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Functional ecology of marine macrobenthic communities

By

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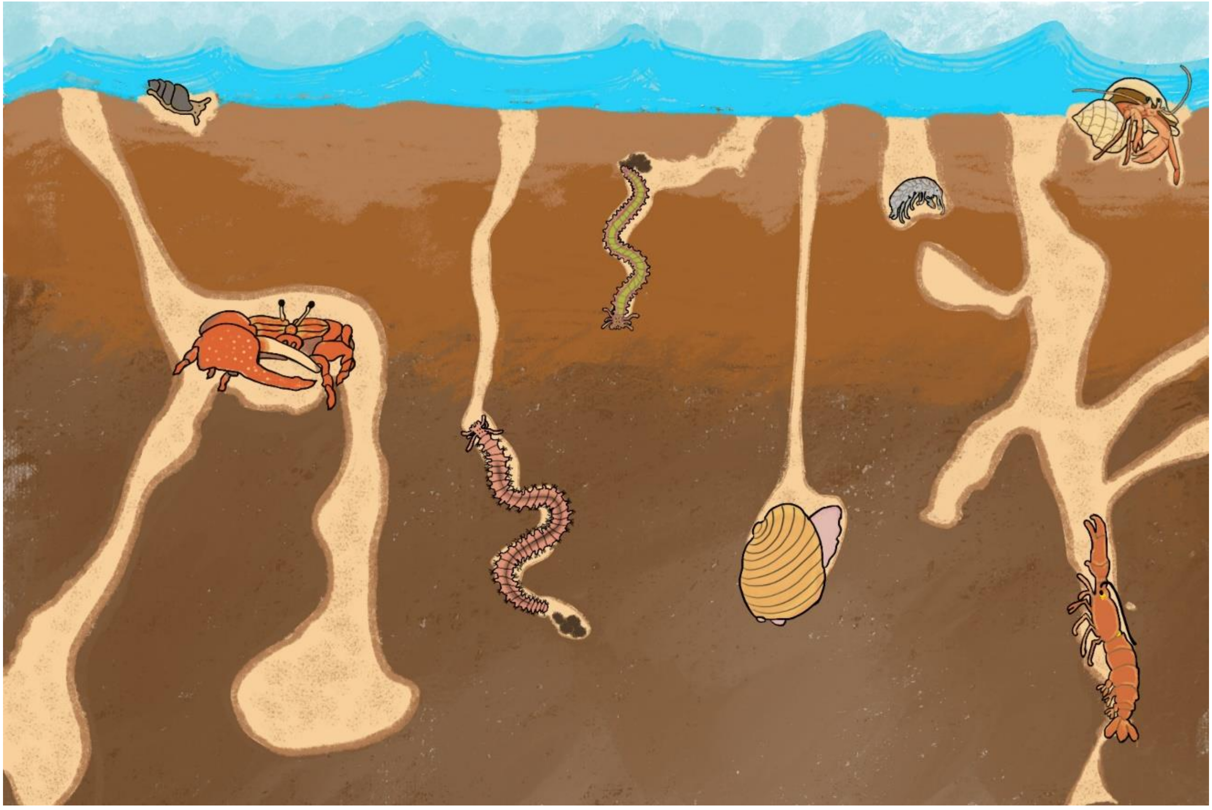
Preface

To my intelligent and beautiful wife, Andrea,

because without you I would not be where I am,

and I would not be who I am.



Marine soft sediment profile showing some macrobenthic organisms performing different activities and its influence on the sediment. Digital illustration by Andrea Barceló.

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Thesis summary

Marine biodiversity is rapidly decreasing worldwide due to human-induced pressures. Climate change, habitat fragmentation, and pollution are the main drivers of biodiversity loss, modifying the abundance, composition and distribution of marine species, and thus the functioning of ecosystems. Over the last decade, assessments on Biodiversity and Ecosystem Functioning have become topical for understanding how changes in biodiversity affect the functioning and services of ecosystems. However, gaps persist in the knowledge of macrobenthic communities' functional ecology in southern temperate ecosystems. This PhD project aimed to understand the functional ecology of benthic communities and investigate the relationship between ecosystem functioning and marine macrobenthic fauna. This thesis provides a global framework on ecosystem functioning and functional approaches, a macrobenthic functional trait database with a step-by-step guide to assist future functional assessments, and a comprehensive implementation of the functional approaches into surveys and experiments to describe macrobenthic functional patterns, sediment nutrient cycling, and buffering capacity of estuarine ecosystems to nutrient loads.

Chapter 2 presents a global review on the topic of ecosystem functioning and functional approaches of marine macrobenthic fauna. A new research weaving method was used. This analysis provided suggestions for unifying the research field, a coherent terminology, methodology and metrics to be used in future, and the application of a generalized framework including the interlinkages among biological traits, ecosystem processes, and ecosystem functioning in marine macrobenthic fauna research. Chapter 3 introduces the South Australian Macrobenthic Traits (SAMT) database, the first comprehensive assessment of macrobenthic fauna traits in temperate Australian waters. Information for >250 macrobenthic taxa was provided, including outcomes from a fuzzy coding procedure for trait classification. An R package for using and analysing the SAMT database was also developed. This study includes an intuitive flow chart for assessing ecosystem functioning highlighting the utility of the SAMT database. Chapter 4 presents taxonomic and functional patterns of benthic macrofauna, and their relationship with environmental conditions. This study elucidated idiosyncratic functional and taxonomic patterns, and the need for complementary perspectives of taxonomic and functional metrics to obtain a holistic understanding of the functioning in marine sediments.

Chapter 5 evaluates changes in macrobenthic fauna, in relation with sediment biogeochemistry across an estuarine-to-hypersaline lagoon ecosystem. This study revealed that macrobenthic communities and functional traits change across an extreme salinity gradient, which correlated with changes in sediment biogeochemistry. This chapter advances the understanding of this relationship, and further highlights the importance of preserving healthy benthic communities to mitigate eutrophication and ensure the functioning of estuarine benthic ecosystems. Chapter 6 presents an *in situ* experiment to investigate whether the bioturbating activity of benthic macrofauna can improve biogeochemical conditions in hostile (i.e. hypersaline, sulfide-rich) sediments. This study indicated that bioturbation by macrobenthic fauna influenced sediment biogeochemistry and remediated hostile conditions in sediment over time, highlighting the importance of benthic macrofauna for improving resilience, and supporting the functioning of estuarine ecosystem.

The integration of the five data chapters demonstrated the functional ecology of benthic communities, providing key knowledge for further functional assessments in southern temperate regions. It also highlighted the importance of including functional perspectives to improve management and conservation plans that ensure healthy functioning of benthic ecosystems.

Declaration

I, Orlando Lam Gordillo, certify that this thesis:

1. Does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and
2. to the best of my knowledge and belief, does not contain any material previously published or written by another person except where due reference is made in the text.

Orlando Lam Gordillo

Acknowledgments

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Chapter 1. General Introduction

Oceans, seas, and coastal ecosystems cover more than 70% of the earth's surface, hosting a wide array of biodiversity (Snelgrove 1999; Zajac 2007). Soft sediment ecosystems are the largest (i.e. in spatial area coverage) habitat on Earth's seafloor, from abyssal plains, the continental shelf, coastal lagoons, estuaries, tidal flats to beaches (Snelgrove 1997; Gray and Elliot 2009). Marine soft sediments are commonly perceived as homogenous, flat, and uninhabited sedimentary habitats. However, these ecosystems are an important component of world's life support system, hosting a vast number of species with highly diversified community assemblages, which are responsible for many ecosystem processes and services (Snelgrove 1997; Gray and Elliot 2009; Thrush et al. 2021).

Most of the organisms inhabiting marine soft sediments are invertebrates living within (infauna) and upon (epifauna) the sediment (Snelgrove 1997; Snelgrove 1999; Thrush et al. 2021). These benthic organisms are often classified into select groups based on a practical size distinction (Mare 1946; Schlacher and Woolridge 1996). This classification includes megafauna, with large invertebrates such as crabs, sea cucumbers, and sea stars; macrobenthic fauna (i.e. macrofauna), with organisms larger than 0.5 mm body size, such as polychaetes, crustaceans and molluscs; meiofauna which are usually interstitial, represented by nematodes and tiny crustaceans from 0.5-0.062 mm body size and; microfauna (microbes), with organisms smaller than 0.062 mm body size that are poorly known (Reise 1985; Snelgrove 1999; Nybakken and Bertness 2005; Thrush et al. 2021).

Macrobenthic organisms are globally distributed (Snelgrove 1997; Gray and Elliot 2009), with latitudinal gradient-patterns showing higher diversity in the tropics and decreasing towards the poles (Roy et al. 1998; Valentine and Jablonski 2015), while macrobenthic biomass is higher in mid-latitudinal zones, and in the Northern Hemisphere compared to the Southern hemisphere (Roy et al. 1998; Ricciardi and Bourget 1999; Cusson and Bourget 2005). Yet, abundance, composition, and distribution of macrobenthic communities are highly influenced by a variety of abiotic and biotic factors. Abiotic factors can include water temperature, water salinity, depth, food availability, sediment organic matter, and sediment grain size (Hillebrand and Matthiessen 2009; Dutertre et al. 2013; Dittmann et al. 2015; Shojaei et al. 2015), while the biotic factors include biological interactions occurring between species, such as predation and competition, as well as promotive interactions (Peterson 1977, 1979; Reise 1985; Thrush 1999; Honkoop et al. 2006). Abiotic and biotic factors strongly interact, promoting physical and biogeochemical changes in soft sediments habitats, which in turn influence the establishment of diverse macrobenthic organisms (Gray and Elliot 2009, Thrush et al. 2021).

Macrobenthic organisms are currently threaten by anthropogenic pressures such as climate change, habitat disturbance, eutrophication, modifying the structure and distribution of their communities (Sala and Knowlton 2006; McCauley et al. 2015). These changes in macrobenthic communities, and in general the alarming loss of biodiversity, are also altering the functioning of ecosystems (Naeem et al. 2002; Hooper et al. 2005). Functional perspectives have been proposed to understand the potential effects of biodiversity loss on the functioning of ecosystem (Díaz and Cabido 2001; Hooper et al. 2005). Functional assessments aim to provide an integrative knowledge on the link between biodiversity, functional traits, and ecosystem functioning. However, the understanding of this relationship in marine ecosystems is still in development, and more assessments using functional perspectives need to be applied for gathering a holistic understanding of how marine macrobenthic organisms are related to the functioning of ecosystems.

This PhD thesis investigate the relationship between macrobenthic fauna and ecosystem functioning using functional perspectives. This study combined the use of functional traits, biological traits analysis, functional diversity, and an *in situ* experiment to provide a holistic understanding of the relationship between marine macrobenthic fauna and ecosystem functioning in soft sediments.

1.1 The role of benthic macrofauna in soft sediments

Marine macrobenthic fauna play a pivotal role in soft sediment ecosystems, as essential providers of ecosystem functioning. They actively disperse and modify soft sediment habitats thorough bioturbation and biological processes such as ingestion, digestion, and excretion, which ultimately promotes suitable conditions (i.e. microhabitats) for microbial activities that contribute to sediment mineralisation and nutrient cycling (Welsh 2003; Lohrer et al. 2004; Snelgrove et al. 2014; Caswell et al. 2018; Thrush et al. 2021; Wyness et al. 2021). The ability of macrobenthic fauna to modify sediment characteristics is directly related to their life history, morphology, physiology and behaviour, i.e. biological traits (Figure 1.1). For example, macrobenthic fauna can enhance sediment oxygenation by bioturbation processes, such as construction (i.e. biomixing) and irrigation (i.e. bioirrigating) of burrows (Kristensen et al. 2012; Mermillod-Blondin 2011; Magni et al. 2009). This increases the surface area of contact between the sediment and water column, promoting biogeochemical exchanges and creating oxidised zones (Welsh 2003; Mermillod-Blondin and Rosenberg 2006; Stief 2013; Bosch et al. 2015). Upward and downward macrobenthic conveyors have an important role on sediment organic matter degradation by physically transporting organic particles between oxic-anoxic zones (Sanders 1958; Aller 1994), modifying the structure of the sediment layers, particle distribution and sediment stability (Rhoads and Young 1970; Anderson 2008; Kristensen et al. 2012).

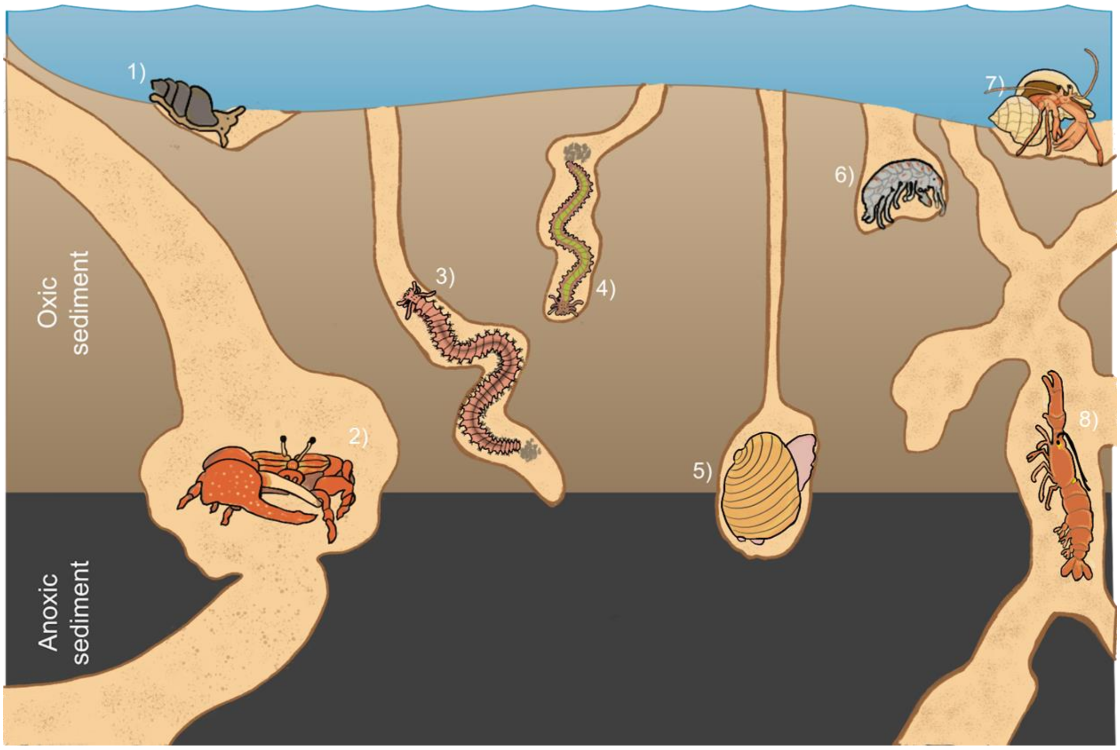


Figure 1.1. Macrobenthic species dispersing and modifying soft sediments based on their functional traits. 1) Snail with limited bioturbation capacity; 2) Fiddler crab bioturbating the sediment by constructing burrows; 3) Burrowing polychaete worm; 4) Polychaete transporting organic matter to the surface; 5) Bivalve filter feeding from the surface; 6) Amphipod modifying the sediment surface; 7) Hermit crab modifying the sediment surface and; 8) A gallery-dweller ghost shrimp.

Macrobenthic organisms are also important secondary and tertiary producers, constituting the link between benthic and pelagic ecosystems, as they function as food resources, transferring energy to higher trophic levels (Gaston et al. 1998; Kristensen et al. 2014). For example, in estuarine lagoon ecosystems polychaetes, amphipods, and small bivalves (i.e. macrobenthic organisms) are key food resources for secondary producers, such as fish and birds (e.g. Horn et al. 2017; Booty et al. 2020; Hensenler et al. 2021).

Furthermore, macrobenthic fauna are often used as powerful bioindicators of environmental change (i.e. ecosystem health) due to their sensitivity to natural and anthropogenic disturbances (Borja et al. 2000; Thrush et al. 2008; Verissimo et al. 2012; Tweedley et al. 2015). The life history, morphology, and physiology characteristics (e.g. limited mobility, long lifespans) of macrobenthic organisms make them adequate for detecting changes in the seafloor (Borja et al. 2004; van der Linden et al. 2016). Several biotic indices have included macrobenthic organisms to assess the ecological health of ecosystems. The AZTI Marine Biotic Index (AMBI; Borja et al. 2000) is the index most frequently used one worldwide with more than 9,000 species included (Borja et al. 2019). AMBI has proved to be an effective measurement assessing the macrobenthic response to several anthropogenic pressures, such as oil spills, sediment removal, and pollution (Borja et al. 2019).

Previous studies that used macrobenthic organisms as bioindicators have reported changes in abundance and diversity of macrobenthic fauna as response to changes in environmental conditions, making them a good proxy for assessing ecosystem health. For example, when an estuary becomes eutrophic, diversity of macrobenthic organisms decreases but the total macrofauna abundance increases (e.g. Pearson & Rosenberg 1978; Tweedley et al. 2012; Tweedley et al. 2015; Ellis et al, 2017). Other studies have shown that densities of macrobenthic molluscs and crustaceans decreased in environmentally stressed conditions, while more tolerant species (e.g. polychaetes) increased (Wildsmith et al. 2011; Beard et al. 2018).

1.2 Traditional macrobenthic assessments and advancement of functional perspectives

Worldwide natural and anthropogenic pressures are affecting the biodiversity (e.g. macrobenthic fauna) of many habitats including benthic ecosystems (McCauley et al. 2015; IPBES 2019). Climate change, habitat disturbance, and pollution, as major drivers of biodiversity loss, have been impacting and modifying species abundance, composition and distribution (McCauley et al. 2015). These changes are also altering the functioning of the ecosystems (Naeem et al. 2002; Hooper et al. 2005). In marine ecosystems, the rate of biodiversity loss is increasing (Sala and Knowlton 2006; McCauley et al. 2015), mainly due to anthropogenic impacts and disturbances, such as extractive processes (e.g. trawling and removal of sediment), pollution, and climate change (van der Linden et al. 2012; Villnäs et al. 2013; Dittmann et al. 2015). These anthropogenic impacts contribute to changes in growth, mortality, recruitment rate, and dispersal ability of macrobenthic species, as well as the macrobenthic community structure (Munguia and Miller 2008; Lohrer et al. 2010, Rodil et al. 2014; Naeem et al. 2012; Villnäs et al. 2013; Dannheim et al. 2014; Shojaei et al. 2015), which ultimately affects the functioning of these ecosystems and services they provide.

Traditional macrobenthic assessments have described the abundance, biomass, community composition, and species distribution of fauna (e.g. Reise 1985; Honkoop et al. 2006; Meadows et al. 2012). These traditional taxonomic-based studies laid the foundation for understanding how changes in benthic biodiversity influence the functioning of an ecosystem (Snelgrove 1997; Thrush et al. 2006; Snelgrove et al. 2014). However, these traditional studies provide limited information about ecosystem properties such as ecosystem functions (Hopper et al. 2006; Pacheco et al. 2011), and the ecological implications of potential macrobenthic biodiversity loss, which makes predicting the influence of biodiversity on ecosystem functioning a challenging task (Naeem et al. 2002; Solan et al. 2004). To fully understand the relationship between macrobenthic fauna and ecosystem functioning, it is essential to adopt a functional perspective (Díaz and Cabido 2001; Hooper et al. 2005; Wright et al. 2006; Legras et al. 2018). Specifically, it is important to determine what these macrobenthic species do in soft sediment habitats (e.g. sediment reworking), as well as how their activities (e.g.

bioturbation) are related with the environmental conditions and functioning of these marine ecosystems.

Ecosystem functioning, defined as the combined effects of all natural processes that sustain an ecosystem (Reiss et al. 2009; Gladstone-Gallagher et al. 2017; Degen et al. 2018), and its relationship with biodiversity, has become increasingly topical over the last few decades motivated by the alarming rate of biodiversity loss. Biodiversity and Ecosystem Functioning (BEF) as a research field emerged in terrestrial ecological studies (Díaz and Cabido 2001; Naeem et al. 2002; van der Plas 2019), was further developed in freshwater ecology research (Lecerf and Richardson 2010; Schmera et al. 2017), and has been increasingly used in marine ecosystems in the last few decades (Snelgrove et al. 2014; Beauchard et al. 2017; Degen et al. 2018; Thrush et al. 2021).

Over the last ten years, BEF research on marine macrobenthic fauna has increased (Figure 1.2), providing further understanding of how changes in biodiversity affect ecosystem functioning and services, and the mechanisms that underpin the macrobenthic biodiversity and functional relationship (see Chapter 2, Lam-Gordillo et al. 2020a for review). Assessments of the relationship between macrobenthic biodiversity and ecosystem functioning have become possible due to the use of functional perspectives. Examples of functional perspectives applied to address the macrobenthic - ecosystem functioning relationships can be found in manipulative experiments (e.g. Stachowicz et al. 2007), seafloor assessments (e.g. Snelgrove et al. 2014, Thrush et al. 2017), frameworks for polar oceans (e.g. Degen et al. 2018), and describing the functioning of mudflats (e.g. Dissanayake et al. 2018).

Functional assessments are based on the use of functional diversity and functional trait analysis. Functional Diversity (FD) has been recognised as the most relevant measure for assessing the relationship between biological diversity, the functioning of organisms, and any links to ecosystem functioning (Díaz and Cabido 2001; Hooper et al. 2005; Wright et al. 2006; de Juan et al. 2015; Lefcheck and Duffy 2015), as FD takes into consideration the value, range, abundance and distribution of functional traits (Tilman et al. 1996; Díaz and Cabido 2001; Reiss et al. 2009).

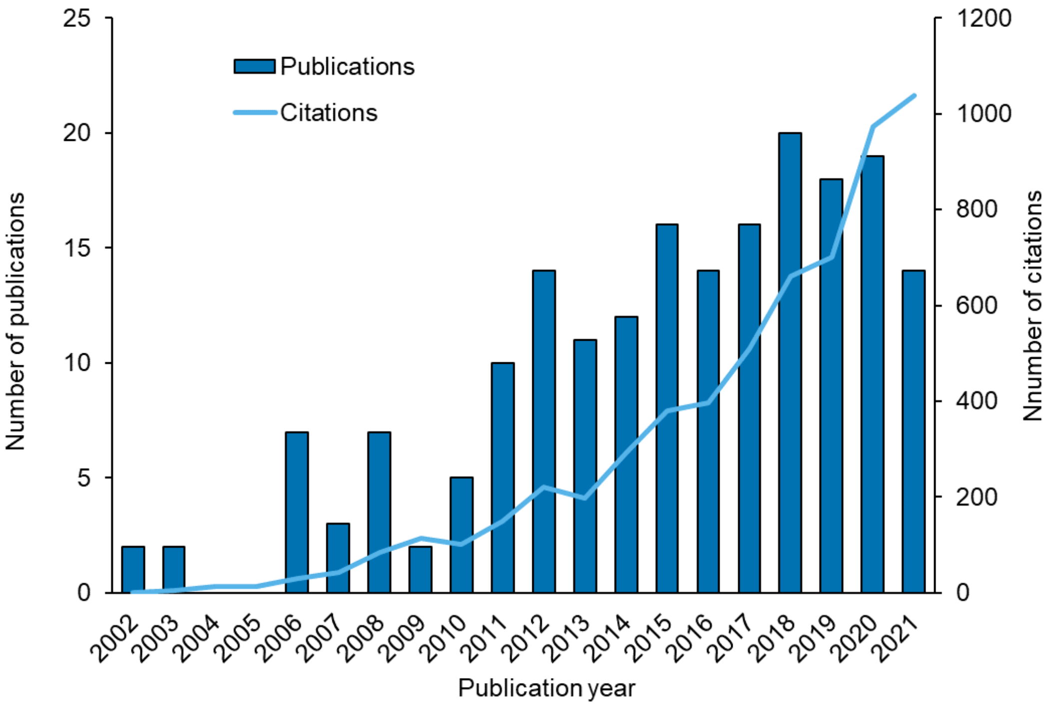


Figure 1.2. Number of peer reviewed publications and citations for ecosystem functioning of marine macrobenthic fauna across time (modified from Lam-Gordillo et al. 2020a).

Functional Diversity was initially split into three components or indices: functional divergence, functional evenness, and functional richness (Villeger et al. 2008). Other indices have been also proposed such as functional identity, functional redundancy, functional dispersion (Mason et al. 2005; Laliberte and Legendre 2010; van der Linden et al. 2012; Mouillot et al. 2013). However, the use of functional perspectives is continuously evolving and other indices for assessing FD and ecosystem functioning have been developed over time (Table 1.1), in order to provide a better understanding of the relationship between biodiversity and ecosystem functioning, as these indices show different facets of the functional traits expressed in a determined community and the way they response to disturbances (Petchey and Gaston 2006; Mouillot et al. 2013; Queiros et al. 2013; Schmera et al. 2017).

Functional assessments (e.g. functional diversity and all its components or indices) are based on the analysis of functional traits and their modalities, also called trait-based approaches (Díaz and Cabido, 2001; Petchey and Gaston 2006). Functional traits are defined as the components of organisms' phenotype that determine its effect on ecosystem functioning (Bremner et al. 2006; Petchey and Gaston 2006; Reiss et al. 2009; Degen et al. 2018). Examples of functional traits include the behaviour, life history, morphology, and physiology characteristics that species can exhibit and influence the functioning of ecosystems, such as bioturbation, body size, feeding mode, living habit, and sediment position (Figure 1.3) (Bremner et al. 2003; 2006).

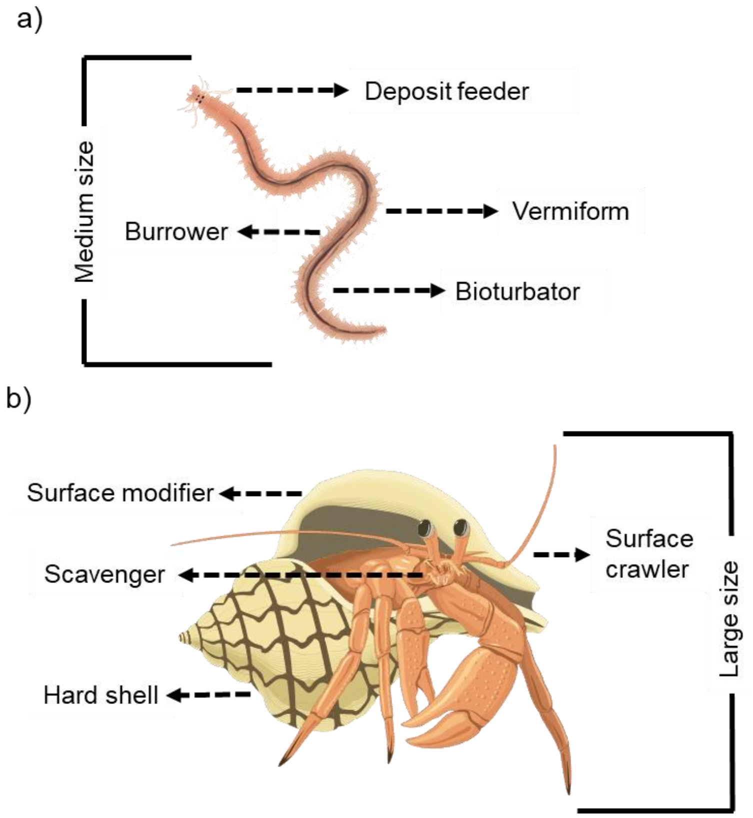


Figure 1.3. Main functional traits modalities of two contrasting macrobenthic fauna. a) Nereid worm (Polychaeta) and b) Hermit crab (Crustacea). Functional traits displayed: Feeding mode (deposit feeder and scavenger); Bioturbation (bioturbator and surface modifier); Body size (medium and large size); Morphology (vermiform and hard shell) and; Living habit (burrower and surface crawler). Symbols used in this figure were retrieved from the Integration and Application Network (ian.umces.edu).

The use of trait-based approaches has been proposed as a powerful tool for assessing biodiversity effects on ecosystem functioning, as trait diversity and variability are related to changes in functions across ecosystems (Díaz and Cabido 2001; Hooper et al. 2005; Bremner et al. 2006). Trait-based approaches rely on the analysis of biological traits (i.e. functional

Table 1.1. Frequently used metrics to measure functional diversity to assess ecosystem functioning of marine macrobenthic fauna.

Name	Description	Reference
Community Bioirrigation Potential	Abundance and biomass data with information about the life traits of individual species or taxonomic groups.	Solan et al. 2004; Queiros et al. 2013.
Functional dissimilarity	The dissimilarity in the functional space occupied by two communities.	Mouillot et al 2013.
Functional dispersion	Abundance-weighted mean distance of individual species to their group centroid (all species community) in multivariate trait space.	Laliberte & Legendre 2010.
Functional divergence	Species deviance from the mean distance to the centre of gravity weighted by relative abundance.	Mason et al. 2005; Villeger et al. 2008; Mouchet et al. 2010.
Functional diversity	The distribution of species and their abundances in the functional space of a given community.	Petchey & Gaston 2006; Mouchet et al. 2010; Mouillot et al 2013.
Functional evenness	The evenness of abundance distribution in a functional trait space.	Mason et al. 2005; Villeger et al. 2008; Mouchet et al. 2010.
Functional identity	The mean value of functional traits, weighted by abundance, across all species present in a given community.	Mouillot et al 2013.
Functional originality	The isolation of a species in the functional space occupied by a given community.	Mouillot et al 2013.
Functional redundancy	Ratio between functional diversity and Shannon diversity index.	de Bello et al. 2007; van der Linden et al. 2012.
Functional richness	The amount of functional space occupied by a species assemblage; Convex Hull Volume.	Mason et al. 2005; Villeger et al. 2008; Mouchet et al. 2010.
Functional specialization	The mean distance of a species from the rest of the species pool in functional space.	Mouillot et al 2013.
Rao's quadratic entropy	Sum of pairwise distances between species weighted by relative abundance	Rao’s 1982; Champely & Chessel 2002; Mouchet et al. 2010.

traits). Biological Traits Analysis (BTA) is a tool to describe variation in trait composition based on the abundances or frequencies of taxa functional traits. In the context of choosing functional traits related to specific aspects of ecosystem functioning (e.g. feeding mode, bioturbation, living habit), BTA has the potential to show how functional traits are related to environmental factors and ecosystem functioning (Bremner et al. 2006; van der Linden et al. 2012).

Addressing the relationship between macrobenthic biodiversity and ecosystem function, the integration of functional traits, biological traits analysis, and functional diversity (and its components), i.e. functional assessment, is also fundamental for informing conservation policy and management of natural ecosystems. Functional assessments provide critical information of the ecological processes occurring in the ecosystem, any changes that have happened, as well as possible future effects. Despite the importance of functional assessments for conservation strategies and management of coastal ecosystems (Miatta et al. 2021), there are many knowledge gaps about macrobenthic communities and their contribution to ecosystem functioning. Theories that describe and evaluate the functional diversity of macrobenthic fauna need to be generated and tested at multiple spatial and temporal scales to provide a better understanding on how an ecosystem is functioning.

Knowledge is also needed on the specific role that macrobenthic organisms play in ecosystems, and how their functional traits are further linked with ecosystem processes, ecosystem functioning, and ecosystem services (Figure 1.4). Those links are key to understanding how macrobenthic communities may adapt and respond to natural or anthropogenic changes, and thus, how these communities are influencing the functioning of ecosystems. Such new information can be used as robust baseline knowledge, which will be useful for improving management of marine resources and ensuring healthy benthic ecosystem functioning.

In temperate southern Australia, several studies addressing the abundance, composition, distribution, and the response of macrobenthic fauna to changing environmental conditions have been undertaken (e.g. Edgar and Barret 2000; Edgar and Barret 2002; Morris and Keough

2003; Macleod et al. 2008; O'Brien et al. 2009; Tweedley et al. 2012; Banks et al. 2013; Tweedley et al. 2015; Lavender et al. 2017). However, the understanding of the relationship between macrobenthic biodiversity and ecosystem functioning in marine soft sediments is still in development. Several gaps persist in the knowledge of macrobenthic fauna – ecosystem functioning, as studies applying functional assessments are still missing. Lack in knowledge of macrobenthic functional traits, terminology and methods used in this research field is also evident. Uncertainties still persist in the interpretation and potential use of the outcomes from functional approaches, for example how future scenarios of biodiversity loss in marine soft sediments will affect the functioning of these ecosystems. Furthermore, theories need to be tested at different spatial and temporal scales, as well as new techniques and methodological analyses needs to be applied to understand the relationship between ecosystem functioning and macrobenthic fauna, i.e. depict the specific influence of these organisms and their functional traits on ecosystem functioning, and to understand how these ecosystems work and change over time.

The aim of this PhD thesis was to understand the functional ecology of marine macrobenthic communities, and investigate the relationship between macrobenthic fauna and ecosystem functioning using functional perspectives, with a general hypothesis stating that greater species and functional diversity will result in high ecosystem functioning. This PhD thesis aims to advance knowledge on macrobenthic – ecosystem functioning, i.e. how macrobenthic fauna influences the functioning of ecosystems, close knowledge gaps on functional traits and functional assessments, and assist in informing conservation and management of marine soft sediments.

Therefore, in this thesis I explored the relationship between macrobenthic fauna and ecosystem functioning in marine soft sediments, created a macrobenthic traits database for southern temperate Australia, described spatial macrobenthic taxonomic and functional patterns; assessed how changes in functional traits correlate with changes in sediment biogeochemistry and; experimentally tested the influence of bioturbation by macrobenthic fauna for remediating hostile sediments.

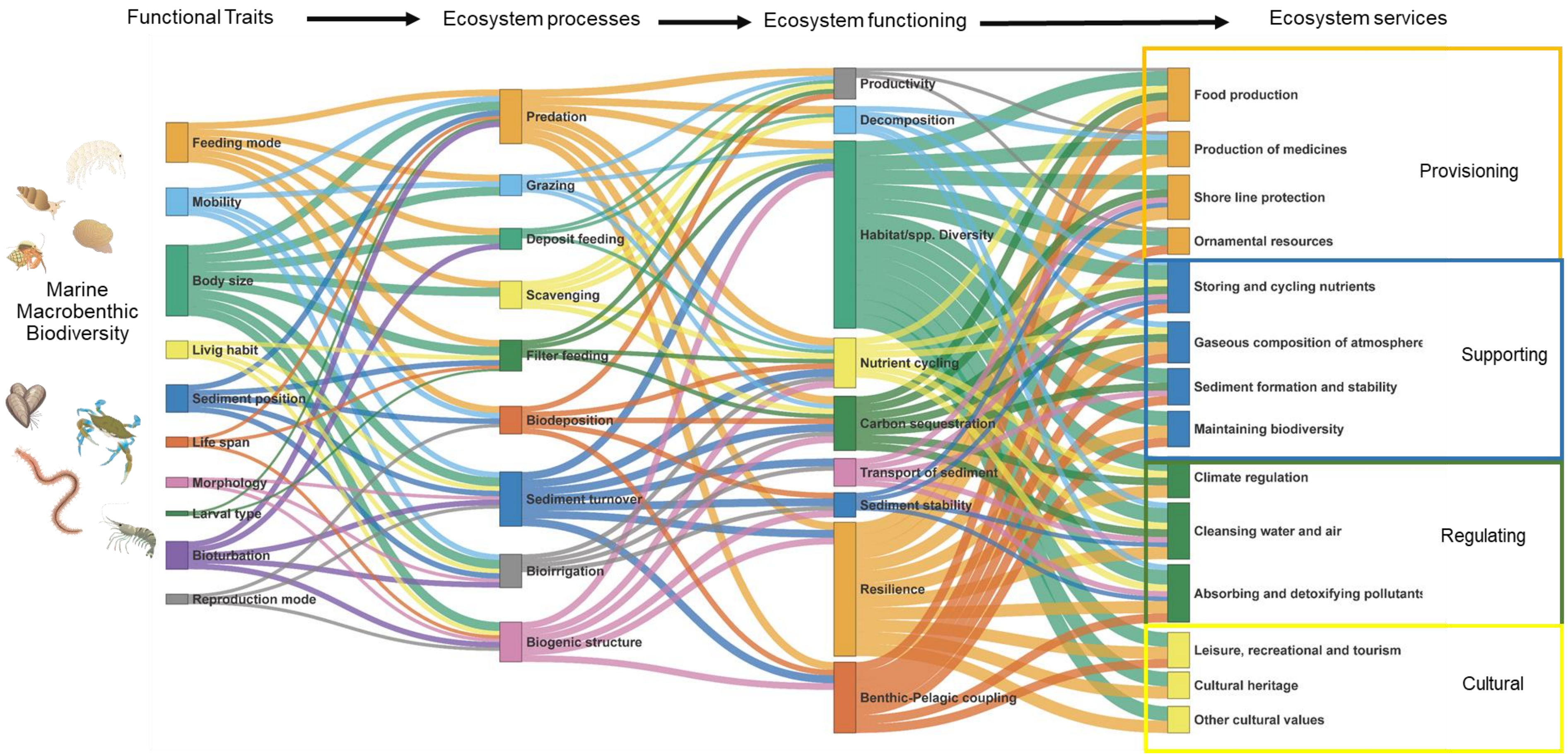


Figure 1.4. Sankey diagram showing the interlinkages among biodiversity of marine macrobenthic fauna, functional traits (selection of the ten most frequently used), ecosystem processes, ecosystem functioning and ecosystem services. This multi-ecosystem linkage is not restricted and can include other functional traits, processes, functioning and services in the expanded literature (modified from Lam-Gordillo et al. 2020a).

1.3 Thesis aim and objectives

The overall aim of this PhD project was to understand the functional ecology of macrobenthic communities, and to investigate the relationship between macrobenthic fauna and ecosystem functioning using functional perspectives. This study combined the use of functional traits, biological traits analysis, functional diversity, and an *in situ* experiment to understand the relationship between marine macrobenthic fauna and ecosystem functioning in soft sediments. This PhD thesis consists of five data chapters (Chapters 2-6) with the following specific objectives and hypotheses:

Chapter 2: To address knowledge gaps on macrobenthic fauna – ecosystem functioning, and the lack of standardization in terminology, methodologies and functional approaches, this chapter aimed to synthesizes the current status of knowledge on the functional approaches of marine macrobenthic fauna and their contribution to ecosystem functioning. Also, I provide a step-by-step framework towards a global consensus in ecosystem functioning and functional approaches of marine macrobenthic fauna.

Chapter 3: To increase the information on functional traits and assist further functional assessments, this chapter aimed to build and introduce the South Australian Macrobenthic Traits (SAMT) database, the first comprehensive assessment of macrobenthic fauna traits in temperate Australian waters. Also, to construct and release an R package for use and analysis of the SAMT database to advance trait-based approaches for southern temperate coastlines.

Chapter 4: To address the limited information on integrative taxonomic and functional assessments, and to contribute to reduce the uncertainties on patterns of taxonomic and functional diversity and their links with ecosystem functioning, this chapter aimed to assess the taxonomic and functional diversity of benthic communities across contrasting habitats (e.g. coastal embayment, gulfs, and lagoon), each representing a typical habitat of the southern temperate Australian coastline, and evaluate the relationships between benthic macrofauna, functional traits and environmental conditions across these habitats. It was hypothesised that (1) taxonomic and functional patterns are distinct across the studied habitats, (2) functional diversity is greater within habitats with a greater number of taxa, and (3) the relationships between taxa, traits and environmental conditions are habitat-specific.

Chapter 5: To investigate how anthropogenic disturbances influences macrobenthic fauna, their functional traits, and sediment biogeochemistry, this chapter aimed to investigate how benthic macrofaunal communities and their functional traits change across an extreme salinity (freshwater to several times seawater concentrations) gradient, and whether there are corresponding patterns in sediment biogeochemistry and nutrient concentrations. It was hypothesised that (1) benthic macrofauna, sediment biogeochemistry and nutrient concentrations will be different across the system, due to the strong salinity gradient, and that (2) pore water nutrient concentrations and sediment biogeochemistry will be correlated with benthic macrofauna, especially those with functional traits that enhance nutrient cycling and sediment redox status.

Chapter 6: To provide a nature-based option for restoration of estuarine ecosystems, and test the functional effect of macrobenthic organisms on sediment biogeochemistry, this chapter aimed to investigate whether restoring the bioturbating activity of the polychaete *Simplisetia aequisetis* (Nereididae) and other macrobenthic fauna, could improve biogeochemical conditions on hostile (i.e. heypersaline, sulfide-rich) sediments through an *in situ* experiment in the Coorong ecosystem. It was hypothesised that hostile conditions will be reduced (e.g. lowered concentrations of sulfide, ammonium, phosphate, organic matter) in sediments with higher than lower density of *S. aequisetis*, and that (2) the hostile conditions will be remediated over time, due to bioturbating organisms oxygenating the sediment, promoting oxidation of sulfide and reduced iron(II).

1.4 Thesis structure

This PhD thesis contains seven chapters following a structured sequence. The first chapter (1) is a general introduction, followed by five data chapters: chapter 2, 3, 4, 5, and 6 (Figure 1.5) that were written as stand-alone manuscripts for peer-reviewed scientific journal publications and formatted consistently to match the layout, purpose and requirements of this thesis. For Chapter 3, published and unpublished records were used to compile the species list for the trait database. All quantitative analyses in Chapters 3,4,5, and 6 were based on targeted sampling undertaken specifically for each chapter with a standardised approach suitable to achieve the objective and address the hypothesis of each investigation. The last chapter (7) is a general discussion of the thesis.

Chapter 1 provides a general introduction on the topic of ecosystem functioning of macrobenthic fauna and showcase the main knowledge gaps. This chapter details general concepts and provides an overview related to marine soft sediment ecosystems, macrobenthic organisms, and functional perspectives. In addition, it provides the aims and structure of this thesis. Some overlap and repetition between this chapter and the data chapters (2-6) is evident as each data chapter was written as individual peer-reviewed manuscript, with some of them already published in scientific journals.

Chapter 2 is a global review on the topic of ecosystem functioning and functional approaches of marine macrobenthic fauna. A research weaving methodology was used to close the gap in the knowledge of macrobenthic fauna – ecosystem functioning, and unifying the terminology, methodologies, and metrics used in the research field. This chapter is published in the scientific journal Ecological Indicators. **Lam Gordillo, O.**, Baring, R., Dittmann, S. 2020. Ecosystem functioning and functional approaches on marine macrobenthic fauna: A research synthesis towards a global consensus. Ecological Indicators 115, 106379. https://doi.org/10.1016/j.ecolind.2020.106379

Chapter 3 addressed the main knowledge gap identified on chapter 2 of a lack on information about functional traits, and the use of trait information for conducting functional assessments. Thus, in this chapter the South Australian Macrobenthic Traits (SAMT) database was compiled and introduced, to provide information on macrobenthic traits in temperate Australian waters. This chapter presented macrobenthic taxa functional trait information, and aimed to assist functional perspectives. This chapter is published in the scientific journal Ecology and Evolution. **Lam-Gordillo, O.**, Baring, R., Dittmann, S. 2020. Establishing the South Australian Macrobenthic Traits (SAMT) database: A trait classification for functional assessments. Ecology and Evolution. 10:14372-14387. https://doi.org/10.1002/ece3.7040

Chapter 4 builds on the information gathered in the two previous data chapters. In this chapter a field study was performed and presents the taxonomic and functional patterns of benthic macrofauna, and their relationship with environmental conditions in eight sites across three different habitats and ~1,260 km of coastline. This chapter presented an integrative study on taxonomic and functional analyses to address the limited information on this topic, and to provide new knowledge on taxonomic and functional diversity, and their links with ecosystem functioning using new statistical methodologies. This chapter is published in the scientific journal Frontiers in Marine Science. **Lam-Gordillo, O.**, Baring R., Dittmann, S. 2021. Taxonomic and Functional Patterns of Benthic Communities in Southern Temperate Tidal Flats. Frontiers in Marine Science, 8. https://doi.org/10.3389/fmars.2021.723749

Chapter 5 presents a localised field study in a region identified by low functional diversity and functional redundancy in the study undertaken in chapter 4, which makes this region of particular interest to understand how changes of macrobenthic fauna influence ecosystem functioning. In this chapter, changes in macrobenthic fauna, in relation with sediment biogeochemistry across an estuarine-to-hypersaline lagoon ecosystem were evaluated, with the aim to investigate how benthic macrofauna and their functional traits change across an extreme salinity gradient, and how this pattern in turn influences sediment biogeochemistry and nutrient concentrations. This chapter is published in the scientific journal Marine Pollution Bulletin. **Lam-Gordillo, O.,** Mosley, L.M., Simpson, S.L., Welsh, D.T., Dittmann, S. 2022. Loss of benthic macrofauna functional traits correlates with changes in sediment biogeochemistry along an extreme salinity gradient in the Coorong lagoon, Australia. Marine Pollution Bulletin. 174 113202. https://doi.org/10.1016/j.marpolbul.2021.113202

Chapter 6 built on the information gathered in chapter 5. This chapter presents an *in situ* experiment to investigate whether restoring the bioturbating activity of benthic macrofauna can improve biogeochemical conditions in hostile sediments (i.e. sulfide-rich, hypersaline). In addition, the experiment conducted in this chapter tested the potential of a nature-based option for the restoration of estuarine ecosystems. This chapter has been submitted to the scientific journal Science of the Total Environment.

The final chapter (Chapter 7) is a general discussion that integrates and summarises the main findings of the data chapters (2-6), describes their implications for conservation and management of marine soft sediments, provide recommendations for further studies on the research field, and concludes the thesis. A reference list for all seven chapters is presented at the end of the thesis, followed by separate appendices for each data chapter. Tables, figures, and appendices are numbered specifically for each chapter in corresponding order.

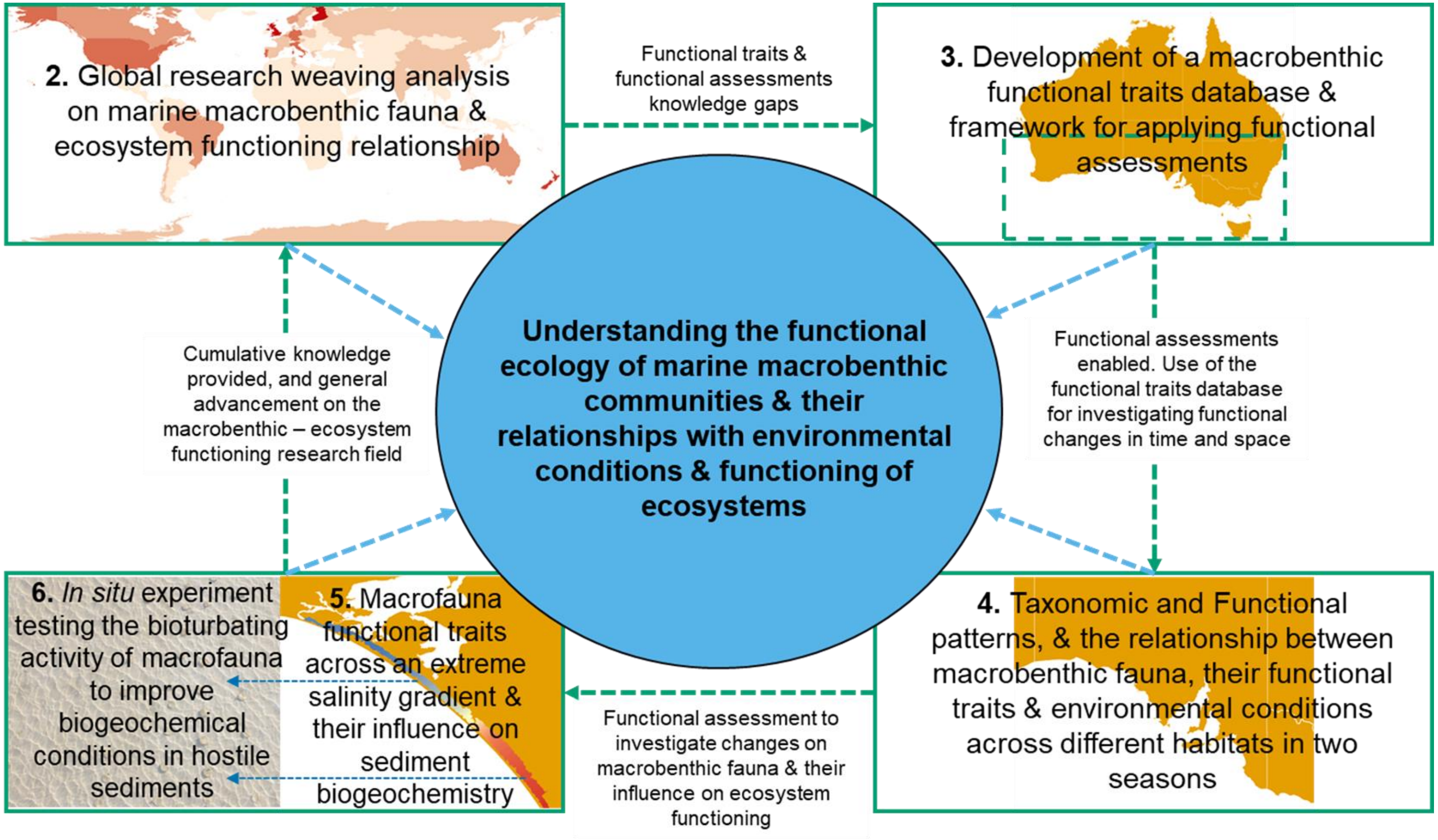
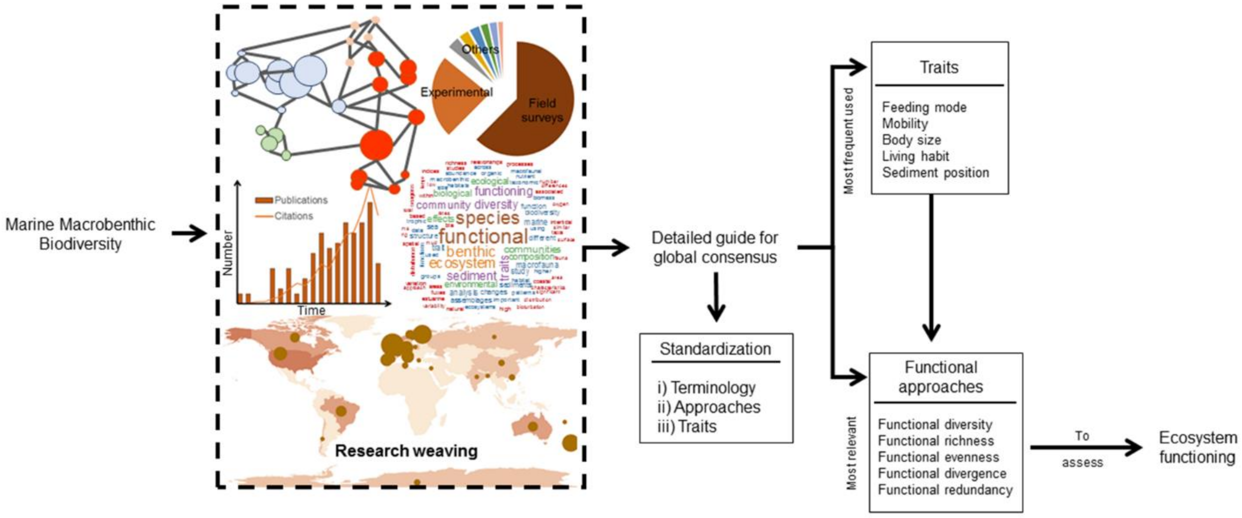


Figure 1.5. Thesis summary flow chart showing the overall aim and the structured sequence of the five data chapters included in this PhD thesis. Data chapters range from global (Chapter 2) to regional (Chapter 3 and 4) and local (Chapter 5 and 6) scale investigations.

Chapter 2. Ecosystem functioning and functional approaches on marine macrobenthic fauna: a research synthesis towards a global consensus



This chapter is published in Ecological Indicators. **Lam Gordillo, O.**, Baring, R., Dittmann, S. 2020. Ecosystem functioning and functional approaches on marine macrobenthic fauna: A research synthesis towards a global consensus. Ecological Indicators 115, 106379. https://doi.org/10.1016/j.ecolind.2020.106379. A copy of the manuscript in the journal format can be found as part of the Appendix A.

Author contributions

Orlando Lam Gordillo: Conceived the ideas and developed the outline for the manuscript, designed the methodology, collected the data, analysed the data, prepared the figures and tables, wrote the manuscript and corresponding author.

Sabine Dittmann – primary supervisor: Guidance on the project development, discussion of project ideas, contribution to drafting manuscript, and critical refinement.

Ryan Baring – co-supervisor: Discussion of project ideas and contribution to drafting manuscript.

Abstract

The global trend in losing biodiversity is affecting ecosystems due to changes in their functions and services. Biodiversity and Ecosystem Functioning has become increasingly topical over the last decades, and still a developing research field. Marine macrobenthic fauna are important providers of ecosystem functioning by regulating the fluxes of energy and matter. However, anthropogenic impacts have triggered changes in their structure and function at the community and ecosystem level. Despite advances in recent years, a wider application of biodiversity and ecosystem functioning relationship in benthic communities has been restrained by missing information on biological traits of species and inconsistencies in terminology, methodologies and approaches used. This review synthesizes the current status of knowledge on the functional approaches of marine macrobenthic fauna and their contribution to ecosystem functioning, using a new method named research weaving analysis. We thus provide a research synthesis combining bibliometric analysis and systematic mapping (spread of evidence). We described advancements in the current knowledge and synthesized the most common functional approaches, terminology and numerical methodologies used. A conceptual step-by-step guide is presented to assist future assessments of ecosystem functioning for marine macrobenthic fauna, and suggestions made for coherent use of terminology, trait selection and metrics to measure ecosystem functioning. The analyses presented will support the development of a framework to conduct globally comparable analyses of ecosystem functioning in marine benthic ecosystems.

Keywords: Biological traits, bibliometrix, ecosystem function, functional diversity, macrofauna, research weaving.

2.1 Introduction

Biodiversity is declining worldwide causing changes in ecosystem functioning and services (Sala and Knowlton 2006; Wright et al. 2006; Butchart et al. 2010; McCauley et al. 2015; IPBES 2019). Over the last few decades, the rate of biodiversity loss and changes in ecosystems have motivated research towards understanding the relationship between Biodiversity and Ecosystem Functioning (BEF). Research directions have included investigations on ecological processes and how changes in biodiversity affect ecosystem functioning and services, elucidating the mechanisms that underpin the biodiversity and functional relationship (Naeem et al. 2002; Hooper et al. 2005; Reiss et al. 2009; Cadotte et al. 2011; van der Plas 2019).

Ecosystem functioning is defined as the combined effects of all natural processes that sustain an ecosystem (Table 2.1). The concept of Biodiversity and Ecosystem Functioning emerged in the early 1990’s (Naeem et al. 1994; Tilman et al. 1996), and has evolved since then, but mainly in terrestrial (Diaz and Cabido 2001; Tilman et al. 2014; van der Plas 2019) and freshwater ecology (Lecerf and Richardson 2010; Schmera et al. 2017). A large body of research shows that greater diversity leads to an increase in the number of expressed biological traits and greater effects on ecosystem functioning, compared to less diverse assemblages that have poor functional expression (Chapin et al. 2000; Hooper et al. 2005; Hillebrand and Matthiessen 2009; Reiss et al. 2009; Snelgrove et al. 2014). The strength and direction of the BEF relationship can, however, be highly variable and subject to environmental context (Strong et al. 2015; Thrush et al. 2017; van der Plas 2019).

In order to assess the BEF relationship several approaches have been used. Functional diversity (FD) is the most relevant measure for understanding the relationship between biological diversity, the functioning of organisms, and the links to ecosystem functioning (Díaz and Cabido 2001; Hooper et al. 2005; Wright et al. 2006; Lefcheck and Duffy, 2015; Legras et al. 2018). Functional diversity is defined as the value and range of functional traits (Table 2.1) and has been quantified by grouping species with shared taxonomic, physiological and morphological characteristics (Wright et al. 2006). The number of ways to measure FD is continually evolving, but usually split into three main components; (1) functional richness, (2) functional evenness, and (3) functional divergence (Petchey and Gaston 2006; Mouchet et al.

2010; Legras et al. 2018, see Table 1 for definitions). However, numerous other metrics to measure FD have been developed over time (e.g. community bio-irrigation potential, community weight means, functional complementary, functional redundancy, functional regularity and Rao's Quadratic Entropy) (Petchey and Gaston 2006; Cadotte et al. 2011; Queiros et al. 2013; Song et al. 2014; Schmera et al. 2017).

Table 2.1. Terminology used in the context of Biodiversity-Ecosystem Functioning and suggested definitions for (a) general terms and (b) trait specific terms.

Key terms	Definition
(a) General terms	
Biodiversity	The extent of all genetic, taxonomic and ecological diversity over all spatial and temporal scales (Reiss et al. 2009; Snelgrove et al. 2014).
Ecosystem functioning	The combined effects of all natural processes that sustain an ecosystem (Reiss et al. 2009; Degen et al. 2018; Gladstone-Gallagher et al. 2019).
Ecosystem goods and services	The ecosystem services are the conditions and processes through which natural ecosystems sustain and fulfil human life. The ecosystems goods are products obtained from ecosystems. In general, both are products of ecosystem functioning that are of value to humans, or with benefits that humans obtain from ecosystems (Reiss et al. 2009; Snelgrove et al. 2014; Degen et al. 2018).
Ecosystem process	Changes in energy and matter over time and space through biological activity, within the ecosystem, due to abiotic (physical and chemical) and biotic (organism) factors and interactions (Reiss et al. 2009).
Ecosystem modelling	The development and analysis of mathematical and statistical models of ecological processes (Pittroff and Pedersen 2005).
Functional divergence	Degree to which the maximum abundance of functional traits deviate from the centre of the functional space within the same community (Mason et al. 2005; Mouchet et al. 2010; Schmera et al. 2017).
Functional diversity	The value and range of functional traits that influence ecosystem functioning (Tilman et al. 1997; Diaz and Cabido 2009; Reiss et al. 2009; Schmera et al. 2017; Degen et al. 2018).
Functional evenness	Distribution of abundance among functional traits (Mason et al. 2005; Mouchet et al. 2010; Schmera et al. 2017).
Functional richness	Amount of functional trait space occupied by an assemblage of multiple species (Mason et al. 2005; Mouchet et al. 2010; Schmera et al. 2017).
(b) Trait terminology	
Trait	Any morphological, physiological or phenological feature measurable at species level.

Biological trait	A defined and measurable (presence/absence, or fuzzy coding) property of organisms, usually at the individual level and used comparatively across species (Reiss et al. 2009; Degen et al. 2018).
Functional trait	Component of an organisms’ phenotype that determines its effect on ecosystem functioning; also referred to as functional characters (Petchey & Gaston 2006; Reiss et al. 2009; Degen et al. 2018; Weiss & Ray 2019).
Effect traits	Expression of a trait that shapes how organisms affect ecosystem functioning (Beauchard et al. 2017; Degen et al. 2018)
Response traits	Traits that determine how organisms respond to changes in the environment (Degen et al. 2018)
Trait modalities	Categories in which any trait can be subdivided.

Functional diversity generally involves knowledge of the components of biodiversity that influence ecological processes or ecosystem functioning (Petchey and Gaston 2006; Shmera et al. 2017), whereby approaches that measure FD are usually based on functional traits (Diaz and Cabido 2001; Petchey and Gaston 2006; Hillebrand and Matthiessen 2009). Functional traits are the components of an organisms’ phenotype that determine its effect on ecosystem functioning (Petchey and Gaston 2006; Reiss et al. 2009; Degen et al. 2018; Weiss and Ray 2019). Functional traits can be selected by either (1) incorporating a wide range of information on biological traits regardless of the taxonomic group (Cadotte et al. 2011; Verissimo et al. 2012) or, (2) selection of an appropriate set of traits that depend on the specific objectives and processes to be measured in any particular study (Reiss et al. 2009).

Marine macrobenthic communities in soft sediments are important providers of ecosystem functioning. They regulate the fluxes of energy and matter and are bioindicators of ecosystem health due to their sensitivity to natural and anthropogenic disturbance (Borja et al. 2000; Reiss et al. 2009; Snelgrove et al. 2014; de Juan et al. 2015; Lefcheck and Duffy, 2015). Anthropogenic disturbances such as trawling, dredging or pollution, can affect growth, mortality, recruitment rate and dispersal ability of benthic species (Lohrer et al. 2010; Naeem et al. 2012; Villnäs et al. 2013; Dannheim et al. 2014; Shojaei et al. 2015), altering the structure and functioning of benthic communities (Worm et al. 2006; van der Linden et al. 2012; Thrush et al. 2017), and therefore ecosystems.

Efforts have been made to understand, describe and measure BEF relationships for macrobenthic fauna in marine ecosystems, using manipulative experiments (Stachowicz et al.

2007), analysing the seafloor biodiversity-ecosystem functioning (Snelgrove et al. 2014), creating frameworks for polar oceans (Degen et al. 2018), and describing the functioning of mudflats (Dissanayake et al. 2018). However, several gaps persist in the knowledge of ecosystem functioning in benthic communities, arising from missing information on the biological traits of specific species, and inconsistency in terminology, methodologies and approaches used (Tyler et al. 2012; Strong et al. 2015; Thrush et al. 2017; Paterson et al. 2019). A framework describing the links between macrobenthic fauna, biological traits, ecological processes and ecosystem functioning and services is thus still missing.

In order to advance a more coherent approach in BEF of marine macrobenthic fauna, we present a research weaving analysis, combining bibliometric analysis with systematic mapping (Nakagawa et al. 2019). This novel approach allowed an advanced and visualised synthesis of the research to date about the connection between biological traits, ecological processes, and ecosystem functions. Through the systematic review of BEF literature on marine macrobenthic fauna around the world, we provide an overview on the spread of evidence and bibliographic analysis. We further analysed the literature content under several categories to identify how ecosystem functioning and functional diversity are currently conceptualized and measured. To enhance comparability between studies, we encourage the use of a general and standardized approach that includes coherent terminology, quantitative methods for choosing biological traits, and consistent use of metrics to measure ecosystem functioning. We also provided a conceptual step-by-step guide to assess ecosystem functioning for marine macrobenthic fauna.

2.2 Methods

2.2.1 Literature and database mining

The databases SCOPUS (Elsevier; elsevier.com) and Web of Science (WoS, Thompson Reuters; webofknowledge.com) were used to compile all studies published before November 2019. The literature searches were performed using the tool ‘combination of sets’ (WoS) and ‘combine queries’ (SCOPUS), which allowed us to find the articles that contained any of all the possible combinations using the following terms: ‘macrofauna’, ‘macroinvertebrate(s)’, ‘macrobenthic’, ‘ecosystem function(ing)’, ‘ecosystem multifunctionality’, ‘functional diversity’, ‘functional traits’, ‘biological traits’; in the fields of ‘Article title, Abstract, Keywords' for SCOPUS and; in 'topics' (Article title, Abstract, Author, Keywords and Keywords plus) for WoS. This search resulted in 1,813 published studies (1,092 in SCOPUS, all of them were in WoS). Within these results, a primary examination of the titles and abstracts was done, retaining only the publications that met the following criteria of: (1) environment (marine habitat), (2) organisms (all macrobenthic fauna), (3) statistically tested, and (4) study type (e.g. only scientific peer-reviewed publications), yielding a total of 239 publications. A second and final examination of the publications was done where we carefully read through each article to verify its relevance to ecosystem functioning of marine macrobenthic fauna, resulting in 93 publications that did not meet the required criteria. In addition, a cross-referencing of the publications gathered additional publications outside of the initial review process (3 publications), resulting in a final total of 149 publications on the research field of ecosystem functioning and functional diversity of marine macrobenthic fauna that included soft and hard bottom marine habitats (Table S1 in Appendix A).

2.2.2 Review style and data analyses

To investigate the relationship of marine macrobenthic biodiversity and ecosystem functioning, we performed a new systematic approach named 'research weaving'. This type of research synthesis combines bibliometrics and systematic mapping, summarizing and visualizing the information content, history and networks across and within publications of a specific topic (Nakagawa et al., 2019).

Bibliographic analyses were performed using the bibliometrix-R package (Aria and Cuccurullo, 2017) in R v3.5.0 (R development Core Team, 2018). An author collaboration network was created using a 'fruchterman' method base on the top 35 authors with more collaborations. For the co-citation network, we used the 25 most co-cited publications and a 'fruchterman' method. The thematic map of keywords was performed using a co-word analysis based on the authors key words.

2.2.3 Review categories and general statistics

The database used for this review was analysed in three ways: (1) Using Clarivate Analytics (Web of Science), the general statistics of citations, web of science categories, source titles (i.e. journal titles), and research areas were obtained; (2) the Bibliometix-R package (Aria and Cuccurullo, 2017) was also used for collecting additional information: number of publications per year, annual percentage growth rate, number of publications per country (single and multiple), and number of publications per author and; (3) information from different categories was extracted by reading each of the peer-reviewed publications included in our dataset. Although, this strategy is time consuming, it was preferred to the option provided in Clarivate Analytics, obtaining information unavailable from automated search. For example, these categories were based on the location where the studies were undertaken, in contrast with automatic sorting that uses the authors' affiliation. Publications were categorised by type of study separating; experimental manipulation, field surveys, distribution modelling, ecological modelling, meta analysis, methods, reviews and tool evaluations. Publications were also grouped by the ecosystem type where the study took place, irrespective of the spatial and temporal scale and only focusing on the predefined ecosystems beach, coastal, offshore (including deep sea), estuary, laboratory, mangrove, and seagrass. In another category, publications were classified according to their study organisms; macrobenthic communities as combinations of groups of multiple taxa or groups of particular taxa such as Annelida, Decapoda, Echinodermata and Mollusca. When analysing the publications, we identified that ecosystem functioning was addressed in different ways, so a classification was created to allocate each publication. As the terminology used for biological traits varies throughout the literature, a classification of traits and their modalities was performed. The variety of numerical methods for assessing ecosystem functioning was further analysed based on the publications reviewed, and sorted by their most common use (see Supplementary data Table S2). Finally, an approach category was identified; methodological approach (i.e. taxonomic diversity vs functional diversity), spatial approach (i.e. differences between sites), temporal approach (i.e. differences across time), and experimental approaches.

2.3 Bibliometric influence and evidence of BEF for macrobenthic fauna

2.3.1 Geographical and temporal spread of evidence

Investigations of marine macrobenthic fauna and their contributions to ecosystem functioning have increased due to growing interest in the field, and the value of functional perspectives for environmental decision making (e.g. van der Linden et al. 2016). The majority of studies were performed in the Northern Hemisphere (115 publications), compared to 29 publications from the Southern Hemisphere. Only five publications had a global perspective as they included information (e.g. organisms) from multiple continents (Figure 2.1A).

When publications were classified based on the continent where the studies were conducted, 62% of all publications were from Europe (93 articles), based on strong collaborations of authors from universities across Europe (e.g. Bremner et al. 2003; van der Linden et al. 2012; Norkko et al. 2013; Villnäs et al. 2018), creating networks for the advancement of ecosystem functioning of marine macrobenthic fauna. In comparison, Oceania was represented by 13.6% of the publications, followed by North America with 8.7%, while BEF was less frequently studied in South America (4.7%), Asia (4.7%), Africa (1.3%), and Antarctica (1.3%) (Figure 2.1A).

The number of peer-reviewed publications and citations on ecosystem functioning of marine macrobenthic fauna across time.

A total of 29 countries had performed investigations into ecosystem functioning of marine macrobenthic fauna. Most publications on BEF, combining both single and multiple country collaborations, were from the United Kingdom (26 publications), Finland (18 publications) and New Zealand (15 publications) (Figure 2.1B). Due to the high number of publications, the United Kingdom was also identified as the country that collaborates most with other countries.

Ecosystem functioning of marine macrobenthic fauna was first raised in the 1990s, identifying traits and functions of specific macrobenthic species (e.g. Posey 1990). However, it was not until 2002 that studies about ecosystem functioning of macrobenthic fauna included broader concepts, applicability and multiple traits per macrobenthic species (e.g. Bolam et al. 2002; Bremner et al. 2006; Bremner 2008). In 2004-2005 no publications on this theme were recorded, but since 2005 there has been a general increase (Figure 2.1C) with an average annual growth rate in publications of 9.7%. The number of citations in this research field has also grown, with a total of 3,705 citations across the 17 years period (Figure 2.1C).

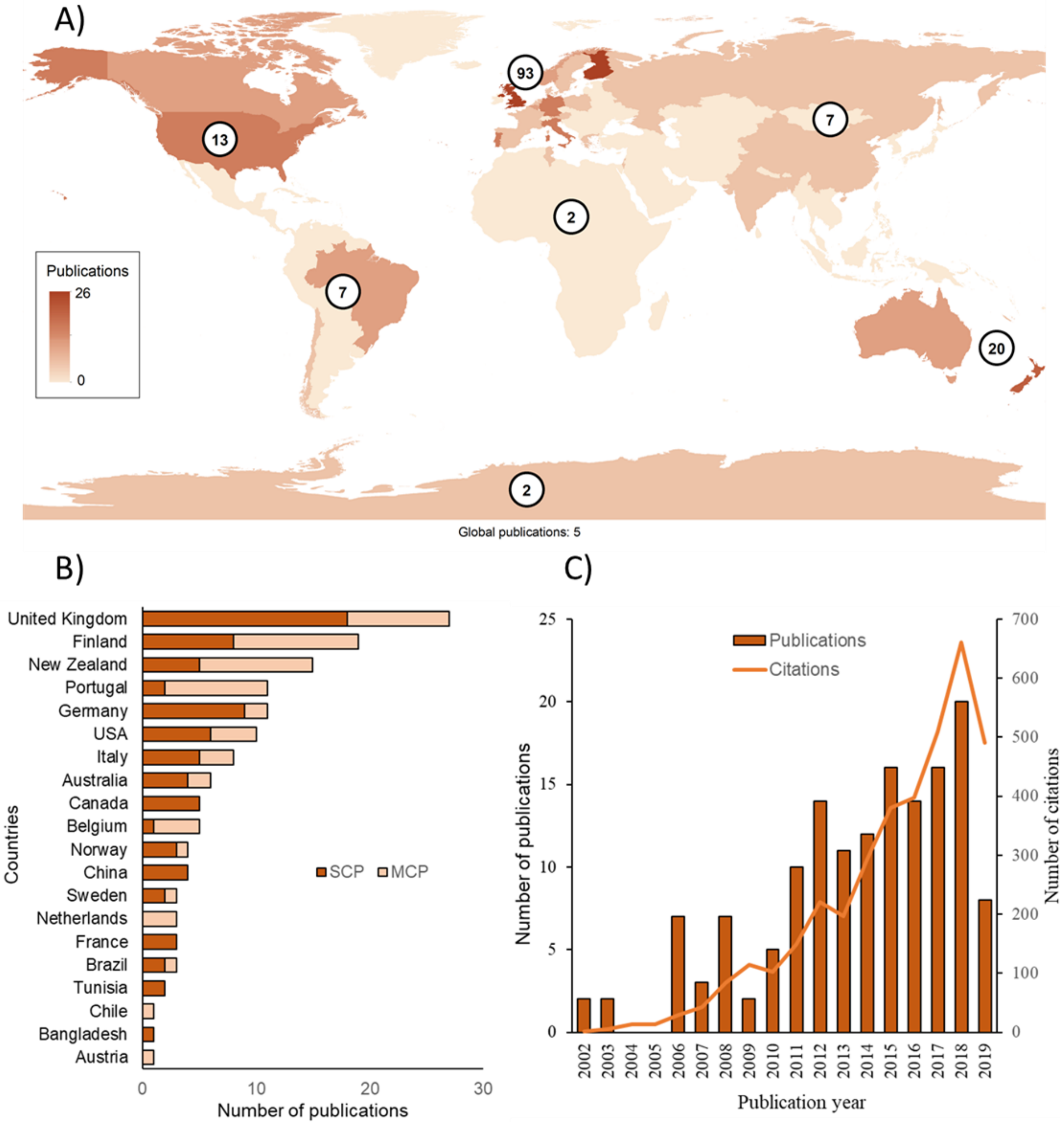


Figure 2.1. Spread of evidence of studies on ecosystem functioning of marine macrobenthic fauna. A) Geographical distribution of the origin of the publication of the included studies. Numbers inside of circles represent the number of publications per continent. Colour intensity is proportional to the number of first authors affiliated to a given country. B) The top 20 most productive countries; SCP: single country publication; MCP: multiple country publication. C)

2.3.2 Bibliographic analysis

Ecosystem functioning of marine macrobenthic fauna have been addressed worldwide (Figure 2.1), and even though the bibliographic influence is strongly interconnected, the field is dominated by six principal authors with 10-11 publications each contributing to 41% of the publications collectively (Figure 2.2A). The author collaboration network displayed four groups of interlinked collaborations (Figure 2.2B; Figure S1 Appendix A). These groups reflected the strong collaboration within Europe (Figure S1 Appendix A). The co-citation network analysis based on the publications' references showed three well defined author groups based on seven central publications (Figure 2.2C; Figure S2 Appendix A). These publications were often cited because they pioneered theoretical foundations about ecosystem functioning (Solan et al., 2004, Hooper et al., 2005), or stated fundamental information about macrobenthic response, including biological factors, to organic enrichment (Pearson and Rosenberg 1978), and created or developed the methodologies for using biological traits in marine macrobenthic fauna (Chevene et al. 1994; Bremner et al. 2003; Bremner et al. 2006; Bremner 2008) (Figure S2 Appendix A).

Publications on ecosystem functioning have been classified into different categories (Table 2.2). Around 31% of the publications on ecosystem functioning of marine macrobenthic fauna were primarily classified as Marine Freshwater Biology. Ecosystem functioning publications have also been categorised as ecology (18%), oceanography (17%), as well as environmental sciences (15%).

Publications of marine macrobenthic fauna and ecosystem functioning were found in 46 journals. The majority of the articles were published in two research journals: Ecological Indicators (Elsevier) with 18 publications and Marine Ecology Progress Series (Inter-Research Science Publisher) with 16 publications. However, another eight journals contained a considerable number (e.g. 6-13 each) of publications in this field (Table 2.2).

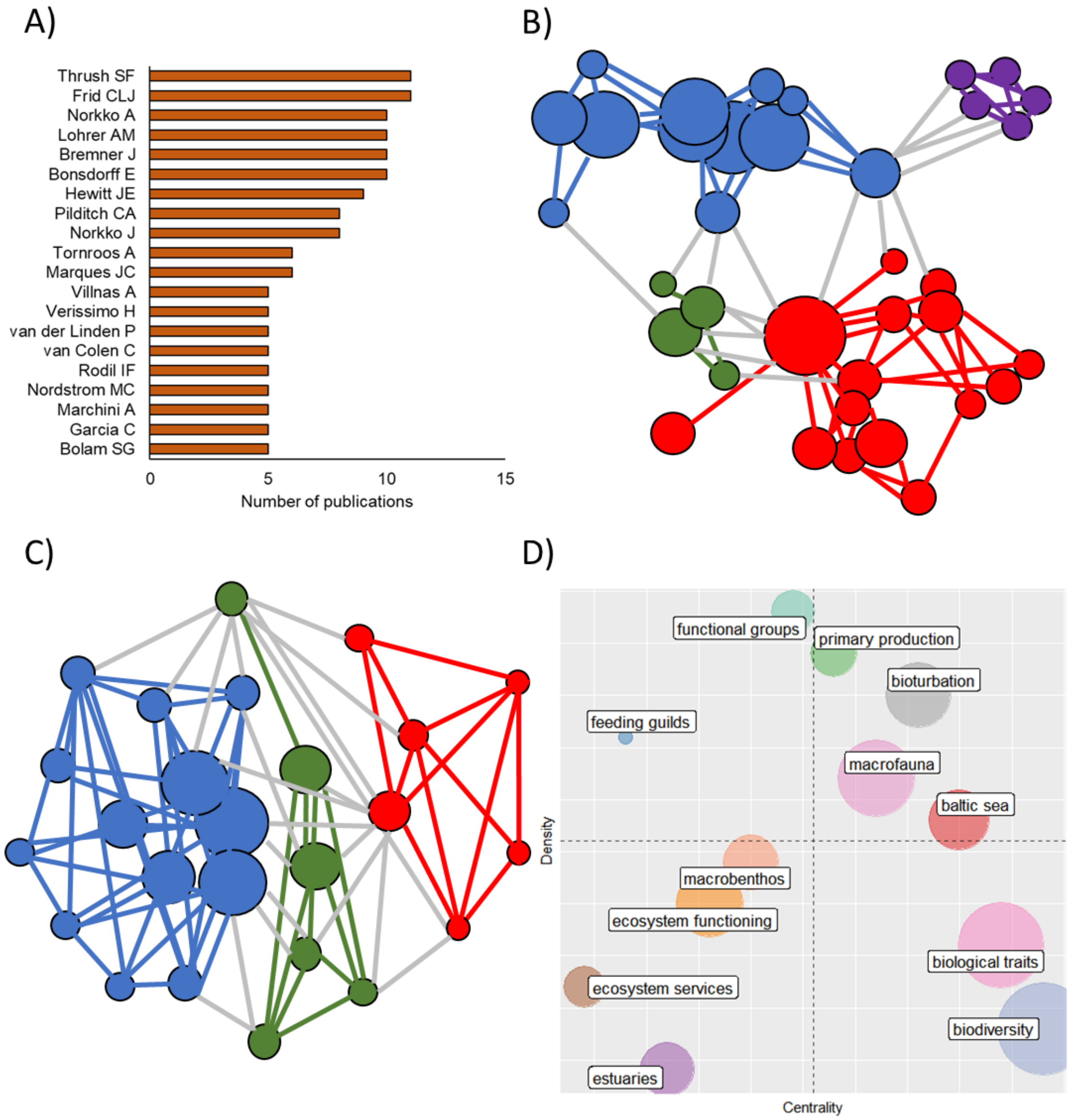


Figure 2.2. Bibliographic analysis of publications on ecosystem functioning of marine macrobenthic fauna. A) Most productive authors. B) Author collaboration network. Nodes represent relations between the top 35 authors in terms of the numbers of authored publications in the dataset; line connections are co-authorships; nodes size is proportional to the number of publications; node colours represented strongest associations between networks. For visualisation, labels are shown in Figure S1 Appendix A. C) Co-citation network based on publication references. Nodes represent relations between cited publications using the top 20 most cited authors; node size is proportional to the number of times the article was cited; nodes colours represented strongest associations between networks. For visualisation, labels are shown in Figure S2 Appendix A. D) Thematic map of keywords based on co-word analysis through authors keyword co-occurrences.

Table 2.2. Number of publications on ecosystem functioning of marine benthic fauna for the top 10 web of science categories and journals.

Web of Science category	No.	Journal	No.
Marine Freshwater Biology	88	Ecological Indicators	18
Ecology	52	Marine Ecology Progress Series	16
Oceanography	49	Journal of Sea Research	13
Environmental Sciences	43	Journal of Experimental Marine Biology and Ecology	10
Biodiversity Conservation	21	Marine Environmental Research	8
Multidisciplinary Sciences	12	Plos One	8
Toxicology	8	Marine Pollution Bulletin	8
Geosciences Multidisciplinary	7	Estuarine, Coastal and Shelf Science	7
Evolutionary Biology	3	Marine Ecology and Evolutionary Perspective	6
Fisheries	3	Ecosystems	6

The most frequently used terms for studying ecosystem functioning of marine macrobenthic fauna emerging through a co-word analysis from keywords are presented in a thematic map (Figure 2.2D). According to Cobo et al. (2011) themes in the upper-left quadrat are highly developed and very specialized themes (e.g. functional groups, feeding guilds); in the upper-right quadrat are the motor-themes, themes well developed and important for structuring the research field (e.g. macrofauna and bioturbation); themes in the bottom-left quadrat represent emerging themes, themes that need development due to the research field is growing towards them (e.g. ecosystem functioning, ecosystem services); and themes in the bottom-right quadrat are basic themes (e.g. biological traits, biodiversity).

2.4 Current status of research into ecosystem functioning and functional diversity of marine macrobenthic fauna

The reviewed publications were analysed using several categories to summarise the current state of the research field. Analysing by the category ‘type of study’ revealed that most of the publications on ecosystem functioning of marine macrobenthic fauna were based on field surveys (62% of publications) and experimental manipulation (24% of publications) (Figure 2.3A). Using the category ‘ecosystem type’ revealed that most of the studies were conducted on the coast/offshore, which included tidal flats and deep sea environments (56% of publications), and in estuaries with 33% of publications (Figure 2.3B). Also, a large proportion of publications (68%) performed their research in subtidal environments, and only 31% of them were performed in intertidal environments (n=136 publications). In addition, the majority of the publications were performed on soft sediments (97 % of publications), and only 3% on hard bottom habitats (n=143).

The category 'study organisms' showed that the majority of publications analysed multiple taxa (e.g. 98% of all publications), yet, a number of publications used particular groups of taxa (Figure 2.3C).

Grouping the publications by the 'ecosystem function' they investigated that the majority focused on species diversity and its influence on ecosystem functioning (46% of all publications), and comparatively less publications investigated other aspects, such as those related with resilience and biological traits (13% each) (Figure 2.3D).

For the category 'approach', four main directions for addressing ecosystem functioning were identified: (1) methodological approach, including publications which compared differences between taxonomic diversity and functional diversity; (2) spatial approach, referring to publications which examined differences in functional diversity between sites; (3) temporal approach, which identified publications where differences in functional diversity were assessed across time (e.g. seasons, years) and; (4) experimental approach, which included publications where manipulations of the environment and organisms were applied (Table 2.3).

Table 2.3. Approaches in assessing ecosystem functioning of marine macrobenthic fauna. Methodological: Taxonomic diversity vs functional diversity; Spatial: differences between sites; Temporal: differences across time; Experimental: manipulation of the environment and organisms.

	Methodological approach	Spatial approach	Temporal approach	Experimental approach
Number of publications (n)	30	78	26	36
Significant differences	15	70	24	36
No significant differences	15	8	4	0

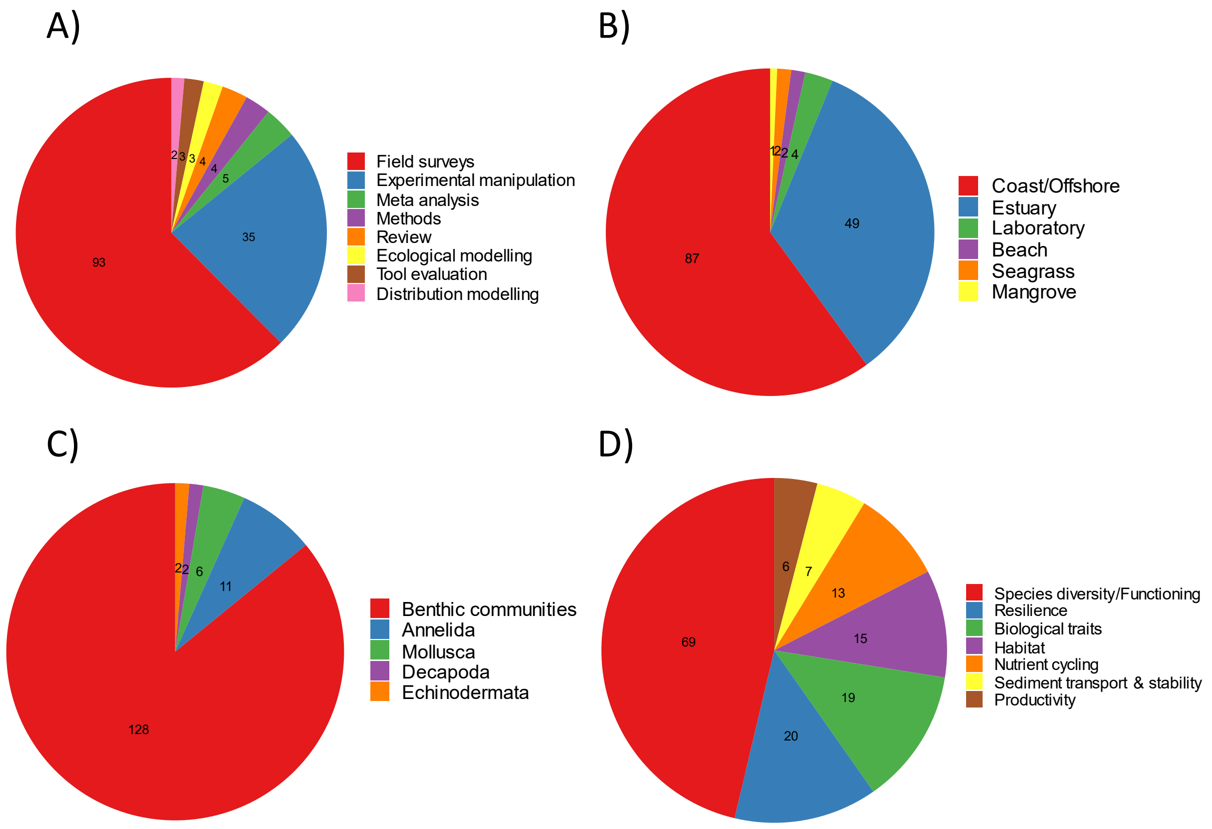


Figure 2.3. Pie charts summarising the attributes found in the publications on ecosystem functioning of marine macrobenthic fauna communities. A) Number of publications per type of study. B) Number of publications per ecosystem type where the studies where performed (n=145). C) Number of publications per taxa. D) Broad categories of ecosystem functioning that were studied. The numbers in each sector of the pie charts indicates the number of publications, with 149 papers reviewed for the analysis. For B), the ecosystem type studied could only be assigned to 145 publications.

A methodological approach was used in 20% of the publications. Most of these publications found a positive relationship between taxonomic and functional diversity (e.g. Bolam 2014; Wong and Dowd 2015), but differences between taxonomic and functional diversity emerged as well (e.g. Belley and Snelgrove 2016; Kokarev et al. 2017). This aligns with Cadotte et al. (2011) who demonstrated that the relationship between taxonomic and functional diversity is not positive in every case. A spatial approach was applied in 52% of the publications, and most of the publications described significant differences in functional diversity between sites (Table 2.3; e.g. Liu et al., 2019). Only a low proportion of publications

(19%) applied a temporal approach, and most of those publications found significant temporal differences (Table 2.3; e.g. Taupp and Wetzel 2019). Lastly, 24% of publications applied experimental approaches to their research, and all found significant relationships between macrobenthic species and sediment condition with the most common trend showing changes in nutrient cycling depending on the number and type of species involved in the experiments (e.g. Norkko et al. 2013; Thrush et al. 2017).

2.5 Towards unifying research on ecosystem functioning of marine macrobenthic fauna

2.5.1 Terminology and definitions

The research field of ecosystem functioning uses particular terminology, however, the terms used and their underlying concepts lack uniformity and robustness and in most of the cases definitions are not provided at all (Bremner 2008; Degen 2018; Weiss and Ray 2019), leading to confusion in understanding and wrong assumptions (e.g. Macleod et al. 2008; Bolam 2014; Rezek et al. 2017). We suggest that it is imperative to specify and define the terminology used in publications, as a coherent terminology can simplify the future progression of this research field at a global scale. As a consensus for terminology, we propose definitions for key terms on ecosystem functioning of marine macrobenthic fauna, presenting Table 2.1 to guide further studies, based on terms most frequently used and important for assessing ecosystem functioning (e.g. Table 2.1; Beauchard et al. 2017; Degen 2018).

2.5.2 Biological traits

With growing interest in BEF for marine macrobenthic fauna the complexity of trait categories used has increased (Bremner 2008, Beauchard et al. 2017). The majority of publications analysed relied on biological traits to assess macrobenthic fauna (78% of publications, or 115 publications). We identified that 129 publications used biological trait categories, and 10 of 26 were the most frequently used. Out of the biological traits most often used in publications, feeding mode was the most frequent trait (87% of publications), followed by mobility, body size and living habit (60.5%, 58% and 56% of publications respectively).

Considering that the selection of biological traits will always depend on the specific objectives of any particular study (Reiss et al. 2009), multiple biological traits have been identified through our dataset (Table 2.4). In some cases, different traits have been proposed, but with the same theoretical meaning as already established traits (e.g. Tornroos and Bonsdorff 2012; Darr et al. 2014, synonyms in Table 2.4), resulting in a lack of consistency across publications.

For a better comparability and coherent understanding of biological traits, it is necessary to use a standardized framework of biological trait categories. Some examples are the framework proposed by Bremner et al. (2003; 2006); Beauchard et al. (2017) which is not specific to macrobenthic fauna; Degen et al. (2018) which is specific to polar oceans; or the one we propose in Table 2.4, where traits are specified along with their synonyms (different theoretical meaning found through the literature), and the categories or modalities, providing a robust baseline for the standardization of the research field.

Another issue emerging from our literature review is the procedure for the selection of biological traits, as most of the publications used only those traits where information was available for species studied. Quantitative methods for choosing traits and weighting traits have been developed (Petchey and Gaston 2006), however refinement of traits is still needed. For many species of marine macrobenthic fauna, knowledge gaps on their biological and ecological information complicate biological trait allocation.

In addition, due to the lack of identification keys for many benthic macroinvertebrates, studies with varying levels of taxonomic resolution and the inclusion of morphospecies make selection of biological traits even more difficult (Bremner 2008; Beauchard et al. 2017; Degen et al. 2018). Recently, Weiss and Ray (2019) proposed a standardized method when selecting biological traits, providing a guide to support functional ecological comparisons across taxa. Alongside the issues concerning the selection of traits, and trait, biological and ecological information for several macrobenthic organisms, it is also important to consider the completeness representation of fauna among studies to perform adequate comparisons. However, further research using such an approach still needs to be done to verify its validity.

Table 2.4. Most frequently used traits for the study of marine macrobenthic fauna, in the context of ecosystem functioning, encountered in the literature. Effect and response traits are presented, 'x' indicates when a trait has an influence on ecosystem functioning ('Effect'), and/or is influenced by changes in the ecosystem ('Response'). Synonyms of the traits are given due to the large variety of terms used. Some examples of modalities are provided, but there could be more in the expanded literature. The sequence of traits in the table is arranged from most to least frequent use. * refers to modalities where classes are defined depending on the aim of the study.

Traits	Effect	Response	Synonyms	Modalities
Feeding mode	x	x	Feeding	Browser
			Feeding habit	Carnivore-Omnivore
			Feeding strategy	Deep deposit feeder
			Feeding type	Deposit feeder
			Trophic mode	Dissolved matter/symbionts
			Trophic group	Filter feeder
				Filter/suspension
				Grazer/scraper
				Opportunist/scavenger
				Parasite/commensal
				Predator
				Sub-surface deposit feeder
				Surface deposit feeder
				Suspension
Mobility		x	Adult dispersal	Freely motile in/on sediment
			Adult mobility	Limited free movement
			Motility	Mobile
				None
				Sedentary
				Semi-mobile
				Semi-pelagic
				Sessile/attached
				Tubicolous
Body size	x	x	Body length	Size classes*
			Body mass	
			Individual size	
			Maximum size	
			Normal adult size	
			Potential size	
			Size	
Living habit	x	x	Adult life habit	Attached/sessile
			Habit	Burrower
				Free living
				Surface crawler
				Swimmer
				Tube dwelling

Sediment position	x	x	Environmental position Living location Living position Local habitat Position in sediment	Attached to hard substrate Below oxygenated zone Epifauna Infauna Interface Oxygenated zone Pelagic Profound surface Surface
Life span		x	Adult longevity Life duration Longevity	Age classes*
Morphology	x	x	Body design Body form Body shape	Conical Cylindric Erect Flat Flattened Globulose Hard exoskeleton Hard shell Irregular Rectangular Round Soft Soft protected Upright Vermiform
Larval type		x	Development mechanism Larvae Larval development	Direct Lecithotrophic Planktotrophic No larvae
Bioturbation	x	x	Sediment transport Sediment reworking Sediment mixing	Biodiffusor Bioirrigator Conveyer belt transport Deep mixing Diffusive mixing No bioturbation Regenerator Surface deposition Surface mixing Surface modifier Transport Upward/downward conveyor
Reproductive mode		x	Reproductive technique	Asexual Gonochoristic Hermaphrodite

				Oviparous
				Ovoviviparous
				Sexual broadcast spawning
				Sexual direct development
				Sexual ovigerous
				Sexual shed eggs
				Sexual spawning
Reproductive frequency		x	Reproduction per year	Annual
				Biennial
				Continuous
				Seasonal
Movement method		x	Type of movement	Burrowing
				Crawling
				Jumping
				None
				Swimming
				Walking
Degree of attachment		x		None
				Permanent
				Temporary
Propagule dispersal	x	x		Benthic dispersal
				Pelagic dispersal
Habitat	x	x	Habitat	Above sediment 3D structures
			Habitat creation ability	Action-sediment accretion
			Habitat structure	Action-sediment removal
				Below sediment 3D structures
				Burrow dwelling
				Creating troughs, trampling on sediment
				Forming biogenic epibenthic structures
				Form-settlement/attached site
				Form-shelter
				Hole/pit
				Mound
				Non-permanent burrow
				None
				Permanent burrow
				Surface dwelling
				Tube dwelling
Body flexibility		x		Degrees classes*
Sexual differentiation		x		Gonochoristic
				Hermaphrodite
Indicator role		x	AMBI-Bentix	First-order opportunistic
				Indifferent
				Second-order opportunistic
				Sensitive
				Tolerant

Salinity preference		x		Oligohaline (0-5)
				Mesohaline (5-18)
				Polyhaline (18-30)
				Euhaline (30-40)
				Hyperhaline (>40)
Sociability	x	x		Colonial
				Gregarious
				Solitary
Migration	x	x	Dispersal habit	Life stage migration
				Non-migratory
				Seasonal migration
Substratum affinity		x		Grain sediment classes*
Productivity				Low
				Medium
				High
Hypoxia sensitivity		x		Low
				Medium
				High

2.5.3 Consistency in numerical methods

A large variety of methodologies and approaches for addressing ecosystem functioning of marine macrobenthic fauna has been identified (e.g. van der Linden et al. 2012; Belley and Snelgrove 2016; Gusmao et al. 2016; Baldrighi et al. 2017). Out of all publications, 86% used at least one numerical method to assess ecosystem functioning out of 39 different numerical metrics which were applied in the reviewed publications. However, only 17 numerical metrics were found in more than five publications (see Appendix A Table S2 for a full list). The numerical methods more recurrently used as a proxy for ecosystem functioning were taxonomic diversity (65 publications), abundance (59 publications) and biological traits (56 publications), taking into consideration that in the majority of the publications a combination of multiple numerical methods was used.

The variety in numerical methods found across studies was due to differences between authors, geographic areas, taxonomic groups and study type. Applying several metrics to measure how an ecosystem functions is not always practical. The wide variety of methods used, and the lack of accurate definitions that we identified across the publications, revealed the need for consistency to measure ecosystem functioning. For example, some publications used taxonomic diversity and abundance as a measure for ecosystem functioning (e.g. Lohrer et al. 2010; Pratt et al. 2015), whereas functional diversity was found less often, although functional diversity is the key component of biodiversity for reliably studying ecosystem functioning (Hooper et al. 2005; Wright et al. 2006; Legras et al. 2018).

To avoid misinterpretations in the fast-growing field of BEF research on marine macrobenthic fauna, it is imperative to standardize the metrics and methods used, including achieving complete representation of fauna. Therefore, we suggest following the most important and previously established methodological frameworks when assessing ecosystem functioning (Table 2.5). Otherwise, results from different studies and geographical areas cannot be reliably compared, which may mask significant information or lead to wrong conclusions (Petchey and Gaston 2006; Bremner 2008; Snelgrove et al, 2014).

2.6 Outlook

With ecosystem functioning of marine macrobenthic fauna growing as a research field, our analysis revealed the complexities of multiple methodologies and usage of terminology, creating discrepancies across publications. Such inconsistencies limit the potential of comparing and exploring study outcomes between different geographical areas.

Here, we provide a conceptual step-by-step guide on approaching ecosystem functioning for marine macrobenthic fauna (Figure 2.4). The following steps are imperative for advancing the research field: (1) Defining the terminology used in each publication to avoid misinterpretations and wrong conclusions. Although most of the terms are widely used, a global consensus on their definitions for ecosystem functioning in marine macrobenthic fauna is lacking. To facilitate more consistent use of terminology, we propose to use the definitions presented in Table 2.1.

(2) Selection of biological traits that are most suitable to address the study aims, based on species information available and previously standardized frameworks. The overview presented in Table 4 can be used as a standardised resource base for information about traits, synonyms, traits-modalities, and whether traits can indicate an effect or a response at ecosystem level (see also Bauchard et al. 2017; Degen et al. 2018; Weiss and Ray 2019).

Table 2.5. Frequently used measures to assess of ecosystem functioning on marine macrobenthic fauna encountered in the literature. Rank; A: Suggested by the authors based on the outcomes from the research weaving analysis; B: According to number of appearances in the publications analysed.

Rank		Name	Id	Description	Formula	Source
A	B					
1	8	Functional diversity	FD	Four steps are required: (i) obtaining a trait matrix, (ii) transform the first matrix into a distance matrix, (iii) create a dendrogram clustering the distance matrix, and (iv) calculate the total branch length of the dendrogram.	$FD = i'.h2$	Petchey and Gaston 2002; Mouchet et al. 2010.
2	7	Rao's quadratic entropy	Q	Sum of pairwise distances between species weighted by relative abundance.	$Q = \sum_{i-1}^{S-1} \sum_{j-j+1}^{S-1} dijpipj$	Rao's 1982; Champely and Chessel 2001; Mouchet et al. 2010.
3	15	Functional Richness	FRic	The amount of functional space occupied by a species assemblage; Convex Hull Volume.	Quick hull algorithm	Mason et al. 2005; Villeger et al. 2008; Mouchet et al. 2010.
4	13	Functional Evenness	FEve	The evenness of abundance distribution in a functional trait space.	$Feve = \frac{\sum_{i=1}^{S-1} \min\left(PEWi, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$	Mason et al. 2005; Villeger et al. 2008; Mouchet et al. 2010.
5	17	Functional divergence	FDiv	Species deviance from the mean distance to the centre of gravity weighted by relative abundance.	$FDiv = \frac{\Delta d + \overline{dG}}{\Delta\lvert d\rvert + dG}$	Mason et al. 2005; Villeger et al. 2008; Mouchet et al. 2010.
6	10	Functional redundancy	FR	Ratio between FD and H'.	$FR = FD/H'$	de Bello et al. 2007; van der Linden et al. 2012.

7	16	Functional dispersion	FDis	Abundance-weighted mean distance of individual species to their group centroid (all species community) in multivariate trait space.	$FDis = \frac{\sum ajzj}{\sum aj}$	Laliberte and Legendre 2010.
8	5	Fuzzy Correspondence Analysis	FCA	Fuzzy coding approach, scoring species according to their biological traits. A fuzzy variable takes values of type a = (a1, . . . , ak) giving the importance of k categories.		Chevenet et al. 1994; Bremner et al. 2006.
9*	3	Biological Trait analysis	BTA	Three numerical matrices are required: (i) taxa abundance in each site; (ii) biological traits of the taxa; and (iii) the combination of the previous two matrices.		Statzner et al. 1994; Bremner et al. 2003.
10	12	Community Bioirrigation Potential	BIPc	Abundance and biomass data with information about the life traits of individual species or taxonomic groups	$BPc = \sum_{i=1}^{n} \sqrt{\frac{Bi}{Ai\ x\ Ai\ x\ Mi\ x\ Ri}}$	Solan et al. 2004; Queiros et al. 2013.
11	6	Shannon diversity Index	H'	The proportion of species *i* relative to the total number of taxa (p_i) is calculated, and then multiplied by the natural logarithm of this proportion ($\ln p_i$)	$H' = -\mathrm{K} \sum_{i=1}^{R} pi \log pi$	Shannon 1948; Spellerberg and Fedor 2003.
12	9	Pielou's index	J'	quantifies how equal the community is numerically	$J' = \frac{H'}{H'max}$	Pielou 1996.
13	2	Abundance	A	Number of organisms found in sample.	-	-
14	1	Taxonomic diversity	S	Number of taxa found in a sample.	-	-
15	4	Biomass	B	Ash-free Dry Weight (AFDW).	-	-

*BTA is a measure required to calculate other functional metrics.

(3) We recommend that numerical methodologies should follow an ordered system, prioritizing the use, at least, of one of the top six measures to assess ecosystem functioning (see ranks A in Table 2.5). Of those measures, functional diversity is the most relevant for understanding the links between ecosystem functioning and marine macrobenthic fauna.

(4) Outcomes from ecosystem functioning assessment can be used as valuable tools for informing conservation policy and management of natural ecosystems.

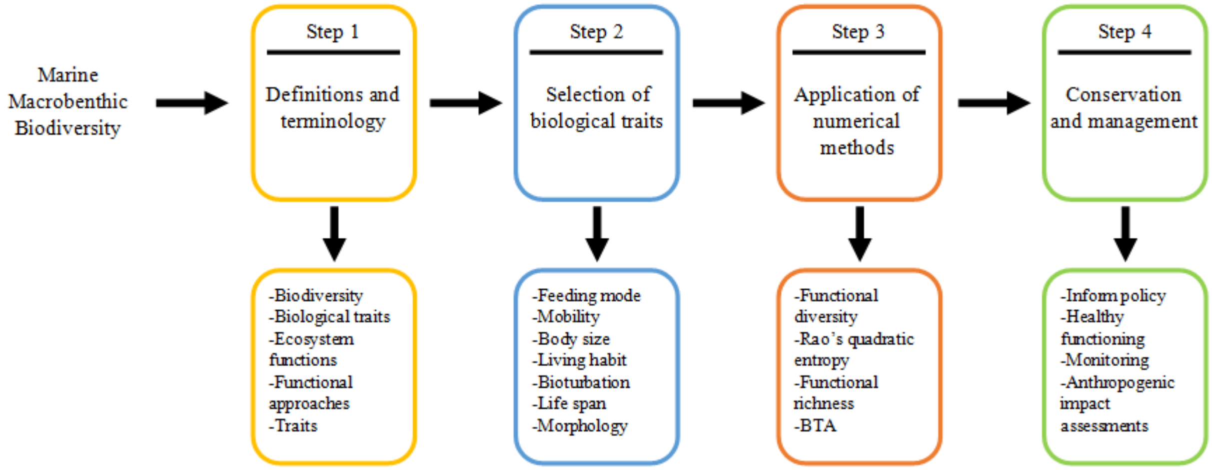


Figure 2.4. Conceptual step-by-step guide for assessing ecosystem functioning of marine macrobenthic fauna.

We also suggest, for a full understanding of how an ecosystem is functioning, to develop more specific approaches, where the complex interlinkages across traits, ecosystem processes, ecosystem functions and services are considered. Single or multiple traits can influence several ecosystem functions, or one ecosystem function could be affected by several traits. For example, body size as a biological trait category influences several ecological processes such as predation, scavenging and bioturbation, which can then affect single or multiple functions in the ecosystem (e.g. productivity, nutrient cycling and sediment transport) and, depending on the ecosystem functions involved, one or more ecosystem services (Figure 2.5).

2.7 Concluding remarks

In this review, we presented the first ecological synthesis that uses the approach of research weaving for analysing the ecosystem functioning and functional diversity of marine macrobenthic fauna. Thus, we provide a detailed description of the influence and evidence of the current knowledge of ecosystem functioning in marine macrobenthic fauna.

The analysis revealed that advances in this research field are challenged by multiple knowledge gaps, several different theoretical ideas, terminology and methods used. The patchiness in research globally further indicated that BEF for benthic communities is understudied in many geographical areas. The heterogeneity in terminology, lack of consistency in selection of biological traits, different completeness of representation of fauna, and inconsistencies in numerical methodologies, make it difficult to extrapolate and compare findings on ecosystem functioning of marine benthic ecosystems, potentially leading to wrong conclusions. Therefore, we have proposed a conceptual guide suggesting the use of standardized terminology, selection of biological traits and numerical methodologies. We also emphasize the need to address the complex interlinkages between biological traits, ecological processes, ecosystem functions and services, to improve our understanding and management of these ecosystems.

With the advancement of technology, and with the willingness to expand established worldwide collaborations and research networks, the availability of information and resources (e.g. trait databases, methodologies) in this research field will only increase. However, consensus on standardised approaches is mandatory for reducing the knowledge-gap in ecosystem functioning of marine macrobenthic fauna on a global scale.

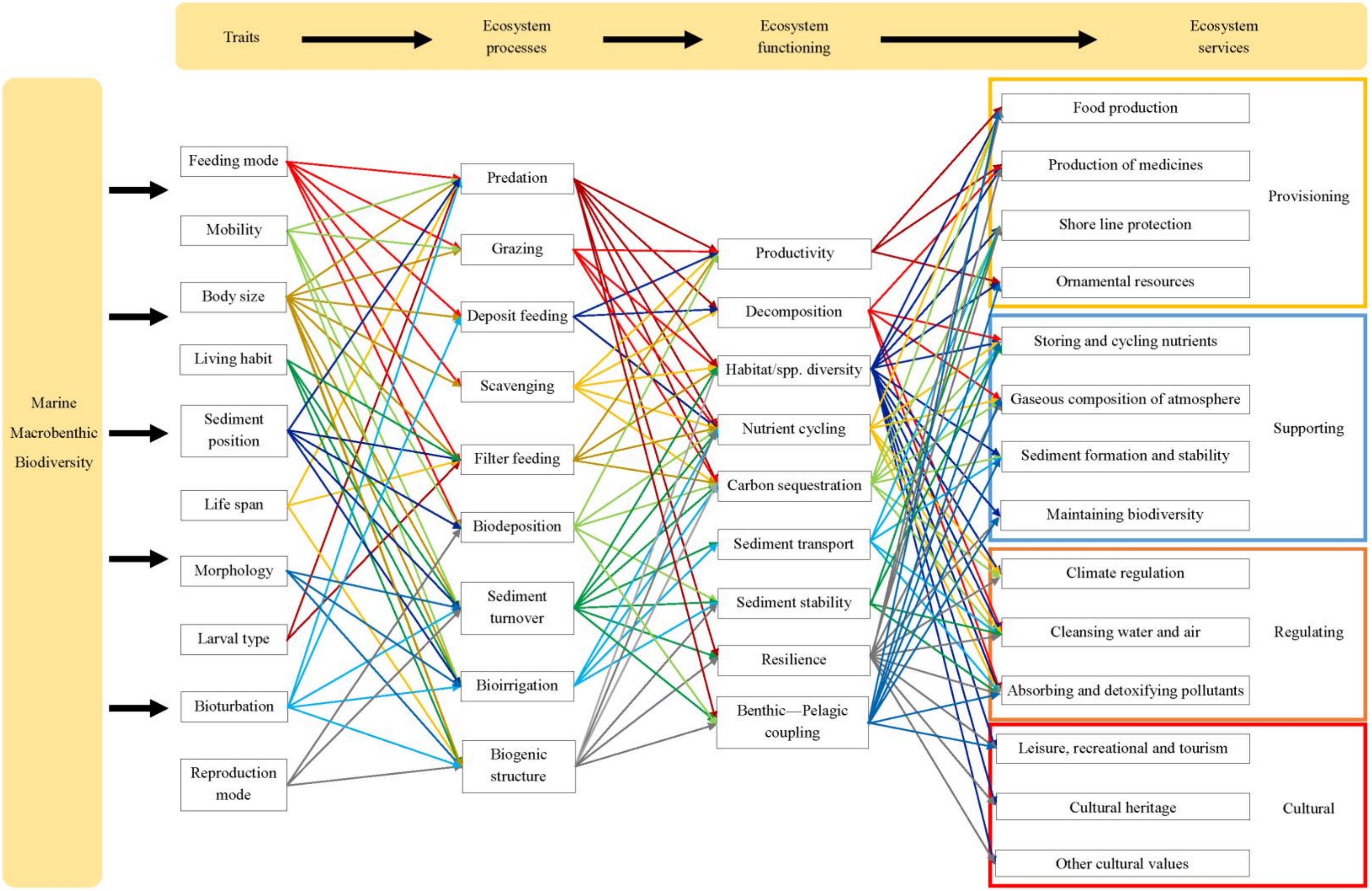
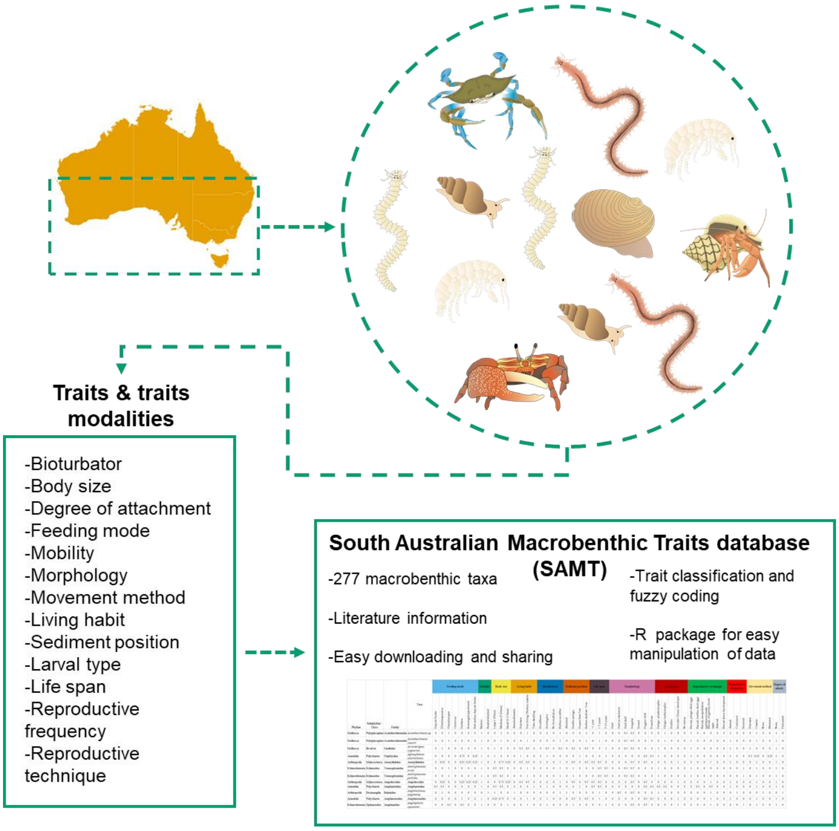


Figure 2.5. Interlinkages among biodiversity of marine macrobenthic fauna, traits (the ten most frequently used, see Table 2.4), ecosystem processes, ecosystem functioning and ecosystem services. Note that this multi-ecosystem linkage is not restricted and can include other traits, processes, functioning and services in the expanded literature. Information was collated from: Norling et al. 2007; Bremner 2008; Townsend et al. 2011; Norkko et al. 2013; Queiros et al. 2013; Snelgrove et al. 2014; Song et al. 2014; Clare et al. 2015; Frid and Caswell 2016; Weigel et al. 2016; Beauchard et al. 2017; Thrush et al. 2017; van der Linden et al. 2017; Dissanayake et al. 2018; Kun et al. 2019.

Chapter 3. Establishing the South Australian Macrobenthic Traits (SAMT) database: a trait classification for functional assessments



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Author contributions

Orlando Lam Gordillo: Conceived the ideas and developed the outline for the manuscript, collated the data, developed R package, wrote the manuscript and corresponding author.

Sabine Dittmann – primary supervisor: Guidance on the project development, discussion of project ideas, contribution to drafting manuscript, and critical refinement.

Ryan Baring – co-supervisor: Discussion of project ideas, contribution to drafting manuscript.

Abstract

Trait-based approaches are increasingly used as a proxy for understanding the relationship between biodiversity and ecosystem functioning. Macrobenthic fauna are considered one of the major providers of ecosystem functions in marine soft sediments, however, several gaps persist in the knowledge of their trait classification, limiting the potential use of functional assessments. While trait databases are available for the well-studied North Atlantic benthic fauna, no such trait classification system exists for Australia. Here, we present the South Australian Macrobenthic Traits (SAMT) database, the first comprehensive assessment of macrobenthic fauna traits in temperate Australian waters. The SAMT database includes 13 traits and 54 trait-modalities (e.g. life history, morphology, physiology, and behaviour), and is based on records of macrobenthic fauna from South Australia. We provide trait information for more than 250 macrobenthic taxa, including outcomes from a fuzzy coding procedure, as well as an R package for using and analysing the SAMT database. The establishment of the SAMT constitutes the foundation for a comprehensive macrobenthic trait database for the wider southern Australian region that could facilitate future research on functional perspectives, such as assessments of functional diversity and changes to ecosystem functioning.

Keywords: Biological traits, ecosystem functioning, functional group, benthos, macrofauna, Australia.

3.1. Introduction

Trait-based approaches have become topical in ecological research for understanding the relationship between species (biodiversity) and ecosystem functioning, ecosystem processes, ecosystem services, or responses to anthropogenic disturbances (Bremner et al. 2003; Bremner et al. 2006; Bolam et al. 2016; Cano-Barbacil et al. 2019; Weiss and Ray 2019). Trait-based approaches are also used to measure several functional indices (e.g. functional diversity: functional divergence, functional redundancy, functional richness), and can be used to perform analyses across species pools from distinct geographical areas (Mason et al. 2005; Mouchet et al. 2010; Degen and Faulwetter 2019; Lam-Gordillo et al. 2020). Functional approaches are based on different subsets of traits (i.e. species characteristics) as a proxy of ecosystem functioning (Bremner et al. 2006; Bremner 2008).

Traits can be defined as properties of organisms that can be measured, usually at the organism level and used comparatively across species. Examples of traits are the life history, morphology, physiology, and behaviour characteristics that species can exhibit (Bremner et al. 2006; Petchey and Gaston 2006; Reiss et al. 2009; Degen et al. 2018; Lam-Gordillo et al. 2020a). Selection of traits is flexible and should include an appropriate range of traits relevant to the specific research question, i.e. capture the characteristics of organism for the ecosystem processes under investigation (Petchey & Gaston 2006; Costello et al. 2015; Beauchard et al. 2017; Lam-Gordillo et al. 2020a).

The use of traits has gained momentum in marine ecology with a growth in published research in recent years, which has improved the understanding of the functioning of marine ecosystems (Costello et al. 2015; Cano-Barbacil et al. 2019; Castro et al. 2019; Lam-Gordillo et al. 2020a). The increased interest in traits has been particularly evident in the assessment of macrobenthic communities (Beauchard et al. 2017; Degen et al. 2018; Dissanayake et al. 2018; Lam-Gordillo et al. 2020a). Macrobenthic invertebrates have long been recognized as important providers of ecological processes and ecosystem functions in soft sediments due to their capability to enhance recycling of nutrients, modifying sediment properties (e.g. bioturbation, exchange processes). They are also useful bioindicators of pollution and other environmental stressors (Reiss et al. 2009; Shojaei et al. 2015; Liu et al. 2019; Dissanayake et al. 2019).

Throughout the literature, several traits have been proposed to assess the relationship between macrobenthic fauna and ecosystem functioning, however, there are no standardised definitions for traits. In addition, the deficiency on species trait information, data accessibility, and different levels of taxonomic resolution, make the selection and use of traits even harder (Lam-Gordillo et al. 2020a). In order to address these issues, some frameworks for assessing biological traits in marine fauna have been suggested, as well as standardised guidelines for the analysis and interpretation of this information (Beauchard et al. 2017; Degen et al. 2018; Lam-Gordillo et al. 2020a).

The southern Australian coast is the longest east-west temperate coastline in the southern hemisphere with a diversity of sedimentary habitats (Short 2020). However, information about traits of macrobenthic fauna from this region is scarce or non-existent (Lam-Gordillo et al. 2020a). The limited information about traits, combined with gaps in the taxonomic knowledge of southern Australian benthic species has limited the use of functional assessments for management and conservation purposes, as well as understanding benthic ecosystem functioning in this part of the world.

Here, we present the South Australian Macrobenthic Traits database (SAMT), to advance trait-based approaches for southern temperate coastlines. The trait information provided is based on previous studies for comparability and presented in an easily accessible database for downloading and sharing amongst researchers (Costello et al. 2015; Beauchard et al. 2017; Degen et al. 2018; Lam-Gordillo et al. 2020a). In addition, we present a flow chart detailing the step-by-step process of assessing ecosystem functioning and highlighting the utility of the SAMT database for accomplishing this task. This is the first comprehensive assessment of traits of the South Australian macrobenthic fauna, with the aim to facilitate further research across southern Australian temperate marine waters on functional perspectives, elucidating patterns on functional diversity and detect changes in ecosystem functioning.

3.2. Methods

3.2.1 Data acquired

A dataset was compiled from previous projects led by the senior author on macrobenthic fauna in soft sediments of South Australia (Appendix B Table S1), from 37 different localities within this region (Figure 3.1). The dataset encompasses quantitative records of taxa recorded from inter- and shallow sub-tidal soft sediments in coastal embayments, lagoons and inverse estuaries, representative of coastal sedimentary habitats along the arid and warm temperate coastline of southern Australia.

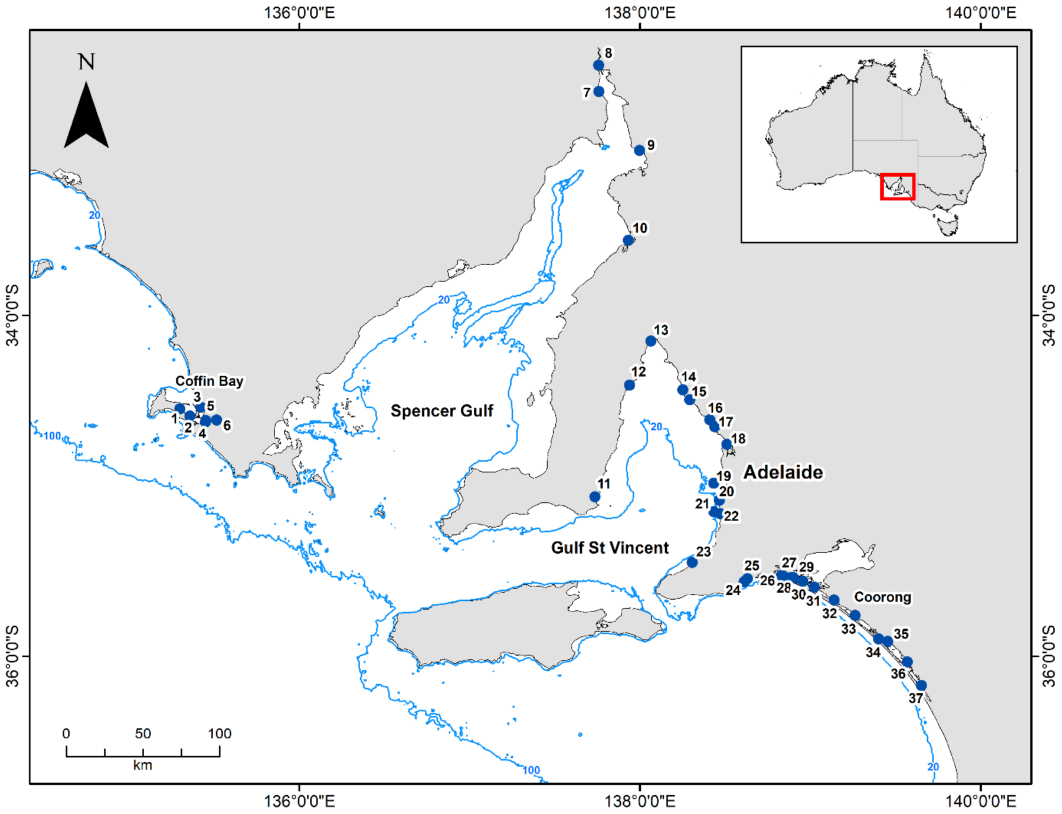


Figure 3.1. Localities of South Australia from where information about taxa traits were used in this study. 1) Port Douglas; 2) Eely Point; 3) Mount Dutton Bay; 4) Long Beach; 5) Crinoline Point; 6) Kellidie Bay; 7) Blanche Harbor; 8) Curlew Point; 9) Port Germain; 10) Fisherman Bay; 11) Coobowie; 12) Tiddy Widdy; 13) Port Arthur; 14) Port Parham; 15) Thompson's Beach; 16) Middle Beach; 17) Port Gawler; 18) Section Bank; 19) Glenelg; 20) Port Stanvac; 21) Port Noarlunga; 22) Onkaparinga; 23) Normanville; 24) Hindmarsh River; 25) Inman River; 26) Monument Rd; 27) Tarni Warra; 28) Hunters Creek; 29) Mundoo Channel; 30) Ewe

Island; 31) Pelican Point; 32) Mulbin Yerrok; 33) Noonameena; 34) Parnka Point; 35) Villa de Yumpa; 36) Jack Point; 37) Loop Rd.

3.2.2 Selection of traits

Selection of traits was based on the most commonly used traits for assessing macrobenthic fauna (Lam-Gordillo et al. 2020a), ensuring that the selected biological traits could be compared across studies (Degen and Faulwetter 2018), geographical areas (Bremner et al. 2006), and are applicable to most benthic taxa (Costello et al. 2015). The selected traits capture the four subject areas "Biology", "Habitat", "Life-history" and "Larval" introduced by Costello et al. (2015) to structure trait categories. In total, based on Lam-Gordillo et al. (2020a), 13 traits and 54 trait-modalities were assessed (Table 3.1).

3.2.3 Trait allocation

Trait data were gathered from various published online sources, depending on the availability of information for each taxon. When trait information on a particular taxon was missing, its trait values were inferred from the nearest phylogenetic neighbour. For example, if no trait information was available at the species level, trait information was used from another species within the same genus; if information was unavailable at genus level, we considered information at family level. Additional considerations such as taxa distribution, resemblance, and expert judgment were also applied (see Appendix B Table S2-3).

3.2.4 Fuzzy coding of traits

Each of the taxa analysed were scored depending on the affinity that a taxon displayed with a trait-modality using a fuzzy coding procedure (Chevenet et al. 1994, Bremner et al. 2006, Bremner 2008). A scoring range from 0 – 1 was used, with 0 being no affinity and 1 being high affinity to a trait. For example, coding the trait 'Feeding mode' for *Aglaophamus australiensis* (Polychaeta), considered that *A. australiensis* is mostly a predatory species, however it also exhibits some degree of sub-surface deposit feeding, giving a fuzzy coding of 0.75 as predator, and 0.25 as sub-surface deposit feeder, completing the full allocation of 1 for the feeding mode trait.

Table 3.1. Details of 13 traits and 54 trait-modalities included in the South Australian Macrobenthic Traits (SAMT) database.

Subject area	Traits	Modalities	Definition	Function and processes	Reference
Biology	Bioturbator	Biodiffusor Bioirrigator No bioturbation Surface modifier	Transport processes & modification of sediments by organisms that directly/ indirectly affect sediment composition.	Nutrient cycling, sediment reworking, organic matter re-generation, influence on biogeochemistry.	Kristensen et al. 2012; Queiros et al. 2013; Beauchard et al. 2017; Degen & Faulwetter 2018; Liu et al. 2019.
	Body size	Large (>20 mm) Medium (5-20 mm) Small (0.5-5 mm)	Maximum body size as adult.	Influence on productivity, habitat facilitation, sediment reworking, oxygen consumption.	Costello et al. 2015; Beauchard et al. 2017; Degen & Faulwetter 2018, Liu et al. 2019.
	Degree of attachment	None Permanent	Organism ability to attach to a substratum.	Influence on metabolic production, trophic support, habitat facilitation.	Bremner 2008; Liu et al. 2019.
	Feeding mode	Deposit feeder Filter/suspension Grazer/scraper Omnivore Predator Scavenger/opportunist Sub-surface deposit feeder	The mode of food acquisition.	Nutrient cycling, resource utilization & facilitation, species demographic control, trophic support.	Costello et al. 2015; Beauchard et al. 2017; van der Linden et al. 2017; Degen & Faulwetter 2018; Liu et al. 2019.
	Mobility	Mobile Sessile/attached	Degree of movement.	Nutrient cycling, sediment reworking, trophic support, food source.	Costello et al. 2015; Degen & Faulwetter 2018; Liu et al. 2019.
	Morphology	Hard Hard exoskeleton Hard shell Irregular, Round Soft / Fragile Vermiform	External features & structural robustness of an adult organism.	Sensitivity, food source, habitat facilitation, survival to disturbances, sediment reworking.	Beauchard et al. 2017; Degen & Faulwetter 2018, Liu et al. 2019.

	Movement method	Burrower Crawler None Swimmer	Organism type of movement as an adult.	Nutrient cycling, sediment transport, dispersal, recolonization, migration, ability to escape predation.	Beauchard et al. 2017; Degen & Faulwetter 2018, Liu et al. 2019.
	Living habit	Burrower Free living / Surface crawler Tube dwelling	Organism mode living as an adult.	Nutrient cycling, sediment transport, dispersal, habitat creation & facilitation.	van der Linden et al. 2017; Degen & Faulwetter 2018; Liu et al. 2019.
Habitat	Sediment position	Attached Bentho-pelagic Deeper than 3 cm Surface shallow <3 cm	Organism relative position on the sediment.	Nutrient cycling, sediment transport, habitat creation & facilitation.	Costello et al. 2015; Beauchard et al. 2017; van der Linden et al. 2017; Degen & Faulwetter 2018, Liu et al. 2019.
Larval	Larval type	Pelagic -planktotrophic Pelagic lecthrotophic Benthic Brooder / Direct developer No larvae	Larval type & feeding mode.	Food source, ability of species dispersal, influence in nutrient cycling.	van der Linden et al. 2017; Degen & Faulwetter 2018, Liu et al. 2019.
	Life span	<1 year 1-3 years 3-10 years	Organism maximum life span as an adult.	Community dynamics, resilience of organisms, reproduction, productivity.	Beauchard et al. 2017; van der Linden et al. 2017; Degen & Faulwetter 2018, Liu et al. 2019.
Life-history	Reproductive frequency	Annual Continuous Seasonal	Times that the organism reproduces over time.	Demographic resilience, population stock.	Beauchard et al. 2017; Degen & Faulwetter 2018.
	Reproductive technique	Sexual, pelagic shed eggs Sexual, benthic shed eggs Sexual, encapsulation Sexual, Asexual	The mode organism reproduces, mechanism of fertilization & propagules released.	Species dispersal, carbon transport, demographic resilience.	Costello et al. 2015; Beauchard et al. 2017; Degen & Faulwetter 2018.

3.2.5 Case study: assessment of the SAMT database

To elucidate the utility of the SAMT database on the assessment of ecosystem functioning, a functional assessment encompassing four main regions across South Australia was performed. The regions selected were Coffin Bay (locality 1,3,4 and 6), Spencer Gulf (locality 9-10), Gulf St. Vincent (locality 14-17), and the Coorong (locality 28,31-33) (Figure 3.1). For this case study we only selected information on macrobenthic fauna from intertidal mudflats. At each locality, samples for benthic macrofauna were taken a handheld PVC corer (83.32 cm^2 surface area), pushed it into the sediment up to 20 cm depth, with 15 replicates haphazardly taken per locality. All sediment samples were sieved through 500 µm mesh size in the field and preserved in 70% ethanol until further processing. Trait selection was made in the context of ecosystem functioning, thus, we analysed only traits that influence the functioning of ecosystems (i.e. effect traits) that included; bioturbator, body size, feeding mode, morphology, living habit, and sediment position (Lam-Gordillo et al. 2020). It is important to note that the functional analyses are an exemplification of the potential use of SAMT database, and outcomes need to be carefully considered.

Macrobenthic fauna were analysed using both traditional biodiversity metric and functional approaches. The traditional biodiversity approaches included the analysis of taxonomic richness (S) and Simpson diversity index (1-λ) on macroinvertebrate abundances. For the functional approach; trait richness, Simpson index and functional diversity (as Rao's quadratic entropy: RaoQ) were calculated on macroinvertebrate trait data. Diversity analyses and graphics were performed using R (R Core Team, 2017) and the packages “vegan” (Oksanen et al. 2019), “FD” (Laliberté et al. 2014), and “ggplot2” (Wickham, 2016). A univariate one-factor PERMutational ANalysis Of VAriance (PERMANOVA) using Euclidean distance for the single variable (either effect traits, taxa or trait based diversity index), permutation of residuals under a reduced model and 9999 permutations was used to test for significant differences across regions (Anderson et al. 2008). All PERMANOVA tests were carried out using PRIMER v7 with PERMANOVA+ add on.

3.3. Results

3.3.1 Taxa included

In total, we generated trait information for 277 taxa (see Appendix B Table S4 for a full list of taxa). The number of taxa varied (i.e. range from 4 to 142 per site, mean of 28) across the 37 localities of South Australia, with the greatest numbers from subtidal sediments in Gulf St Vincent (Appendix B Figure S1). Different levels of taxonomic identification were assessed, 152 at the species level, followed by 28 at genus level, 86 at family level, and the remaining 11 taxa at higher levels (order, class or phyla; Appendix B Figure S2a). The phylum with most records was Mollusca (112 records, 40% of all taxa), followed by Arthropoda (94 records, 34% of all taxa) and Annelida (45 records, 16% of all taxa), with the remaining 10% belonging to other taxa (Echinodermata 15 taxa, one to three taxa each for Chordata, Sipunculida, Nemertea, Cnidaria, Porifera and Brachiopoda; Appendix B Figure S2b). Although Mollusca was the phylum with the highest number of records overall, Annelida was the phylum with the most records across localities (i.e. 43% of all sites) (Figure 3.2).

3.3.2 Data sources

The information on traits was retrieved from diverse peer reviewed and expert sources, and a database was generated for easy interpretation and useability (Figure 3.3; Trait source table in "https://doi.org/10.6084/m9.figshare.12763154"). Including all the traits assessed, 90% of the information was provided from primary literature that included 48% from South Australian literature, 29% from Australian literature and 13% from overseas literature. The remaining 10% of information was obtained from reputable resources online (Appendix B Table S2). However, the source of trait information varied between types of traits (Figure 3.4a). Across taxonomic levels, most of the trait information was available at the family (42%) and species (38%) levels, with proportionally less at the order/class and genus levels (11% and 9% respectively; Figure 3.4b). It also emerged that the traits larval type, life span, reproductive frequency and technique are less studied for the macrobenthic fauna from Australia (Figure 3.4).

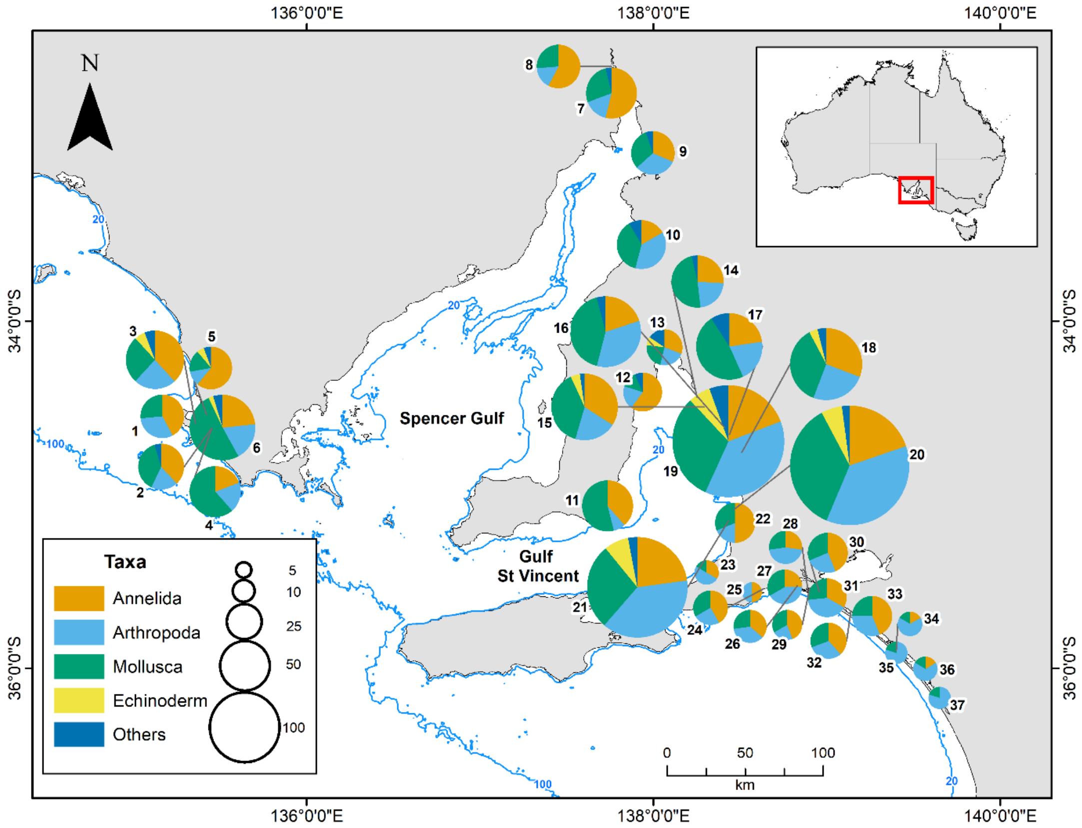
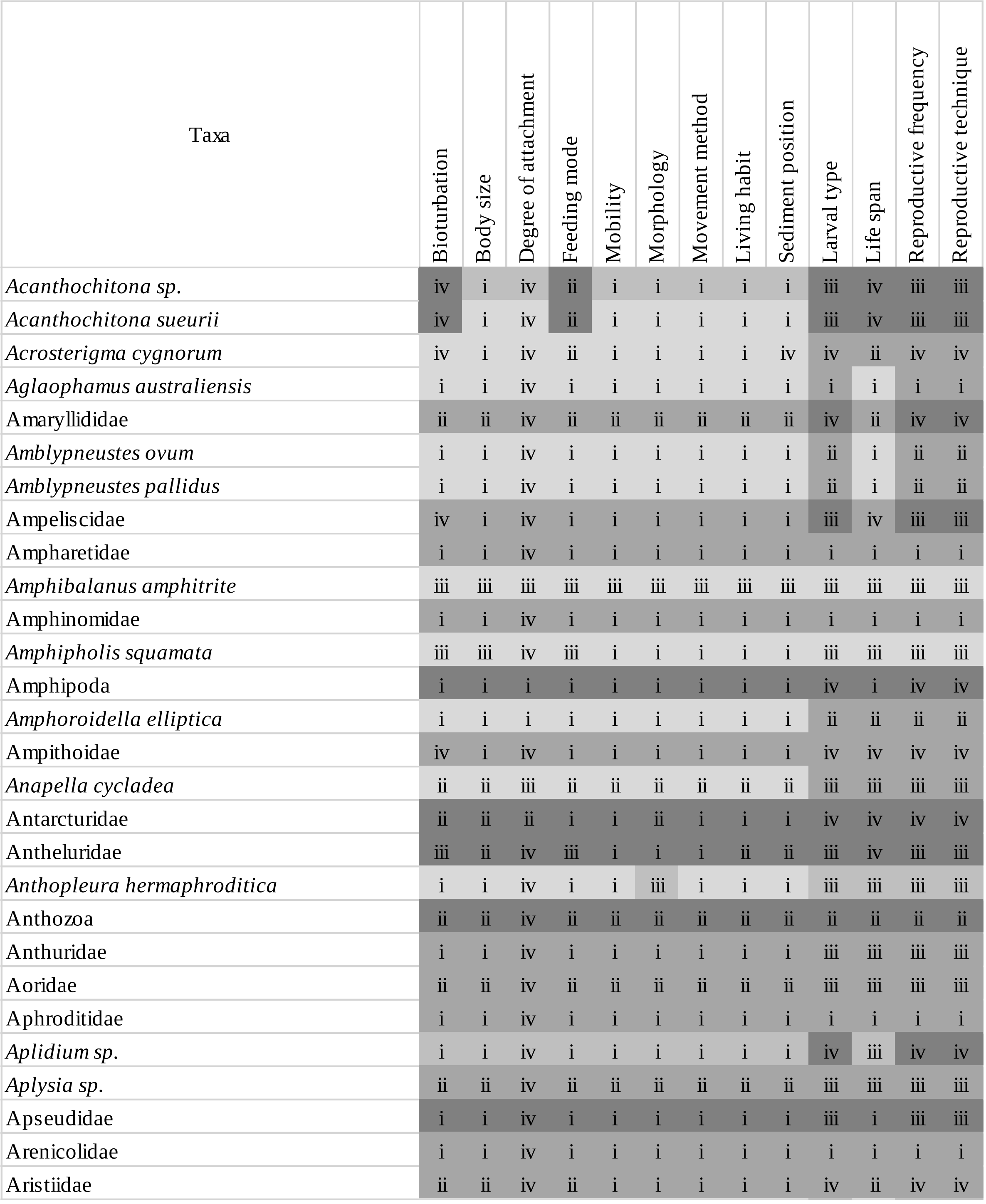


Figure 3.2. Number of taxa per locality of South Australia. Circle size is proportional to the number of taxa. 1) Port Douglas; 2) Eely Point; 3) Mount Dutton Bay; 4) Long Beach; 5) Crinoline Point; 6) Kellidie Bay; 7) Blanche Harbor; 8) Curlew Point; 9) Port Germain; 10) Fisherman Bay; 11) Coobowie; 12) Tiddy Widdy; 13) Port Arthur; 14) Port Parham; 15) Thompson's Beach; 16) Middle Beach; 17) Port Gawler; 18) Section Bank; 19) Glenelg; 20) Port Stanvac; 21) Port Noarlunga; 22) Onkaparinga; 23) Normanville; 24) Hindmarsh River; 25) Inman River; 26) Monument Rd; 27) Tarni Warra; 28) Hunters Creek; 29) Mundoo Channel; 30) Ewe Island; 31) Pelican Point; 32) Mulbin Yerrok; 33) Noonameena; 34) Parnka Point; 35) Villa de Yumpa; 36) Jack Point; 37) Loop Rd.



Taxa	Bioturbation	Body size	Degree of attachment	Feeding mode	Mobility	Morphology	Movement method	Living habit	Sediment position	Larval type	Life span	Reproductive frequency	Reproductive technique
Acanthochitona sp.	iv	i	iv	ii	i	i	i	i	i	iii	iv	iii	iii
Acanthochitona sueurii	iv	i	iv	ii	i	i	i	i	i	iii	iv	iii	iii
Acrosterigma cygnorum	iv	i	iv	ii	i	i	i	i	iv	iv	ii	iv	iv
Aglaophamus australiensis	i	i	iv	i	i	i	i	i	i	i	i	i	i
Amaryllididae	ii	ii	iv	ii	ii	ii	ii	ii	ii	iv	ii	iv	iv
Amblypneustes ovum	i	i	iv	i	i	i	i	i	i	ii	i	ii	ii
Amblypneustes pallidus	i	i	iv	i	i	i	i	i	i	ii	i	ii	ii
Ampeliscidae	iv	i	iv	i	i	i	i	i	i	iii	iv	iii	iii
Ampharetidae	i	i	iv	i	i	i	i	i	i	i	i	i	i
Amphibalanus amphitrite	iii	iii	iii	iii	iii	iii	iii	iii	iii	iii	iii	iii	iii
Amphinomidae	i	i	iv	i	i	i	i	i	i	i	i	i	i
Amphipholis squamata	iii	iii	iv	iii	i	i	i	i	i	iii	iii	iii	iii
Amphipoda	i	i	i	i	i	i	i	i	i	iv	i	iv	iv
Amphoroidella elliptica	i	i	i	i	i	i	i	i	i	ii	ii	ii	ii
Ampithoidae	iv	i	iv	i	i	i	i	i	i	iv	iv	iv	iv
Anapella cycladea	ii	ii	iii	ii	ii	ii	ii	ii	ii	iii	iii	iii	iii
Antarcturidae	ii	ii	ii	i	i	ii	i	i	i	iv	iv	iv	iv
Antheluridae	iii	ii	iv	iii	i	i	i	ii	ii	iii	iv	iii	iii
Anthopleura hermaphroditica	i	i	iv	i	i	iii	i	i	i	iii	iii	iii	iii
Anthozoa	ii	ii	iv	ii	ii	ii	ii	ii	ii	ii	ii	ii	ii
Anthuridae	i	i	iv	i	i	i	i	i	i	iii	iii	iii	iii
Aoridae	ii	ii	iv	ii	ii	ii	ii	ii	ii	iii	iii	iii	iii
Aphroditidae	i	i	iv	i	i	i	i	i	i	i	i	i	i
Aplidium sp.	i	i	iv	i	i	i	i	i	i	iv	iii	iv	iv
Aplysia sp.	ii	ii	iv	ii	ii	ii	ii	ii	ii	iii	iii	iii	iii
Apseudidae	i	i	iv	i	i	i	i	i	i	iii	i	iii	iii
Arenicolidae	i	i	iv	i	i	i	i	i	i	i	i	i	i
Aristiidae	ii	ii	iv	ii	i	i	i	i	i	iv	ii	iv	iv

Figure 3.3. Screenshot of a section of the Traits information sources table. Roman numerals indicate sources' origin, and cell shading specify the taxonomic level of the information. i: South Australian literature; ii: Australian literature; iii: Overseas literature; iv: online resources. ░ Species level; ▒ Genus level; ▓ Family level; █ Order/Class level.

Full table available in https://doi.org/10.6084/m9.figshare.12763154

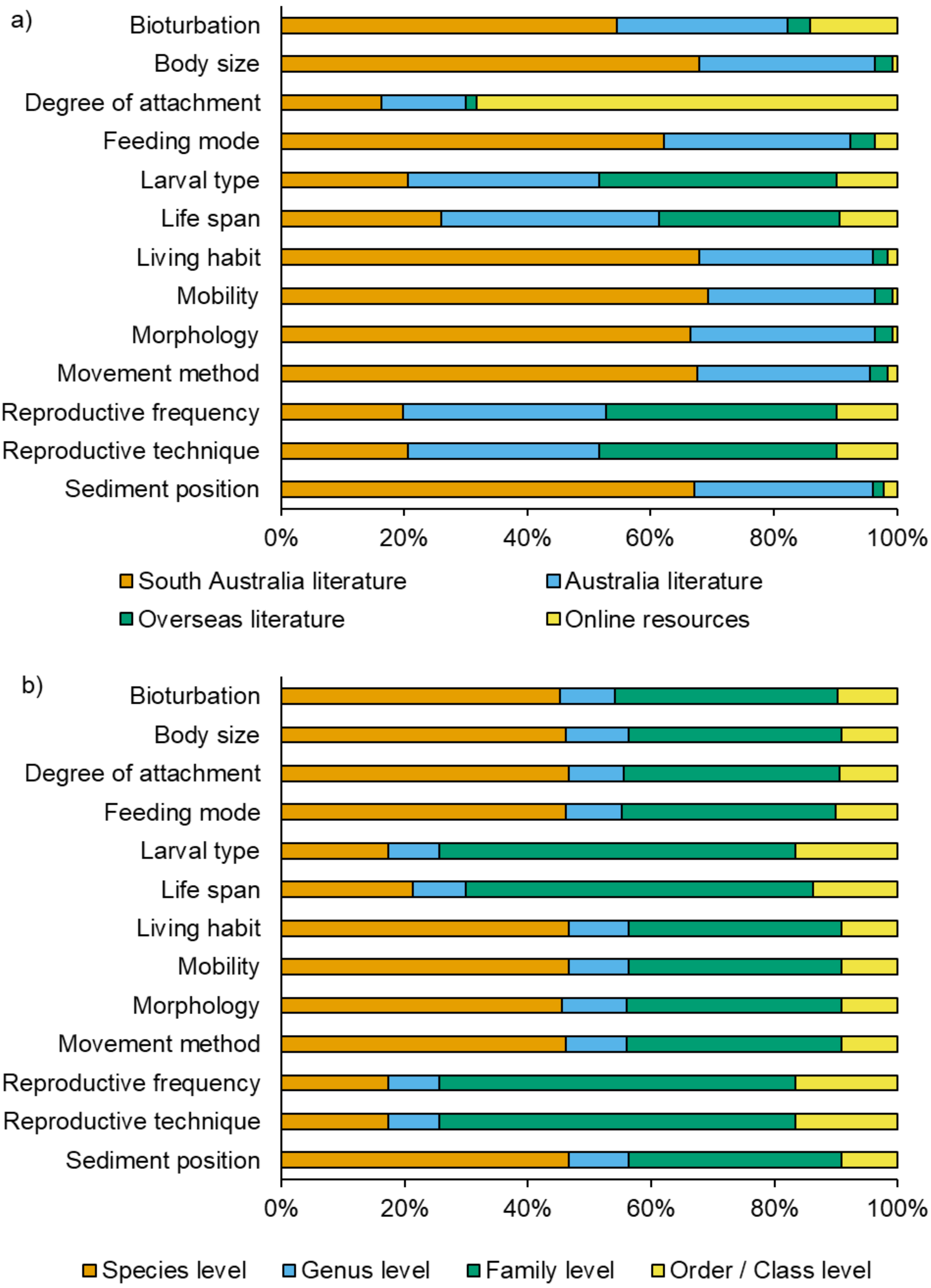


Figure 3.4. Stacked bar graphs showing a) the cumulative percentage of trait information sources, and b) the cumulative percentage of trait information by taxonomic level.

3.3.3 The South Australian Macrobenthic Traits (SAMT) database

Functional trait information (i.e. traits and fuzzy coding classification) for the 277 macrobenthic taxa analysed from the South Australian region are the basis for the SAMT database, which is available as an accessible resource at "https://doi.org/10.6084/m9.figshare.12763154" (see Figure 3.5 for a screenshot of the SAMT database). Along with the database resource, version 1.0.0 of the SAMT R package is provided for assistance in using and analysing the SAMT database. The SAMT v1.0.0 R package is currently available on the repository https://github.com/OrlandoLam/SAMT (see Appendix B-1 for SAMT package user guide). The SAMT database is intended to progress with regular updates of new data by researchers conducting work across southern Australia for easy downloading and sharing.

To illustrate the utility of the SAMT database, we developed a flow chart showing the step-by-step process for assessing the contribution of macrobenthic fauna to ecosystem functioning (Figure 3.6). The first steps are to compile macrobenthic data from diverse sources (e.g. surveys, field sampling, collections, online databases) and allocate the respective trait information to each taxon. The SAMT database reduces the time needed for gathering and finding the taxa trait information and provides the information in one place. Macrobenthic abundance data can be added to the database at any time, and the R package provided within SAMT database can be used for compiling a trait x sample matrix (LQ). Depending on the aim of the study, and with all the matrices compiled, different analyses can be performed using different software (e.g. R, PRIMER), from measuring trait patterns (LQ), relationships between species-traits and the environment, or modelling the interactions between species-traits and the environment (RQL), to calculating functional diversity as a proxy for assessing ecosystem functioning (Figure 3.6).

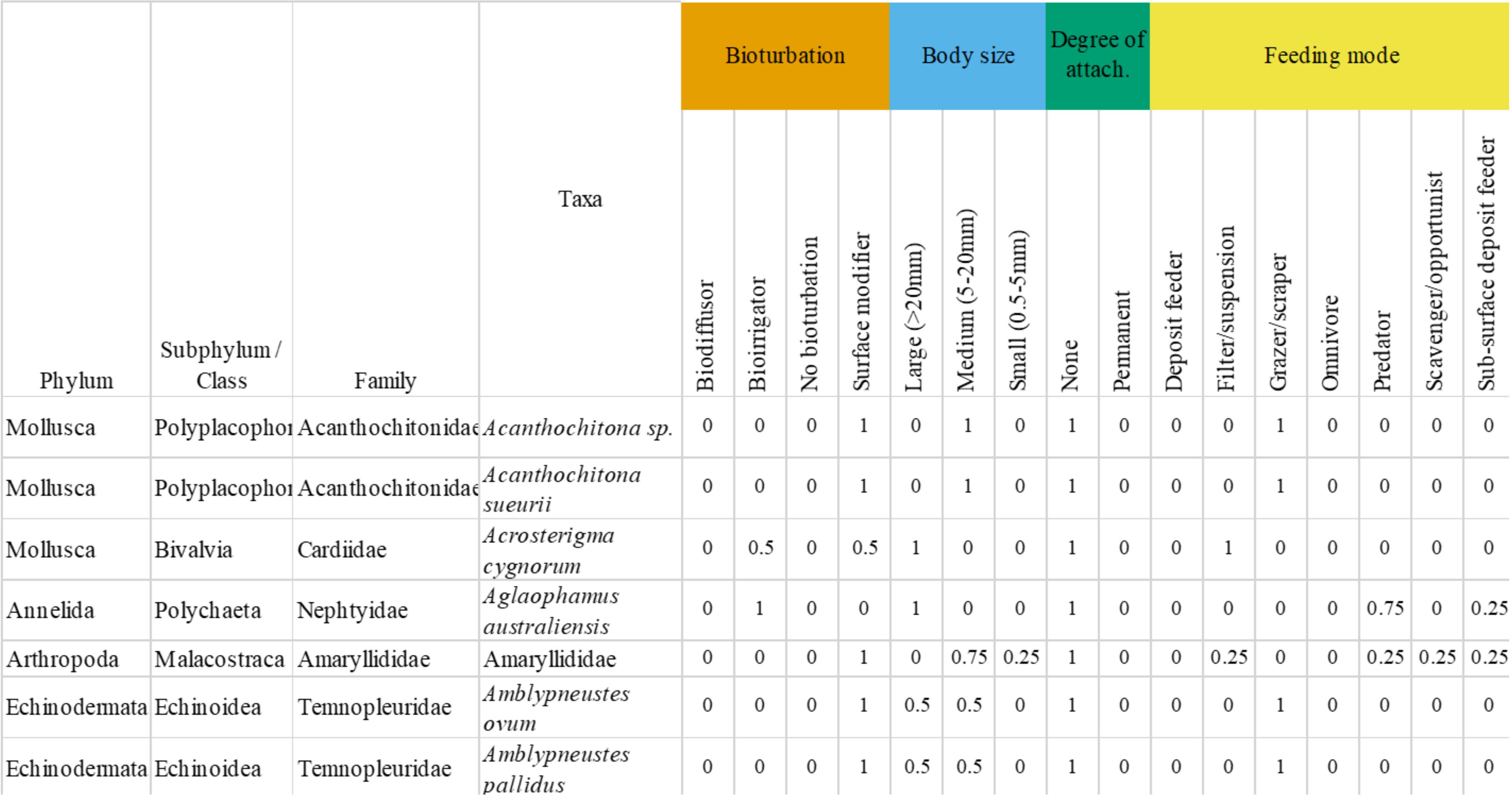
3.3.4 Case study using SAMT database: Preliminary functional perspectives for South Australia waters

The analysis of data from the SAMT database included, on average, 47 of the 54 trait-modalities across all taxa, analysed across the 37 South Australian localities. However, based on the traits and localities analysed, some trait-modalities were expressed more than others due to the different number of taxa present in each locality. Based on effect traits, and grouping the localities into regions (e.g. Coffin Bay, Spencer Gulf, Gulf St. Vincent, Coorong), the majority of the taxa recorded were surface modifiers and bioirrigators (Figure 3.7a), with large body size (Figure 3.7b) and were deposit feeders (Figure 3.7c). The most common morphology were irregular and fragile/soft bodies (Figure 3.7d). The most common living habit was free living/surface crawler and burrower (Figure 3.7e), and most of the organisms inhabited demersal habitats (Figure 3.7f).

Trait expression (i.e. the number of taxa that exhibit a determined trait) differed significantly across the regions (p <0.01, Table 3.2). Considering the six effect traits analysed (e.g. bioturbator, body size, feeding mode, morphology, living habit and sediment position), Coffin Bay, Spencer Gulf and Gulf St Vincent were significantly different in the number of traits present compared to the Coorong region (p <0.01, Table 3.3). Greater similarities in terms of trait expression were found between Coffin Bay, Spencer Gulf and Gulf St Vincent (Table 3.3).

Table 3.2. Test results from univariate one-way fixed factor PERMANOVA to compare trait expression of bioturbation, body size, feeding mode, morphology, living habit, and sediment position across regions. Significant results are shown in bold.

	df	MS	Pseudo-*F*	*P*(perm)
Bioturbation				
Region	3	995.08	8.3728	**0.0009**
Residual	21	118.85		
Body size				
Region	3	1635.6	9.8249	**0.0011**
Residual	21	166.47		
Feeding mode				
Region	3	818.11	7.4907	**0.0035**
Residual	21	109.22		
Morphology				
Region	3	1115.00	7.0205	**0.0023**
Residual	21	158.82		
Living habitat				
Region	3	1136.70	9.0705	**0.001**
Residual	21	125.32		
Sediment position				
Region	3	744.96	7.6826	**0.0022**
Residual	21	96.97		



Phylum	Subphylum / Class	Family	Taxa	Bioturbation				Body size			Degree of attach.		Feeding mode						
				Biodiffusor	Bioirrigator	No bioturbation	Surface modifier	Large (>20mm)	Medium (5-20mm)	Small (0.5-5mm)	None	Permanent	Deposit feeder	Filter/suspension	Grazer/scraper	Omnivore	Predator	Scavenger/opportunist	Sub-surface deposit feeder
Mollusca	Polyplacophor	Acanthochitonidae	*Acanthochitona sp.*	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0
Mollusca	Polyplacophor	Acanthochitonidae	*Acanthochitona sueurii*	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0
Mollusca	Bivalvia	Cardiidae	*Acrosterigma cygnorum*	0	0.5	0	0.5	1	0	0	1	0	0	1	0	0	0	0	0
Annelida	Polychaeta	Nephtyidae	*Aglaophamus australiensis*	0	1	0	0	1	0	0	1	0	0	0	0	0	0.75	0	0.25
Arthropoda	Malacostraca	Amaryllididae	Amaryllididae	0	0	0	1	0	0.75	0.25	1	0	0	0.25	0	0	0.25	0.25	0.25
Echinodermata	Echinoidea	Temnopleuridae	*Amblypneustes ovum*	0	0	0	1	0.5	0.5	0	1	0	0	0	1	0	0	0	0
Echinodermata	Echinoidea	Temnopleuridae	*Amblypneustes pallidus*	0	0	0	1	0.5	0.5	0	1	0	0	0	1	0	0	0	0

Figure 3.5. Screenshot of a section of the SAMT database (South Australia Macrobenthic Traits database). Traits are differentiated by colours**.** Phylum, Subphylum / Class, Family and Taxa tabs are displayed for easy sorting and searching. Note that the full extent of the table is not presented. Full table available in https://doi.org/10.6084/m9.figshare.12763154

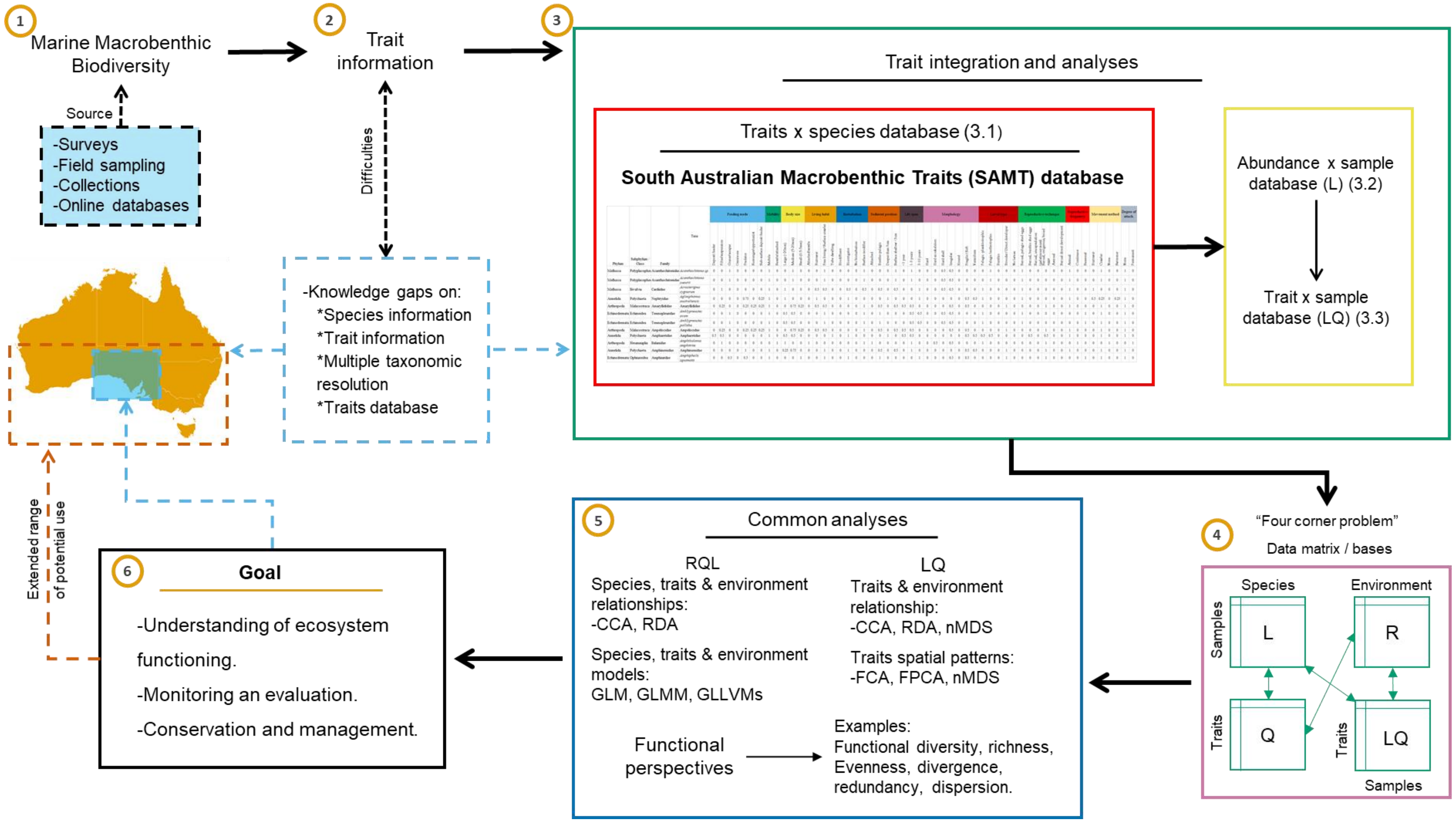


Figure 3.6. Flow chart showing step-by-step processes for assessing ecosystem functioning. Solid colored boxes (green, pink, blue, black) represent the separate task for analyzing trait data and black arrows indicate the logical order for the steps. Red box highlights the essential step for having a macrobenthic fauna trait database for southern Australia. Yellow box shows the complementary information needed. Blue dotted box and arrows show the information provided in this study, and the brown dotted box and arrow show the range of potential use of the information provided.

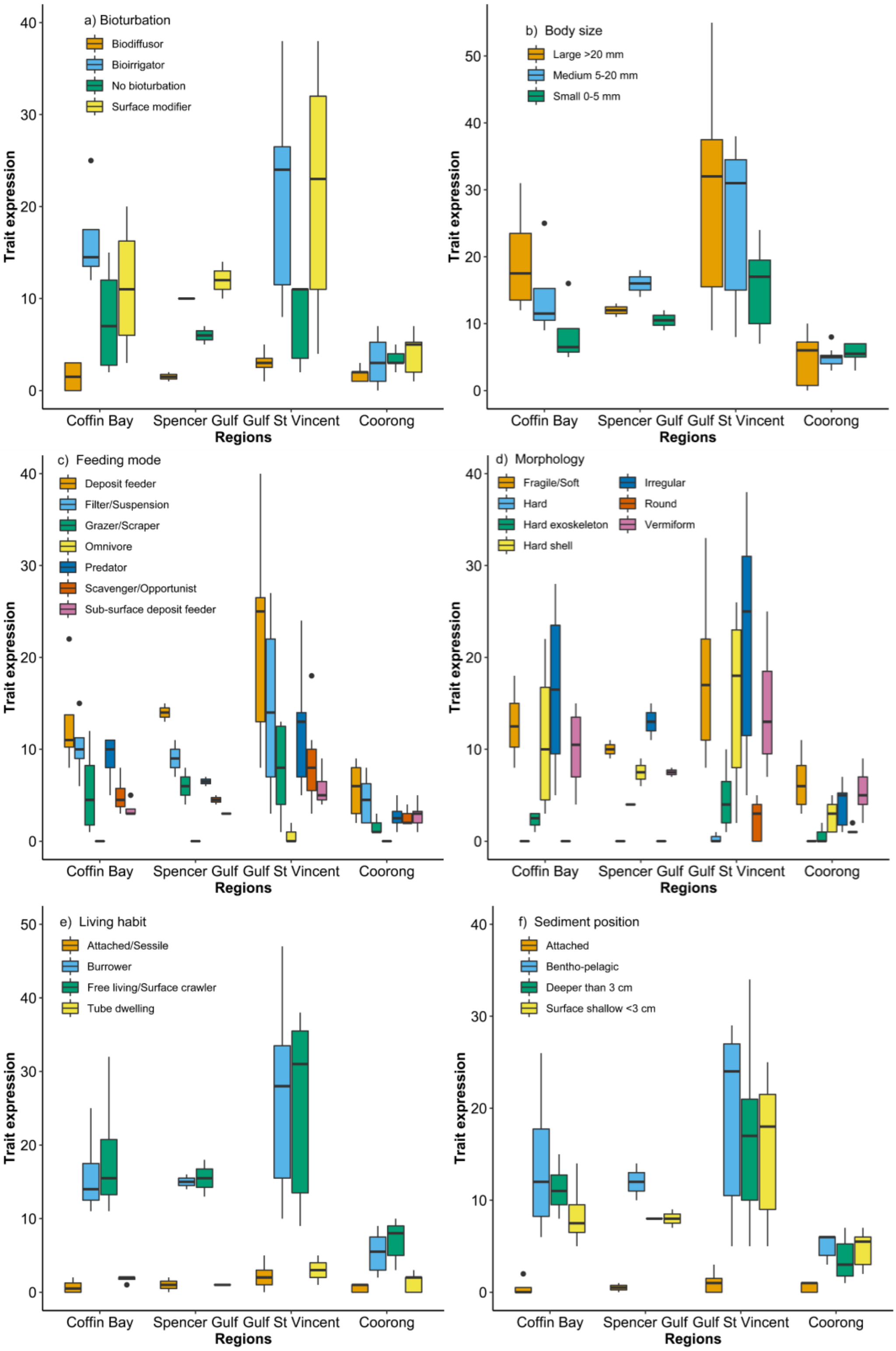


Figure 3.7. Expressed traits across four regions (Coffin Bay, Spencer Gulf, Gulf St. Vincent, Coorong Lagoon) in South Australia. Median, percentiles, upper/lower bounds, and outliers are shown. Traits shown: a) bioturbation, b) body size, c) feeding mode, d) morphology, e) living habit, and f) sediment position.

Table 3.3. Results from univariate pairwise test of bioturbation, body size, feeding mode, morphology, living habit, and sediment position across regions. Significant results are shown in bold.

Pair-wise test	t	*P*(perm)
Bioturbation		
Coffin Bay, Spencer Gulf	0.77	0.6047
Coffin Bay, Gulf St Vincent	1.11	0.2997
Coffin Bay, Coorong	4.39	**0.001**
Spencer Gulf, Gulf St Vincent	1.09	0.3659
Spencer Gulf, Coorong	4.14	**0.0106**
Gulf St Vincent, Coorong	4.78	**0.0002**
Body size		
Coffin Bay, Spencer Gulf	0.85	0.7364
Coffin Bay, Gulf St Vincent	1.32	0.2027
Coffin Bay, Coorong	4.44	**0.0006**
Spencer Gulf, Gulf St Vincent	1.22	0.3086
Spencer Gulf, Coorong	4.35	**0.0109**
Gulf St Vincent, Coorong	5.16	**0.0001**
Feeding mode		
Coffin Bay, Spencer Gulf	0.42	0.9292
Coffin Bay, Gulf St Vincent	1.17	0.2447
Coffin Bay, Coorong	3.81	**0.0006**
Spencer Gulf, Gulf St Vincent	0.93	0.4901
Spencer Gulf, Coorong	3.81	**0.0113**
Gulf St Vincent, Coorong	4.49	**0.0002**

Pair-wise test	t	*P*(perm)
Morphology		
Coffin Bay, Spencer Gulf	0.57	0.7966
Coffin Bay, Gulf St Vincent	0.86	0.4178
Coffin Bay, Coorong	3.69	**0.0003**
Spencer Gulf, Gulf St Vincent	1.07	0.359
Spencer Gulf, Coorong	3.47	**0.0114**
Gulf St Vincent, Coorong	4.5	**0.0003**
Living habit		
Coffin Bay, Spencer Gulf	0.38	0.9319
Coffin Bay, Gulf St Vincent	1.18	0.2785
Coffin Bay, Coorong	4.32	**0.0005**
Spencer Gulf, Gulf St Vincent	1.07	0.3793
Spencer Gulf, Coorong	4.43	**0.0105**
Gulf St Vincent, Coorong	5.01	**0.0001**
Sediment position		
Coffin Bay, Spencer Gulf	0.5	0.9332
Coffin Bay, Gulf St Vincent	1.13	0.281
Coffin Bay, Coorong	3.91	**0.0009**
Spencer Gulf, Gulf St Vincent	1.12	0.3662
Spencer Gulf, Coorong	3.61	**0.0111**
Gulf St Vincent, Coorong	4.61	**0.0003**

The relationship between the macrobenthic fauna (biodiversity) and trait expression (ecosystem functioning) was asymptotic, showing a decreasing effect of adding new species to the ecosystem (Figure 3.8a). Taxonomic and trait richness were significantly different across regions (p <0.01, Table 3.4; Figure 3.8b). The pairwise tests revealed significant differences in taxa richness across all regions except for the pairing of the Gulf St Vincent and Coorong regions (p<0.01, Table 3.5), while differences in trait richness were only identified between Coffin Bay and the other three regions (p <0.01, Table 3.5). The example reveals that trait richness can show greater similarity, whereas macrobenthic fauna assemblages were taxonomically different between regions.

Table 3.4. Test results from univariate one-way fixed factor PERMANOVA to compare Richness (S), Simpson index (1-Lambda') and functional diversity (FD) of macrobenthic fauna across regions. Significant results are shown in bold.

	df	MS	Pseudo-*F*	*P*(perm)
Richness (S)				
Taxa				
Region	3	140.32	23.803	**0.0001**
Residual	203	5.89		
Trait				
Region	3	45.45	4.0587	**0.0094**
Residual	203	11.20		
Simpson index				
Taxa				
Region	3	144.64	23.782	**0.0001**
Residual	203	6.08		
Trait				
Region	3	0.004	21.85	**0.0001**
Residual	203	0.0002		
Functional diversity				
Region	3	352.66	6.9265	**0.0003**
Residual	202	50.91		

Diversity, measured using the Simpson Index (Figure 3.8c), revealed significant differences for taxa and traits across regions ($p < 0.01$, Table 3.4). Coffin Bay was the most significantly different region compared to the other regions based on both taxa and traits (Table 3.5). Based on traits, the Simpson Index was similar between Gulf St Vincent and Spencer Gulf. Based on taxa, the Simpson Index was significantly different between most region pairs except for the Gulf St Vincent and Coorong (Table 3.5). Functional diversity was also significantly different between regions ($p < 0.01$, Table 3.4, Figure 3.8d). In pairwise comparisons, functional diversity was different in Spencer Gulf compared to the other three regions, and in Gulf St Vincent compared to the Coorong ($p < 0.05$, Table 3.5). The case study demonstrated the usefulness of the SAMT database for elucidating functional similarities for taxonomically different benthic assemblages across regions.

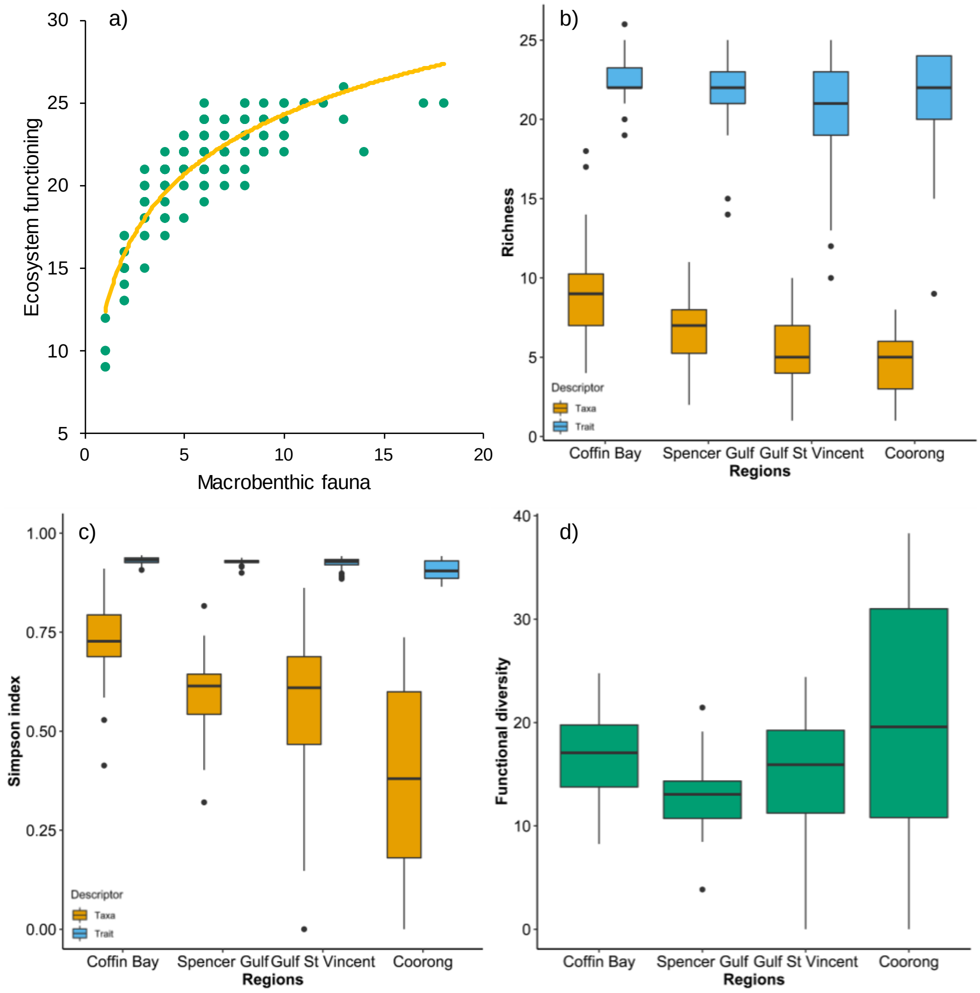


Figure 3.8. a) Correlation and trend line between the macrobenthic fauna (number of taxa) and ecosystem functioning (trait expression) in the main four regions of South Australia. b) Boxplots of the taxonomic and trait richness, c) Simpson index, and d) functional diversity across the four study regions.

Table 3.5. Results from univariate pairwise test of richness (S), Simpson index (1-Lambda') and functional diversity (FD). Only significant differences are shown.

Pair-wise test	t	*P*(perm)
Richness (S)		
Taxa		
Coffin Bay, Spencer Gulf	3.15	0.0028
Coffin Bay, Gulf St Vincent	7.34	0.0001
Coffin Bay, Coorong	6.47	0.0001
Spencer Gulf, Gulf St Vincent	3.04	0.0036
Spencer Gulf, Coorong	3.51	0.0010
Trait		
Coffin Bay, Spencer Gulf	2.34	0.021
Coffin Bay, Gulf St Vincent	3.46	0.001
Coffin Bay, Coorong	2.42	0.017
Simpson index (1-Lambda')		
Taxa		
Coffin Bay, Spencer Gulf	3.15	0.0017
Coffin Bay, Gulf St Vincent	7.34	0.0001
Coffin Bay, Coorong	6.48	0.0001
Spencer Gulf, Gulf St Vincent	3.08	0.0024
Spencer Gulf, Coorong	3.52	0.0004
Trait		
Coffin Bay, Gulf St Vincent	2.30	0.0232
Coffin Bay, Coorong	5.46	0.0001
Spencer Gulf, Coorong	4.52	0.0001
Gulf St Vincent, Coorong	6.09	0.0001
Functional diversity (FD)		
Coffin Bay, Spencer Gulf	4.04	0.0001
Spencer Gulf, Gulf St Vincent	2.06	0.0400
Spencer Gulf, Coorong	3.01	0.0038
Gulf St Vincent, Coorong	3.28	0.0014

3.4. Discussion

Functional approaches have become a requisite for studying ecosystem functioning (e.g. Bremner et al. 2003; Bremner et al. 2006; Bolam et al. 2016; Degen et al. 2018), yet, functional assessments remain hindered by a lack of taxa-specific trait data (Lam-Gordillo et al. 2020a). Compiling trait information of marine macrobenthic fauna is often considered time-consuming and difficult, due to knowledge gaps on the biology and ecology of many species, the lack of identification keys, as well as the scarcity of relevant data (Verissimo et al. 2012; Beauchard et al. 2017; Degen et al. 2018).

The SAMT database we present here aims to close the information gap by enabling a comprehensive assessment of traits for the South Australian macrobenthic fauna. SAMT, and the accompanying R package, will facilitate and enhance further research addressing ecosystem functioning and functional perspectives. The SAMT database provides trait information for 277 macrobenthic taxa and a trait classification for South Australian temperate marine waters. This first iteration of the SAMT database can be used as a part of the framework provided in this paper, with the aim to facilitate functional assessments along Australia's south coast.

The SAMT database is available for easy downloading, sharing and using. However, as in any trait classification, several limitations need to be considered; (i) the structure of the database represents the current taxonomic classification at the time of the analysis, (ii) the taxa included reflect the sampling design (e.g. effort, habitats sampled) of the projects from which the information was retrieved and (iii) the SAMT database is an ongoing project, with continuous updates and refinements as additional taxa and trait information becomes available, resulting in up to date versions of functional trait classifications.

We identified several knowledge gaps in the literature while building the SAMT database. For example, the majority of the information included for 'Larval type' (58%, 160 of 277 taxa), 'Reproduction technique' (58%, 160 of 277 taxa), 'Reproduction frequency' (58%, 160 of 277 taxa) and 'Life span' (56%, 156 of 277 taxa) were based on the family level taxonomic classification, highlighting that basic knowledge about macrobenthic fauna that inhabit southern Australian waters is still very limited in many cases.

The exemplary use of the SAMT database found an asymptotic pattern between the macrobenthic fauna taxa and trait expression (ecosystem functioning), which could be explained by redundancy in these regions. Redundancy can be due to; (i) different species performing the same functioning in the ecosystem, and (ii) adding species to the ecosystem until all functionality (functional traits) is represented (Schulze and Mooney 1993; Loreau et al. 2002; van der Linden et al. 2012). Taxa and trait differences were found in terms of richness and diversity using the Simpson index across all regions, but for comparing particular regions, taxonomically indices varied more than those based on traits across all regions.

Functional diversity (FD), as Rao’s quadratic entropy metric, was significantly different across regions, highlighting greater FD in the Coorong and the lowest FD in Spencer Gulf. This pattern could be explained by the Coorong region having the greatest abundance of individuals and the most similar community compared to the other regions, aligning with the properties of the Rao’s quadratic entropy metric, that bases its calculations on the proportion of the abundance of taxa present and the measure of dissimilarities between them (Rao 1982; Botta-Dukát, 2005). The case study represents an example of the usefulness to combine both taxa and trait perspectives, as they give complementary insight to ecosystem functioning assessment and identify further research needs. Future targeted studies with consistent design can apply the database and framework presented here to demonstrate the ecological importance of effect traits and advance the understanding of the functionality of ecosystems along the southern Australian coast.

3.5. Conclusion

To date, this is the first study providing a comprehensive assessment of traits for the southern Australian macrobenthic fauna. We highlight that the South Australia Macrobenthic Traits (SAMT) database presented here is a valuable tool to enhance further research on trait-based approaches within southern temperate Australia. The structure of the SAMT database includes 277 macrobenthic taxa so far, is very intuitive and was created for easy downloading, sharing, and using by researchers working on southern temperate benthic ecosystems. The newly developed R package for using and analysing the SAMT database, that can be applied more broadly to link trait and species data. A theoretical framework detailing the step-by-step process for assessing ecosystem functioning is introduced, illustrating the need for taxa-trait information and the use of SAMT database.

The use of the SAMT database should be approached with awareness of its limitations of available taxonomic and trait-based information, as well as ongoing changes to taxonomic nomenclature, traits information, and trait classification as the database evolves. The structure of the SAMT database will remain as simple as possible, avoiding complexity, redundancy, and duplication between traits as it expands to include more taxa, traits and regions. The SAMT database is an ongoing project, where adding more taxa and traits will be continued with expansion into other regions within southern Australia.

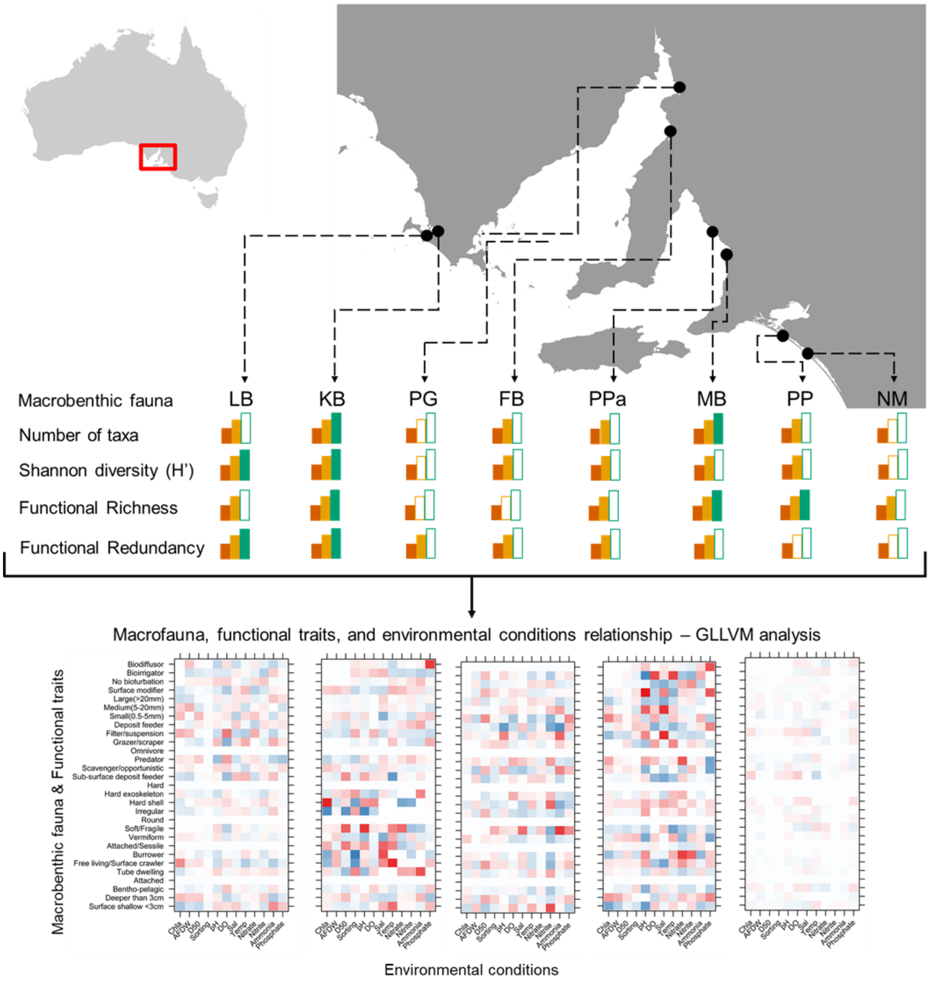
Data availability

Data are available on figshare (https://doi.org/10.6084/m9.figshare.12763154)

Code availability

Code is available on figshare (https://doi.org/10.6084/m9.figshare.12763154) and on the GitHub repository (https://github.com/OrlandoLam/SAMT).

Chapter 4. Taxonomic and functional patterns of benthic communities in southern temperate tidal flats



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Author contributions

Orlando Lam Gordillo: Conceived the ideas and developed the outline for the manuscript, designed the methodology, collected the data, analysed the data, prepared the figures and tables, wrote the manuscript and corresponding author.

Sabine Dittmann – primary supervisor: Guidance on the project development, discussion of project ideas, contribution to drafting manuscript, and critical refinement.

Ryan Baring – co-supervisor: Discussion of project ideas and contribution to drafting manuscript.

Abstract

Coastal ecosystems are vulnerable to anthropogenic disturbances which can cause loss of benthic macrofauna and their ecosystem functioning. Despite the importance of functional assessments for conservation and management, knowledge gaps persist on the generality of how the diversity and functional traits of benthic communities influence ecosystem functioning. We investigated eight sites in three different habitats across ~1,260 km of coastline, to evaluate patterns between taxonomic and functional diversity of benthic macrofauna, and the relationship between benthic macrofauna, functional traits and environmental conditions. A total of 74 benthic macrofauna taxa were identified. Significant differences across sites and season were found for metrics based on taxonomic and functional traits. Multivariate analysis revealed spatial-temporal differences, which were more evident based on taxa than functional traits. Functional diversity also showed spatial and temporal differences and was positively correlated with the number of taxa. The dominant functional traits modalities were deposit feeders, with large (>20 mm) body size, burrowers, bioirrigators, deeper than 3 cm in sediments, and irregular morphology. Novel Generalized Linear Latent Variable Models (GLLVM) uncovered several site-dependent relationships between taxa, traits and environmental conditions. Functional redundancy was lowest in a highly modified lagoon, and highest in a more pristine embayment. The outcomes from this study showed site-dependent patterns of benthic communities based on either taxonomic or functional metrics, highlighting that both perspectives are complementary to obtain a holistic understanding of the functioning in marine sediments under environmental change.

Keywords: Australia, functional traits, ecosystem functioning, macroinvertebrates, GLLVM.

4.1. Introduction

Benthic macrofauna are major providers of ecosystem functioning in marine habitats. They modify soft-sediment habitats through biological processes such as ingestion, digestion, excretion, and bioturbation, which facilitates microbial recycling of nutrients, detoxification of pollutants, and organic matter remineralization (Snelgrove et al. 2014; Shojaei et al. 2015; Caswell et al. 2018; Wyness et al. 2021). Benthic macrofauna also represent a connection between benthic and pelagic ecosystems, and plays an important role in energy transfer to different trophic levels (Pearson and Rosenberg 1978; Kristensen et al. 2014; Murillo et al. 2019). Furthermore, benthic macro-organisms are often used as bioindicators to assess ecosystem "health" due to their sensitivity to natural and anthropogenic disturbances (Borja et al. 2000; Tweedley et al. 2015).

Descriptive and experimental approaches have highlighted that benthic communities are structured by environmental factors (e.g. temperature, water depth, salinity, sediment type, habitat complexity), biological processes (e.g. competition, predation, bioturbation), and ecosystem engineering by benthic macrofauna (e.g. Reise 1985; Honkoop et al. 2006; Meadows et al. 2012). These traditional taxonomic-based studies laid the base for functional assessments of benthic fauna (Snelgrove 1997; Thrush et al. 2006; Snelgrove et al. 2014), which allow the understanding of how changes in benthic biodiversity influence the functioning of an ecosystem. Functional approaches have been increasingly explored to comprehensively understand effects of the alarming loss of biodiversity in terrestrial and marine ecosystems (de Juan et al. 2015; Degen et al. 2018; Gammal et al. 2019; van der Plas et al. 2019). For benthic communities, the use of functional approaches is a powerful tool to investigate Biodiversity and Ecosystem Functioning relationships (BEF), and how these relationships vary spatially and temporally, or under specific environmental conditions (Baldrighi et al. 2017; Beauchard et al. 2017).

Ecosystem functioning, defined as the combined effects of all natural processes that sustain an ecosystem (Reiss et al. 2009; Gladstone-Gallagher et al. 2017; Degen et al. 2018), is commonly analysed by using Functional Diversity (FD) measurements. Functional Diversity considers the variation of functional traits occurring across ecological communities of a given ecosystem based on the activities of organisms (e.g. movement, behaviour, feeding and reproduction; Díaz and Cabido 2001; Reiss et al. 2009; Beauchard et al. 2017; Degen et al. 2018). Several indices have been used to quantify functional diversity, however, there is a lack of consensus on which index is the most appropriate (Mason et al. 2005; Villeger et al. 2008; Mouchet et al. 2010; Lam-Gordillo et al. 2020a).

Functional diversity is usually split into at least three components: functional richness, evenness, and divergence (Mason et al. 2005; Villeger et al. 2008), with several other components recently added (e.g. functional dispersion and functional redundancy) (Laliberté and Legendre et al 2010, van der Linden et al. 2012; Gammal et al. 2020). Functional diversity, and all its main components, are based on the analysis of functional traits and their modalities (e.g. bioturbation, body size, feeding mode, morphology, living habit, sediment position), where species are clustered into groups with shared physiological and morphological attributes (Bremner et al. 2003; Bremner et al. 2006). The functional traits and their modalities studied can be selected in accordance with the processes of interest, the ecosystem type, and the spatial and temporal scale of study (Hooper et al. 2005; Wright et al. 2006; Bremner 2008; Beauchard et al. 2017).

Functional metrics, which are based on functional traits, can be more important to explain ecological processes and ecosystem functioning than taxonomic metrics (Belley and Snelgrove 2016; Mestdagh et al. 2020). Yet, considering both approaches can provide a more robust and holistic knowledge about the structure of benthic communities and functioning of ecosystems. Recent investigations have applied a combination of taxonomic and functional approaches to understand the influence of benthic macrofauna on ecosystem functioning and support management and conservation efforts (e.g. Hajializadeh et al. 2020; Delfan et al. 2021; Shojaei et al. 2021; Nunes de Souza et al. 2021). Results from taxonomic and functional approaches have been similar (e.g. van der Linden et al. 2012; Wong & Dowd 2015; Hajializadeh et al. 2020), but distinct patterns based on either taxonomic or functional diversity emerged as well (e.g. Emmerson et al. 2001; Kraan et al. 2013; Frid and Caswell 2015; Gladstone-Gallagher et al. 2017). These different patterns could result from highly variable relationships between taxonomic and functional diversity subject to the environmental context (Gladstone-Gallagher et al. 2017; Thrush et al. 2017; Gammal et al. 2019), and from presence of key benthic macrofauna functional groups, that is often more important than species diversity per se (Norkko et a. 2013; Thomas et al. 2020).

Despite the importance of functional assessments for conservation strategies (Miatta et al. 2020) and to inform policy and management to ensure healthy coastal ecosystems, several uncertainties still persist in the interpretation and potential use of the outcomes from trait-based and functional approaches in future scenarios of biodiversity loss in coastal ecosystems. Such uncertainties can be reduced with greater understanding of how taxonomic diversity and functional traits present in benthic communities influence ecosystem functioning across different habitats. For example, low functional redundancy can be used to indicate habitats vulnerable to functional loss.

To contribute to the knowledge on patterns of taxonomic and functional diversity and their links with ecosystem functioning (e.g. Gammal et al. 2019; Taupp and Wetzel 2019; Shojaei et al. 2021), this study investigated benthic communities in soft sediments along the southern temperate coast of South Australia, where traits of benthic fauna have been recently compiled (Lam-Gordillo et al. 2020b), which enabled a comparative assessment of taxonomic and functional perspectives.

The aims of this field study were to (i) assess the taxonomic and functional diversity of benthic communities across contrasting habitats (coastal embayment, gulfs, and lagoon), each representing a typical habitat of the southern temperate Australian coastline, and (ii) evaluate the relationships between benthic macrofauna, functional traits and environmental conditions across these habitats. Over two seasons, benthic macrofauna, their functional traits and environmental conditions were assessed in each habitat to provide a comprehensive analysis on their patterns and relationships. It was predicted that (1) taxonomic and functional patterns are distinct across the studied habitats, (2) functional diversity is greater within habitats with a greater number of taxa, and (3) the relationships between taxa, traits and environmental conditions are habitat-specific.

4.2. Methods

4.2.1 Study area

The southern Australian coast is the longest east-west temperate coastline in the southern hemisphere, and harbours diverse sedimentary habitats (Short 2020). The benthic sampling was conducted across eight sites in South Australia, covering three contrasting habitats of this coastline: a coastal embayment (Coffin Bay: Long Beach - LB, Kellidie Bay - KB), gulfs (Spencer Gulf: Port Germein - PG, Fisherman Bay - FB, Gulf St Vincent: Port Parham - PPa, Middle Beach - MB), and lagoon (Coorong: Pelican Point - PP, Noonameena - N) (Figure 4.1, Table 4.1).

4.2.2 Data collection and laboratory procedures

Benthic samples were collected in July 2019 (Austral winter) and January 2020 (Austral summer) at the eight tidal flat sites. South Australia has a Mediterranean climate, with dry summers and winter rain. January is the warmest month of the year with an average air maximum temperature of 29.6 °C, while the coldest month is July with a minimum temperature average of 7.6 °C (Bureau of Meteorology 2021). All sampling occurred at low tide when tidal flats were exposed and accessible from shore. Tides in South Australia are of a unique mixed tidal pattern with tidal range varying from micro-tidal (Coffin Bay, Coorong) to mesotidal (gulfs). The samples for benthic macrofauna were taken using a standard approach with optimal equipment to detect differences in macrobenthic communities (Rodriguez et al. 2007; Eleftheriou and Moore 2013; Valenca and dos Santos 2013; Souza & Barros 2015), and suitable for the research question and habitat. A handheld PVC corer (83.32 cm^2 surface area) was pushed it into the sediment up to 20 cm depth, with 15 replicates haphazardly taken per site. All sediment samples were sieved through 500 µm mesh size in the field and preserved in 70% ethanol until further processing. In the laboratory, samples were sorted and all benthic macrofauna were identified to the lowest possible taxonomic level (i.e. 66.2% to Species, 4.1% to Genus, 28.4% to Family, and 1.4% to Order), and counted.

At each sampling site, environmental conditions known for influencing the abundance, composition and distribution of benthic communities were measured (Hillebrand 2004; Dutertre et al. 2013; Dittmann et al. 2015; Shojaei et al. 2015). Water temperature (°C), salinity, and pH were recorded in the water overlying the mudflat, using a Hannah HI98194 multiparameter meter. Sediment samples were taken for analysing Chlorophyll-*a* (g/m^3), total organic matter content (OM%) and sediment grain size. In addition, sediment pore water was collected for analysing nutrients (Nitrate, Nitrite, Ammonium and Phosphate). Fifteen replicate samples for each environmental parameter were taken at each site within the same area where the sediment samples for benthic fauna were collected.

Chlorophyll-*a* (g/m^3) was determined using a spectrophotometer (Thermo Scientific, Spectronic 200) following the protocols described by Ritchie (2008). The organic matter (OM%) content in sediment was determined by loss on ignition, first drying the sediment to constant weight, followed by burning in a furnace at 450 °C for 5 hrs. Grain size was determined by laser diffraction using a particle size analyser (Malvern Mastersizer 2000). Average values for grain size fractions for each site were entered into the GRADISTAT program v8.0 (Blott and Pye 2001) to obtain the median (D50 µm) and coefficient (sorting σG). Nutrient concentrations (mg/L) of Nitrate (NO_3-), Nitrite (NO_2-), Ammonium (NH_3) and Phosphate (PO_4^3-) were determined using a Skalar SAN ++ SFA segmented flow analyser.

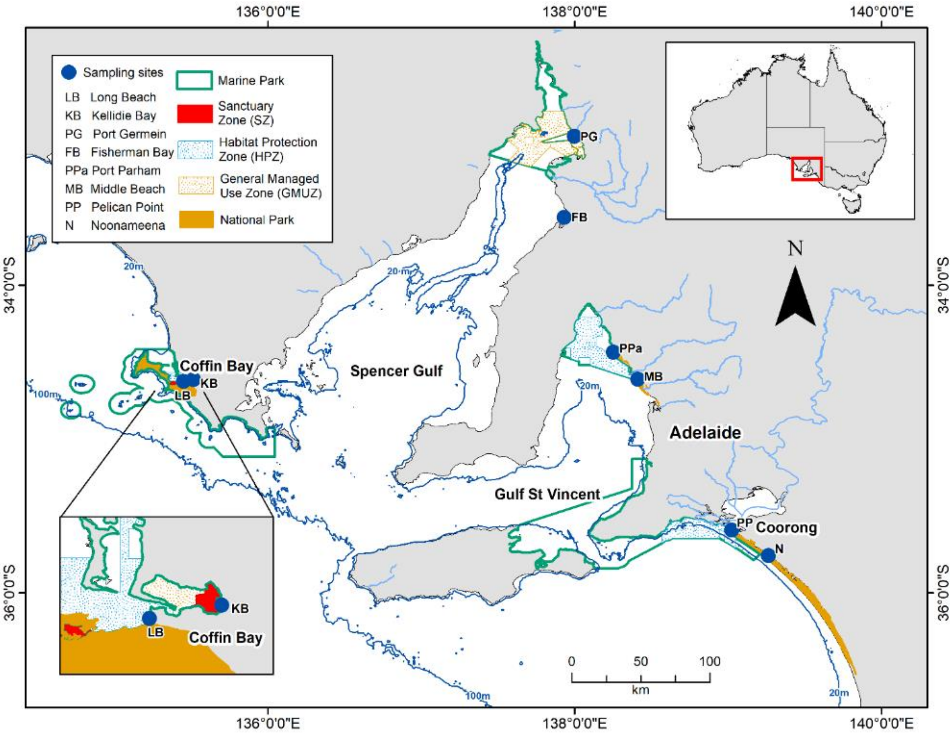


Figure 4.1. Map of the study area showing the eight sites across South Australia from where benthic macrofauna samples were collected. The dark blue lines indicate depths at 20 and 100 m, and the light blue lines indicate the rivers.

Table 4.1. Main habitat characteristics of the eight sampling sites across southern Australia. Sediment description based on Folk and Ward (1957) geometric description. Width (m) refers to the extension of the mudflats from high to low tide mark.

Site	Habitat (Geomorphology)	Protection status	Region	Sediment description	Width (m)
Long Beach	Coastal embayment	Habitat Protection Zone	Coffin Bay	Fine sand, moderately well sorted	~100
Kellidie Bay	Coastal embayment	Sanctuary Zone	Coffin Bay	Fine sand, poorly sorted	~100
Port Germein	Gulf	General Managed Use Zone	Upper Spencer Gulf	Fine sand, poorly sorted	~1000
Fisherman Bay	Gulf	None	Upper Spencer Gulf	Medium sand, poorly sorted	~200
Port Parham	Gulf	Habitat Protection Zone	Upper Gulf St Vincent	Fine sand, poorly sorted	~500
Middle Beach	Gulf	Habitat Protection Zone	Upper Gulf St Vincent	Coarse sand, poorly sorted	~500
Pelican Point	Lagoon	Habitat Protection Zone / National Park / Ramsar site	Coorong	Medium sand, poorly sorted	~200
Noonameena	Lagoon	National Park / Ramsar site	Coorong	Fine sand, moderately sorted	~500

4.2.3 Data analysis

4.2.3.1 Environmental data analysis

Environmental data were square root transformed as needed to approximate normality (except OM, pH and salinity), and then normalised prior to multivariate analysis (Clarke et al. 2014). Spearman correlation (Appendix C Figure S1) and variance inflation factors with a cut-off <3 (VIF) (Appendix C Table S1) were analysed for collinearity among variables and, as no redundant environmental variable was identified, all were included in the analyses. To test for differences between sites and season, univariate PERMutational ANalysis Of VAriance (PERMANOVA) and multiple pair-wise tests were conducted, using Euclidean distance for the single variables in PRIMER v7 with PERMANOVA+ add on software (Anderson et al. 2008). Principal Component Analyses (PCA) were performed separately for summer and winter data to explore spatial and temporal patterns. R software (R Core Team, 2017) and the packages “corrplot” (Wei and Simko 2017), “fmsb” (Nakazawa 2019), “vegan” (Oksanen et al. 2019), were used for conducting the analyses.

4.2.3.2 Selection of traits and trait information

A suite of six functional traits and 29 trait-modalities (Table 4.2) were selected. The functional traits selected describe behavioural, morphological, and physiological attributes of benthic macrofauna, and are considered as effects traits as they are directly or indirectly related to several ecosystem functions including nutrient cycling and sediment transport (Lam-Gordillo et al. 2020a). Trait information was obtained from the South Australia Macrobenthic Trait (SAMT) database (Lam-Gordillo et al. 2020b). The SAMT database applied a fuzzy coding procedure assigning scores from 0 to 1, with 0 being no affinity and 1 being high affinity to a trait (for details see Lam-Gordillo et al. 2020b). This resulted in the compilation of three data matrices (1) “taxa abundance by site matrix”, in this case the data collected from our surveys; (2) “taxa by traits matrix”, obtained from the SAMT database; and (3) the combinations of the previous two: “traits by site matrix” (Bremner 2008; Bremner et al. 2006).

Table 4.2. Traits and traits-modalities selected. Acronyms are used in Figure 4.4.

Traits	Traits modalities	Acronym
Bioturbation	Biodiffusor	Bdiff
	Bioirrigator	Birrig
	No bioturbation	Nbio
	Surface modifier	Surmo
Body size	Large (>20mm)	Lar
	Medium (5-20mm)	Med
	Small (0.5-5mm)	Sma
Feeding mode	Deposit feeder	Defe
	Filter/suspension	Fisus
	Grazer/scraper	Graz/Sc
	Omnivore	Omn
	Predator	Pred
	Scavenger/opportunist	Scav
	Sub-surface deposit feeder	Ssdefe
Morphology	Hard	Hard
	Hard exoskeleton	Haexosk
	Hard shell	Hashell
	Irregular	Irreg
	Round	Round
	Soft / Fragile	Frag/Sof
	Vermiform	Verm

Living habit	Attached/Sessile	Att/S
	Burrower	Burr
	Free living / Surface crawler	Free
	Tube dwelling	Tubdw
Sediment position	Attached	Att
	Bentho-pelagic	Be-pel
	Deeper than 3cm	Deep
	Surface shallow <3cm	Surfsh

4.2.3.3 Taxonomic and functional analysis

The benthic macrofauna was analysed for traditional diversity metrics, including the analysis of taxonomic richness (S), Shannon index (H'; log e) and Pielou's evenness (J') for each site and season using the package "vegan" (Oksanen et al. 2019). For the functional diversity (FD) analyses, the benthic abundance data (taxa abundance by site matrix) were log (1 + *x*) transformed to reduce the influence of dominant taxa without losing the abundance effect. To compare the FD across sites and seasons, the following functional metrics were calculated as a proxy of FD. (i) Functional Richness (FRic), provides the amount of functional space occupied by a community (Mason et al. 2005), i.e. the quantity of traits that are expressed in a habitat. (ii) Functional Evenness (FEve), describes how consistently the taxa abundance is distributed across the expressed traits (Mason et al. 2005). iii) Functional Redundancy (FR), describes the ratio between FD and H', when the ratio decreases, FR increases and *vice versa* (van der Linden et al. 2012), providing information on how common the expressed traits are within a habitat. In addition, community-level weighted means of trait values (CWM) were calculated to compare trait expression across the sites and seasons. Functional metrics and CWM were calculated using the package "FD" (Laliberté et al. 2014) in R software (R Core Team, 2017).

4.2.3.4 Statistical analysis

To elucidate spatial (sites) and temporal (seasons) patterns for each taxonomic (e.g. S, abundance, H', J'), functional metric (FRic, FEve, Fdis, FR) and CWM, univariate PERMANOVA were used with Euclidean distance for the single variables, permutation of residuals under a reduced model, sums of squares type III and 9999 permutations (Anderson et al. 2008). In addition, multiple pair-wise tests were conducted if fixed factors (sites, seasons) or interactions (sites x season) were significant to identify which groupings contributed to differences from PERMANOVA main tests. To assess community structure differences between sites and seasons, Principal Coordinates Ordination (PCO) were performed for the taxonomic and trait data. Species density (taxa abundance) was fourth root transformed, and in both taxa and trait data, a Bray-Curtis similarity resemblance was applied. To assess the relationship between functional metrics and environmental conditions, non-parametric multiple regressions were performed with the DISTLM routine, using Euclidean distances and 9999 permutations (McArdle and Anderson 2001). PERMANOVA, pair-wise tests, PCO and DISTLM analysis were carried out using PRIMER v7 with PERMANOVA add on. To elucidate the direction of the relationships, multiple Spearman correlation analyses were performed using the R package "ggpubr" (Kassambra 2020).

For assessing the response of benthic taxa and functional traits to the environmental predictor variables (fourth corner analysis), several generalized linear latent variable models (GLLVMs) were performed with the R package "gllvm" (Niku et al. 2020). GLLVM extends the basic GLM, handles overdispersion data, includes latent variables to capture the correlation between species, and considers fourth-corner terms to account for species-traits- environment-interactions (Niku et al. 2020; Niku et al. 2021). Further, the fourth-corner approach includes regression of the multivariate abundance against the function of the trait and environment association (Niku et al. 2019). GLLVMs were constructed for fitting multivariate data using a negative binomial distribution as the best fit model (lowest Akaike information criterion – AIC; Appendix C Table S2) (Niku et al. 2019). Level plots were performed for visualizing the interactions between taxa-traits and environmental variables obtained with the GLLVMs using the R package "lattice" (Sarkar 2008).

4.3. Results

4.3.1 Environmental conditions

The environmental conditions varied across sites and seasons (PERMANOVA p <0.01, Figure S2, Table S3). In general, hypersaline conditions were recorded at the gulfs (PG, FB) and lagoon (N) habitats in summer. Sediment grain size (D50 and sorting) was mostly characterized by fine sand at the coastal embayment (LB, KB) and lagoon (N), while the gulfs (FB, MB) had medium to coarse sand. The PCA analyses showed spatial and temporal variation (summer: 40.9%, winter: 47.81% of variability explained by the first two axes) (Figure 4.2). In summer, porewater nutrients separated the lagoon habitat located in the Coorong (N, PP) based on Nitrate and Nitrite, and LB and PG based on Ammonium and Phosphate. MB had larger sediment grain size (D50, sorting) and higher sediment organic matter (Figure 4.2a). In winter, higher porewater nutrient concentrations also separated sites from the Coorong (PP, N due to nitrous oxides), and MB was separated again by sediment grain size (D50), Sorting and organic matter (Figure 4.2b).

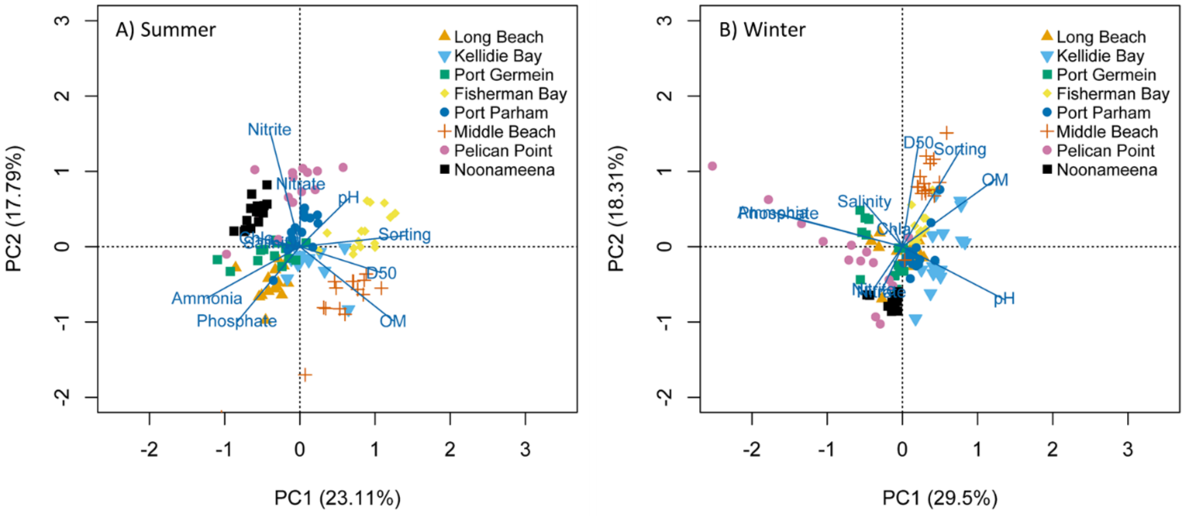


Figure 4.2. Principal Component Analysis (PCA) on the environmental conditions measured at the eight sites across South Australia, in the seasons: a) Summer, and b) Winter.

4.3.2 Abundance of benthic macrofauna

The average abundance recorded was 18,255 (+1,676 SE) ind.m^{-2} across the sampling sites in South Australia. Annelida was the phylum with the greatest abundance overall (44%), followed by Mollusca (41%) and Arthropoda (15%) (Appendix C Table S4). The most abundant polychaete families were Capitellidae (mean: 5,588 ind.m^{-2} +1,091 SE) and Nereididae (mostly *Simplisetia aequisetis* mean: 1,340 ind.m^{-2} +291 SE). *Arthritica semen* (mean: 3,104 ind.m^{-2} +628 SE) and *Salinator fragilis* (mean: 2,205 ind.m^{-2} +288 SE) contributed most to the abundance of Mollusca, while the most abundant arthropods were amphipods (1,536 ind.m^{-2} +466 SE). The total individual densities were significantly different across sites and seasons (PERMANOVA *p*=0.0001; Table 4.3), with significantly higher individual densities at the Coorong lagoon (PP and N), compared to the other six sites (*p*<0.01; Appendix C Table S4 and Figure S3b).

4.3.3 Taxonomic and functional assessment of benthic macrofauna

In total, 74 taxa were found across eight sites in South Australia, belonging to six different phyla. Mollusca was the phylum with the highest number of taxa (42%, 31 taxa), followed by Arthropoda (31%, 23 taxa), and Annelida (23%, 17 taxa), while Cnidaria, Echinodermata and Nemertea were represented by only one taxon each (1.4%) (Appendix C Table S5). The taxonomic metrics (species richness, H’, J’) showed the highest mean values in the coastal embayment habitats (LB, KB) at Coffin Bay, and the lowest mean values in the lagoon (PP, N) at the Coorong (Figure 4.3).

Significant differences between sites and seasons (i.e. the warmest and coldest moth) were found for all three taxonomic metrics (PERMANOVA *p*=0.0001; Tables 4.3). The number of taxa was higher in summer than winter at all the sites (Figure 4.3a). In pairwise comparisons between sites, significant differences in the number of taxa were found for PG and N compared to the other five sites, but only in winter (*p*<0.01; Appendix C Figure S3a).

The Shannon diversity index ranged from 0 to 1.99, with greater values in summer at the coastal embayment habitats (LB, KB), and one site in the gulfs (PG) and lagoon (N) habitat respectively (Figure 4.3b). In pairwise comparisons, the majority of the sites were distinct from each other (*p*<0.01; Appendix C Figure S3c), apart from the two coastal embayment habitats in Coffin Bay. Pielou's evenness index ranged from 0 and 0.97, following the same patter as H’, with greater values at the coastal embayment habitats in summer (Figure 4.3c). In pairwise comparisons, LB and N were significantly different to the other sites (*p*<0.01; Appendix C Figure S3d).

Table 4.3. Test results from univariate one-way fixed factor PERMANOVA to compare number of taxa (richness), abundance, Shannon diversity index (H’), Pielou's evenness index (J’), Functional: Richness, Evenness, and Redundancy across sites and seasons. Significant differences are shown in bold.

	df	MS	Pseudo-*F*	P-value
Number of taxa				
Site	7	61.75	21.47	**0.0001**
Season	1	234.04	81.35	**0.0001**
Site x Season	7	21.54	7.49	**0.0001**
Residual	224	2.88		
Abundance (ind.m^2)				
Site	7	1.19E+10	87.46	**0.001**
Season	1	1.13E+10	83.03	**0.001**
Site x Season	7	5.19E+09	38.22	**0.001**
Residual	224	1.36E+08		
H'				
Site	7	2.79	34.83	**0.0001**
Season	1	0.25	3.08	0.0828
Site x Season	7	0.86	10.72	**0.0001**
Residual	224	0.08		
J'				
Site	7	0.46	29.56	**0.0001**
Season	1	0.35	22.56	**0.0001**
Site x Season	7	0.17	11.12	**0.0001**
Residual	224	0.02		
Functional Richness				
Site	1	374.48	14.39	**0.0001**
Season	7	2589.50	99.52	**0.0001**
Site x Season	7	182.04	6.99	**0.0001**
Residual	224	26.018		
Functional Evenness				
Site	1	0.36	8.65	**0.0001**
Season	7	0.13	3.19	0.0761
Site x Season	7	0.26	6.32	**0.0001**
Residual	224	0.04		
Functional Redundancy				
Site	1	309.42	21.04	**0.0001**
Season	7	118.34	8.04	**0.0018**
Site x Season	7	110.34	7.50	**0.0001**
Residual	224	14.703		

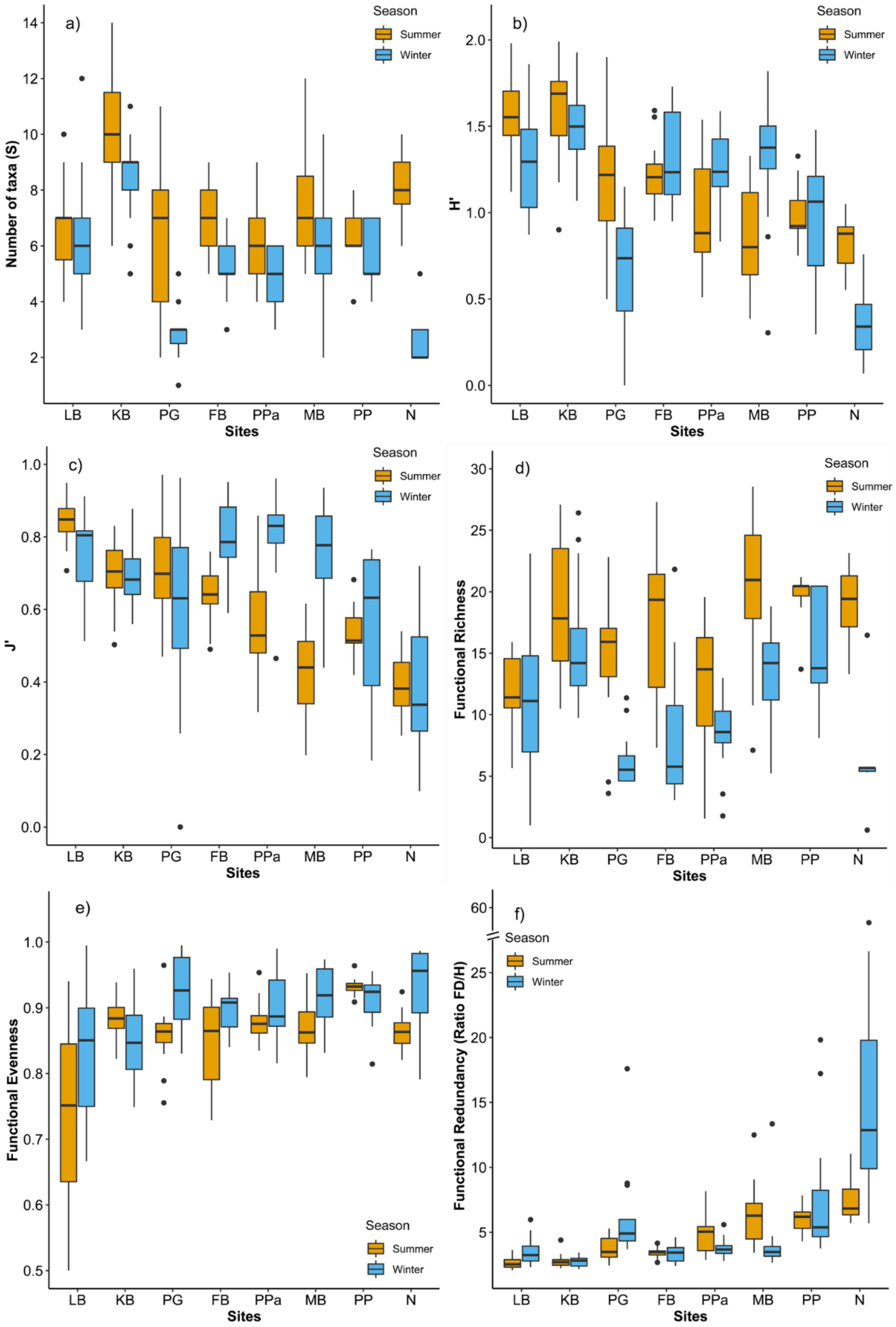


Figure 4.3. Box plots of number of taxa (S), Shannon diversity index (H'), and Pielou's evenness index (J'), Functional Richness, Evenness, and Redundancy across sites and seasons. LB: Long Beach; KB: Kellidie Bay; MB: Middle Beach; PPa: Port Parham; PG: Port Germein, FB: Fisherman Bay; PP: Pelican Point; N: Noonameena.

The most expressed functional trait modalities in the studied benthic communities, based on community-level weighted means (CWM) analyses of trait values, were deposit feeder (feeding mode; contribution: 0.37%), large (>20 mm) body size (contribution: 0.44%), burrower (living habit; contribution: 0.56%), bioirrigator (bioturbation; contribution: 0.56%), sediment position of deeper than 3 cm (contribution: 0.36%), and irregular morphology (contribution: 0.27%) (Figure 4.4-4.5). The CWM values of each compiled functional trait varied significatively across all sites and seasons (Table 4.4, Figure 4.4-4.5). Most of the CWM trait modalities showed significant differences across sites, except for the trait modalities omnivore and hard exoskeleton. In contrast, significant differences across seasons were less evident for trait modalities (Table 4.4). In pairwise comparisons, significant differences in CWM trait modalities were also observed among sites and seasons (Figures 4.4-4.5, Table 4.5, Appendix C Table S6). For example, the functional trait feeding mode showed significant differences in all the trait-modalities at the lagoon habitat (N) compared to all other sites (Appendix C Table S6), and the trait modality sub-surface deposit feeder (feeding mode) and surface shallow <3cm (Sediment position) were significantly different in summer and winter in six of the eight sites analysed (Table 4.5).

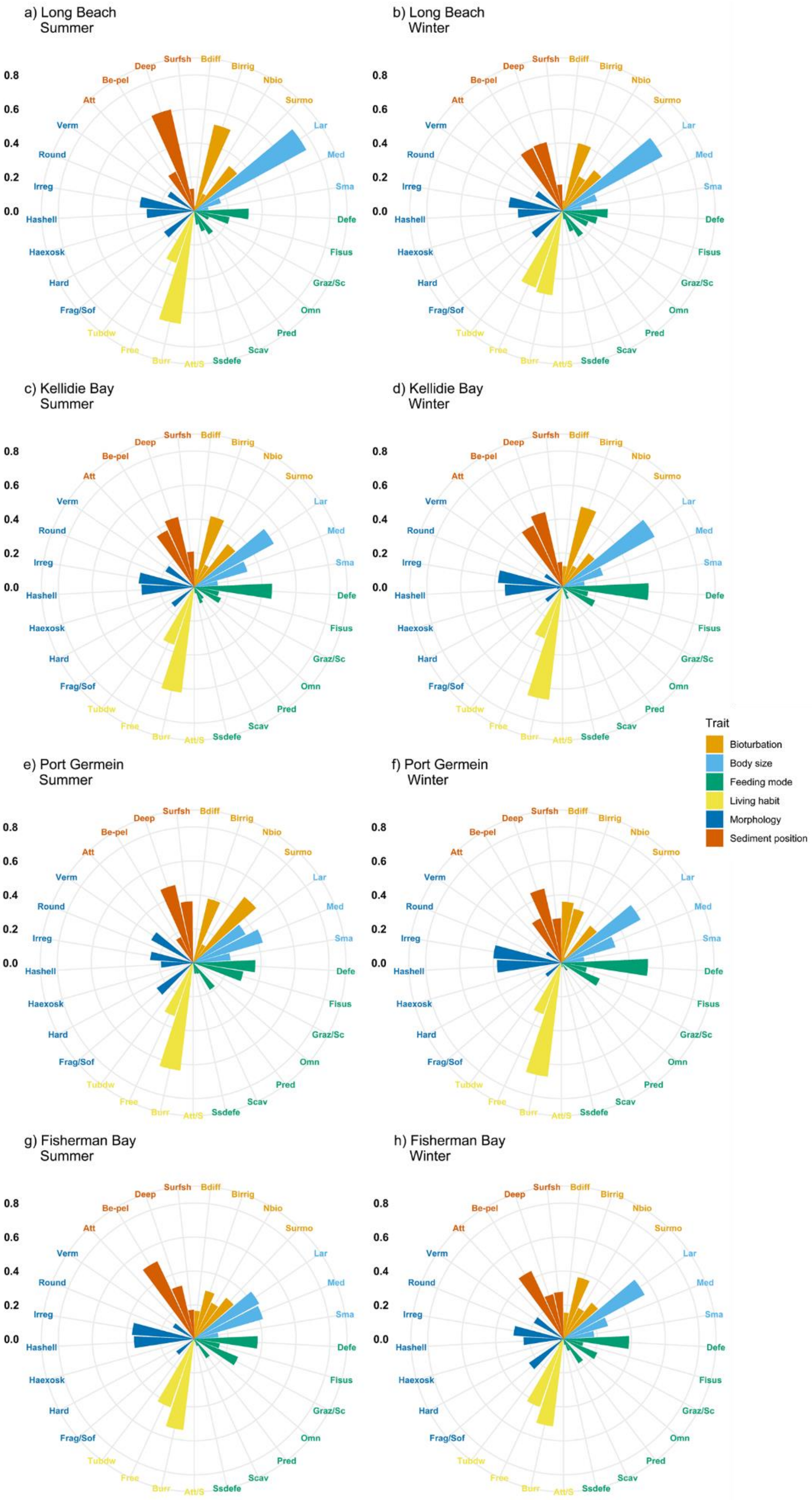
Functional Richness (FRic), Functional Evenness (FEve), and Functional Redundancy (FR) varied significantly across sites (PERMANOVA p=0.0001; Table 4.3). However, FEve was the only metric not significantly different across season (Table 4.3). The greatest FRic values were found in summer at all sites, with greatest FRic values in the gulf habitat at Upper Gulf St Vincent (Figure 4.3d). In contrast, the greatest values of FEve were found in winter at the gulf (PG, PPa), and lagoon (N) habitats. In terms of FR (ratio FD/H'), the greatest values were recorded at the two lagoon habitats in the Coorong, showing the lowest functional redundancy (Figure 4.3e-f). Functional diversity, as FRic, was significant and positively correlated with the number of taxa (R^2= 0.64, p<0.01, Figure 4.6a-b). Although the ratio of FD/H' (i.e. FR) showed a significant relationship with the number of taxa, the relationship was not linear (R^2= 0.13, p<0.01, Figure 4.6c-d). Also, a significant but not linear relationship was identified between FEve and the number of taxa (R^2= 0.17, p<0.01, Figure 4.6e-f). DISTLM analyses revealed that FRic, FEve and FR were mostly influenced by Ammonium, Chlorophyll *a*, sediment grain size (D50), sorting, sediment organic matter content, Nitrite and temperature (Table 4.6).

Table 4.4. Summary of the test results from univariate one-way fixed factor PERMANOVA to CWM trait modalities across sites and seasons. P-values are presented, and significant differences are shown in bold. NC: Not computed.

Trait	Trait modality	Site	Season	Site x Season
Bioturbator	Biodiffusor	**0.0001**	**0.0001**	**0.0001**
	Bioirrigator	**0.0001**	0.0964	**0.0001**
	No bioturbation	**0.0001**	0.8628	**0.0001**
	Surface modifier	**0.0001**	0.3006	**0.0001**
Body size	Large (>20mm)	**0.0001**	0.8339	**0.0001**
	Medium (5-20mm)	**0.0001**	**0.0002**	**0.0001**
	Small (0.5-5mm)	**0.0001**	**0.0001**	**0.0001**
Feeding mode	Deposit feeder	**0.0001**	0.0109	**0.0001**
	Filter/suspension	**0.0001**	**0.0010**	**0.0001**
	Grazer/scraper	**0.0001**	0.8023	**0.0001**
	Omnivore	0.5601	0.2277	0.7073
	Predator	**0.0001**	**0.0048**	**0.0001**
	Scavenger/opportunist	**0.0001**	**0.0025**	**0.0001**
	Sub-surface deposit feeder	**0.0001**	**0.0001**	**0.0001**
Living habit	Attached/sessile	0.0075	0.7358	**0.0002**
	Burrower	**0.0001**	**0.0096**	**0.0001**
	Free living / Surface crawler	**0.0001**	**0.0001**	**0.0001**
	Tube dwelling	**0.0001**	**0.0001**	**0.0001**
Morphology	Hard	NC	NC	NC
	Hard exoskeleton	0.101	0.0320	0.0639
	Hard shell	**0.0001**	**0.0044**	**0.0001**
	Irregular	**0.0001**	0.0429	**0.0001**
	Round	**0.0001**	**0.0001**	**0.0001**
	Fragile/Soft	**0.0001**	0.1578	**0.0001**
	Vermiform	**0.0001**	**0.0001**	**0.0001**
Sediment position	Attached	NC	NC	NC
	Bentho-pelagic	**0.0001**	0.1985	**0.0001**
	Deeper than 3cm	**0.0001**	**0.0001**	**0.0001**
	Surface shallow <3cm	**0.0001**	**0.0001**	**0.0001**

Table 4.5. Summary of PERMANOVA Pair-wise test of CWM trait modalities comparing differences across seasons by sites. P-values are presented, and significant differences are shown in bold. NC: Not computed.

Trait modality	LB	KB	PG	FB	PPa	MB	PP	N
Biodiffusor	0.0808	0.2851	**0.0001**	0.5609	0.9926	0.4877	0.1095	**0.0001**
Bioirrigator	**0.0038**	0.1372	0.2981	0.0209	0.0476	0.857	0.5886	**0.0001**
No bioturbation	**0.0003**	0.8082	0.0246	0.2672	**0.0001**	0.1454	**0.0003**	**0.0001**
Surface modifier	0.4664	0.0155	**0.0001**	0.1987	0.8288	0.364	**0.0001**	**0.0008**
Large (>20mm)	0.0545	0.0403	**0.0004**	**0.0093**	0.9374	0.0638	**0.0004**	**0.0001**
Medium (5-20mm)	0.0607	**0.0062**	**0.0078**	**0.0001**	**0.0089**	0.6922	0.5593	**0.0006**
Small (0.5-5mm)	0.1382	0.6092	**0.0039**	0.0153	**0.0007**	**0.0091**	**0.0001**	**0.0001**
Deposit feeder	0.0500	0.1671	**0.0001**	0.5138	0.4424	0.739	0.0604	**0.0011**
Filter/suspension	0.9546	0.7268	**0.0001**	0.145	0.6975	0.9878	0.3485	**0.0001**
Grazer/scraper	0.1667	0.2035	**0.0001**	0.016	**0.009**	**0.0011**	**0.0061**	0.082
Omnivore	NC	NC	NC	NC	NC	NC	NC	NC
Predator	0.5465	0.0324	**0.0013**	0.1577	0.3533	0.594	0.239	**0.0002**
Scavenger/opportunist	0.9692	0.2551	**0.0012**	0.0933	0.766	0.0744	0.7113	**0.0001**
Sub-surface deposit feeder	**0.0079**	**0.0032**	0.0166	0.0747	**0.0001**	**0.0027**	**0.0001**	**0.0001**
Attached/sessile	0.4852	0.0975	NC	1	1	0.017	NC	NC
Burrower	**0.0006**	0.2789	0.3393	0.4309	0.9166	0.3287	**0.001**	**0.0001**
Free living / Surface crawler	**0.0008**	0.256	0.7733	0.9636	0.5442	0.8337	0.014	**0.0001**
Tube dwelling	0.6939	0.114	**0.0003**	**0.0018**	0.1343	0.5659	**0.0019**	**0.0001**
Hard	NC	NC	NC	NC	NC	NC	NC	NC
Hard exoskeleton	0.3430	**0.0022**	0.2211	0.2039	0.8692	0.5532	NC	NC
Hard shell	0.6447	0.2025	**0.0001**	**0.0001**	**0.0004**	0.0407	**0.0065**	**0.0001**
Irregular	0.8756	**0.01**	**0.0001**	**0.0018**	**0.0006**	0.1223	0.7021	**0.0001**
Round	NC	NC	NC	NC	NC	NC	0.4272	**0.0001**
Fragile/Soft	0.8881	0.0449	**0.0001**	**0.0001**	0.0747	0.4299	0.941	**0.0001**
Vermiform	0.8762	**0.0069**	**0.0001**	0.0318	**0.0002**	0.0236	0.0525	**0.0001**
Attached	NC	NC	NC	NC	NC	NC	NC	NC
Bentho-pelagic	0.0148	0.4107	0.0162	0.0772	**0.0004**	0.5379	**0.0044**	**0.0001**
Deeper than 3cm	**0.0028**	0.4188	0.7602	0.1183	0.4579	0.5157	0.0688	**0.0001**
Surface shallow <3cm	0.4770	**0.0088**	0.0577	**0.0022**	**0.0001**	**0.0054**	**0.0001**	**0.0001**



a) Long Beach Summer

b) Long Beach Winter

c) Kellidie Bay Summer

d) Kellidie Bay Winter

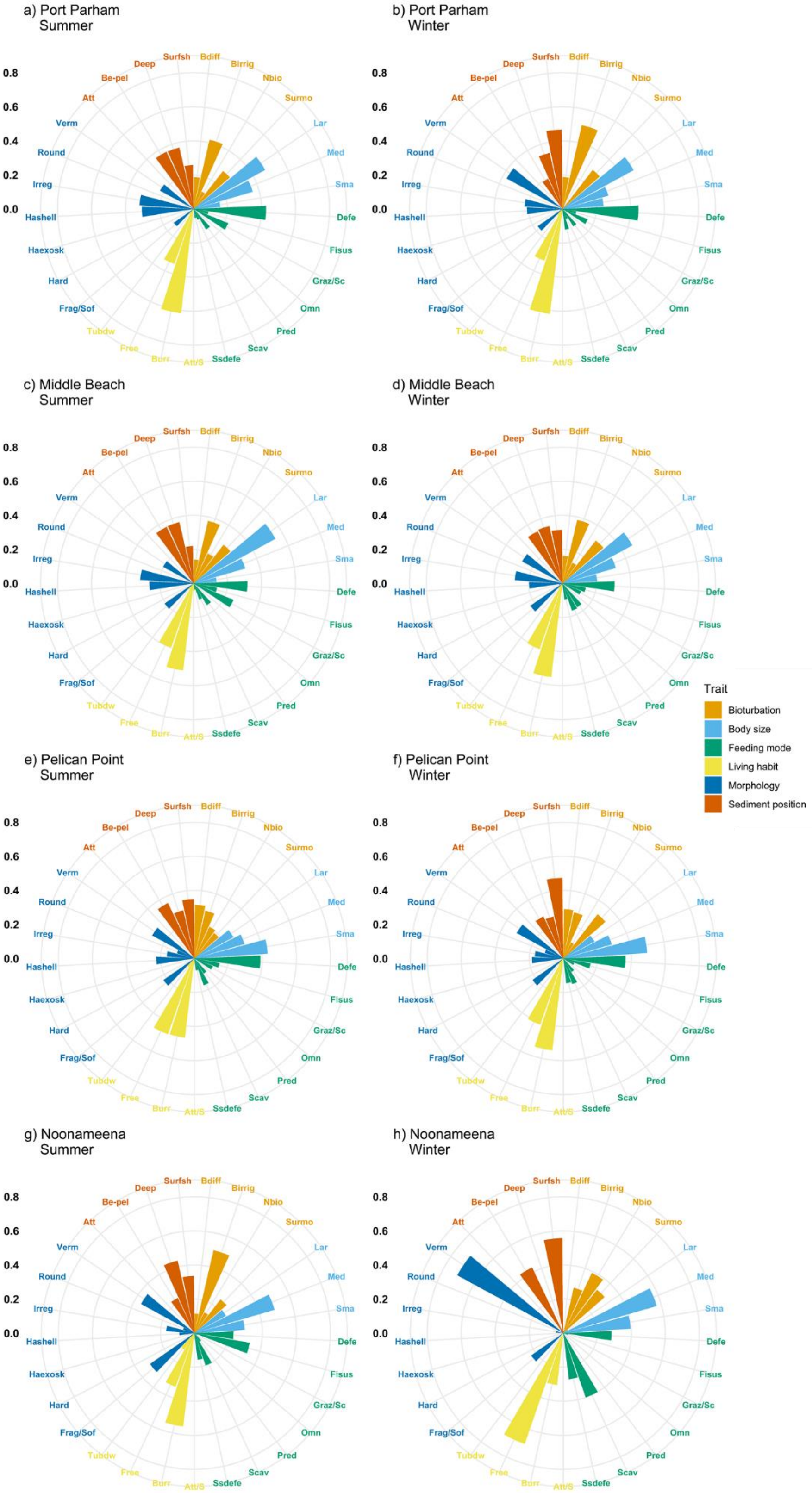
e) Port Germein Summer

f) Port Germein Winter

g) Fisherman Bay Summer

h) Fisherman Bay Winter

Figure 4.4. Community-weighted means (CWM) of trait-modalities expression. Scale represents the percentage contribution to CWM. Trait modalities labels (acronyms) are defined in Table 4.2.



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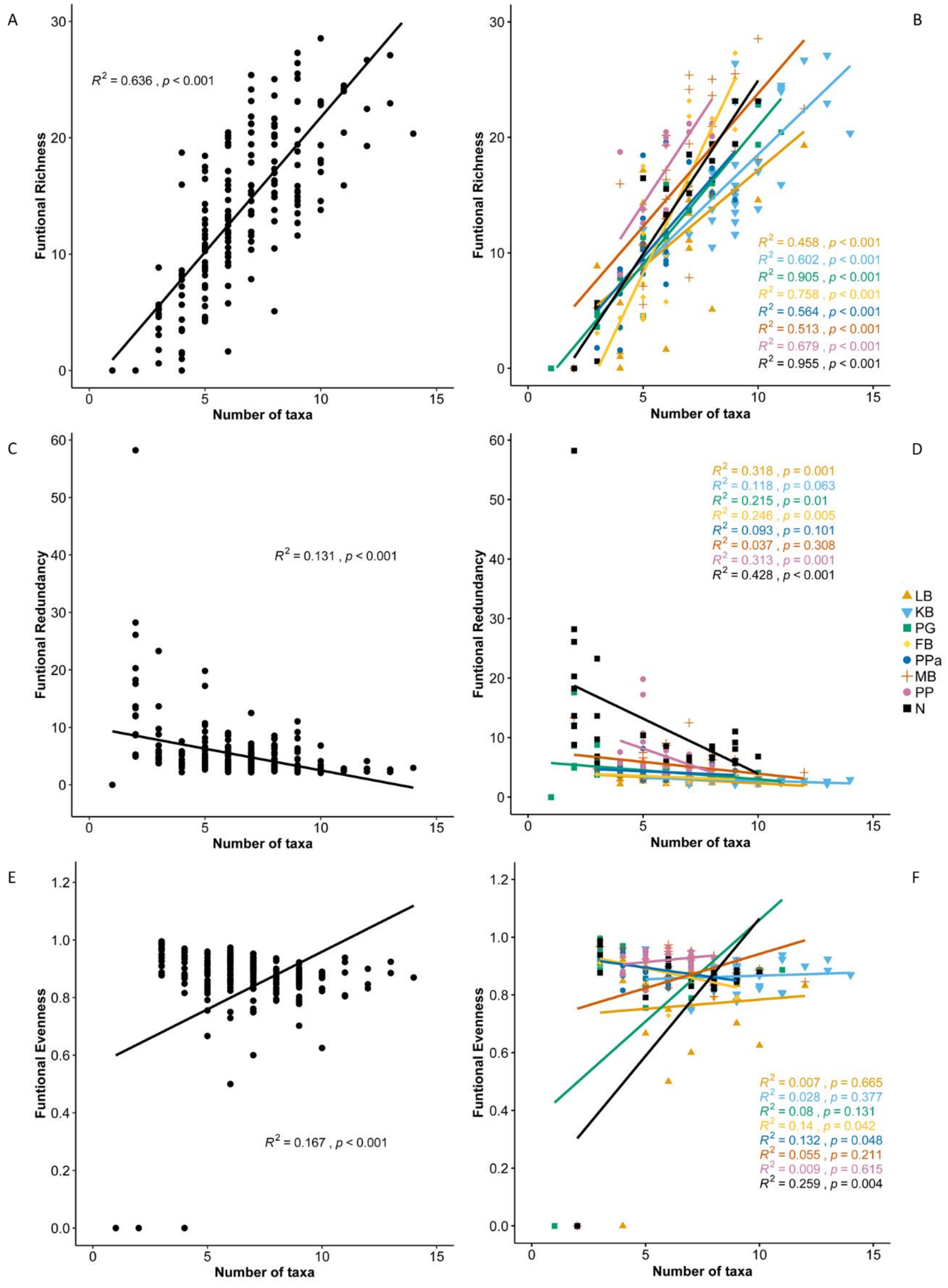


Figure 4.6. Correlation plots between the number of taxa and functional metrics. Lines represent trend lines. LB: Long Beach; KB: Kellidie Bay; MB: Middle Beach; PPa: Port Parham; PG: Port Germein, FB: Fisherman Bay; PP: Pelican Point; N: Noonameena.

Table 4.6. Result of DISTLM forward analysis. Only significant (p<0.01) results are shown.

Variable	R^2	SS (trace)	Pseudo-*F*	P-value	Proportion
Functional Richness	0.35				
Chlorophyll *a*		2172.20	50.979	0.0001	0.176
D50		373.82	7.4517	0.0074	0.030
Sorting		367.52	7.3223	0.0072	0.030
Temperature		2014.50	46.554	0.0001	0.163
Nitrite		488.81	9.8388	0.0015	0.040
Functional Evenness	0.11				
D50		373.82	7.4517	0.0074	0.030
Organic matter		0.54488	9.6673	0.0029	0.040
Functional Redundancy	0.21				
Ammonium		385.12	15.366	0.0092	0.060
Organic matter		1000.80	44.37	0.0001	0.157

4.3.4 Community analyses of benthic macrofauna and functional traits

Significant community differences were detected between sites and seasons for both taxa and functional traits (PERMANOVA *p*=0.0001, Table 4.7). The PCO analysis revealed distinct communities across sites and seasons with 47.7% of the variability in taxa composition, and 64.3% of the variability in trait composition (Figure 4.7). Based on taxa, sites in the Coorong lagoon (PP, N) were separated from other sites, while the gulfs habitats were more closely grouped. A separation according to season was found in KB, FB and PG (Figure 4.7a, appendix C Figure S4a). Less distinction emerged based on traits with the most evident seasonal separation in PG and N (Figure 4.7b, Appendix Figure S4b).

Table 4.7. Test results from multivariate one-way fixed factor PERMANOVA to compare the community structure of taxa and traits composition across sites and seasons. Significant differences are shown in bold.

	df	MS	Pseudo-*F*	P-value
Taxa				
Site	7	61012	68.46	**0.0001**
Season	1	19425	21.8	**0.0001**
Site x Season	7	13569	15.23	**0.0001**
Residual	224	891		

	df	MS	Pseudo-*F*	P-value
Traits				
Site	7	7653	63.5	**0.0001**
Season	1	6781	56.26	**0.0001**
Site x Season	7	2630	21.82	**0.0001**
Residual	224	120		

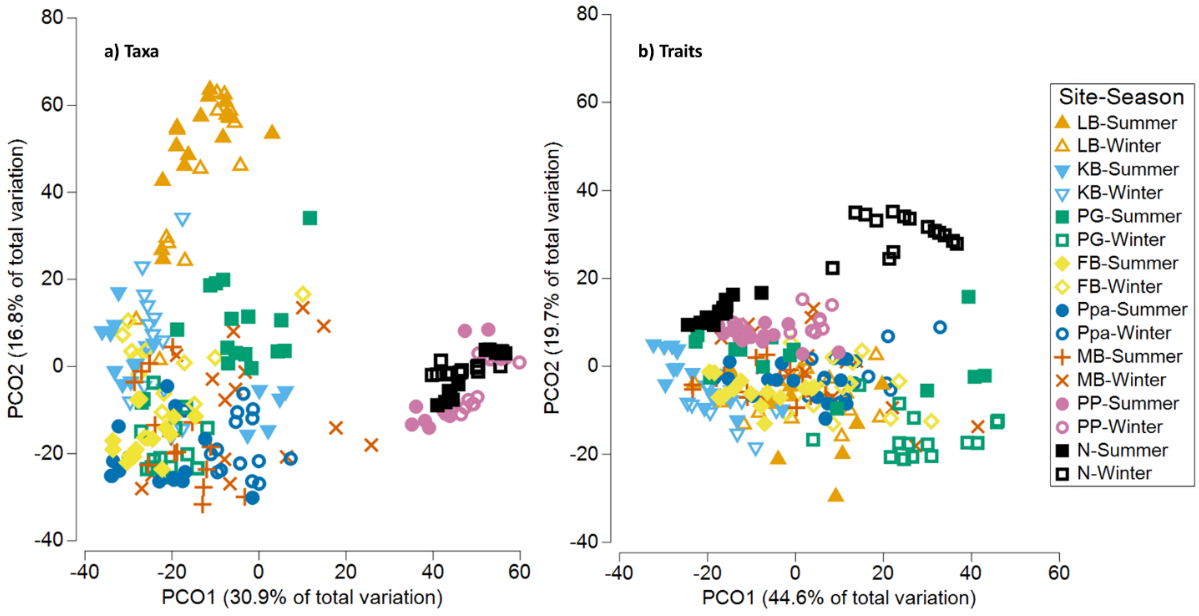


Figure 4.7. PCO (Principal Coordinates Ordination) plots for benthic assemblages across sites and seasons based on the (a) taxonomic and trait (b) composition. LB: Long Beach; KB: Kellidie Bay; MB: Middle Beach; PPa: Port Parham; PG: Port Germein, FB: Fisherman Bay; PP: Pelican Point; N: Noonameena.

4.3.5 Ecosystem functioning – Relationship between benthic macrofauna, functional traits and environmental conditions

Several significant relationships between the benthic taxa, their functional traits and the environmental conditions were identified across sites and season (Figure 4.8, Appendix C Figure S5-12). In general, the interactions were stronger in summer than winter. The stronger interactions were identified at the coastal embayment habitats in Coffin Bay, while the lagoon habitats showed the weakest interactions between benthic macrofauna, traits and environmental conditions (Figure 4.8). The six functional traits and their modalities showed significant interactions with environmental conditions across all sites irrespective of season. At the coastal embayment habitats, the trait modality of small (<0.5 mm) body size was correlated to sediment grain size (D50), sub-surface deposit feeder with Chl *a*, and hard exoskeleton and hard shell with temperature and salinity (Figure 4.8a-b). The gulfs at the Upper Spencer Gulf showed significant relationships between the trait modalities filter suspension, small and medium body size, and pH, salinity, and sediment grain size (Figure 4.8c-d). In the other gulf habitats at the Upper Gulf St Vincent, significant relationships were found between the trait modalities deposit feeder, hard exoskeleton and Chl *a*, with correlations between large body size and tube dwelling to salinity and temperature, and burrower to Nitrate (Figure 4.8e-f). At the lagoon habitats in the Coorong, the magnitude of the interactions between benthic macrofauna traits and environmental conditions was lower compared to the other sites. In PP interactions between the trait modalities biodiffusor, surface shallow <3cm and temperature were identified, as well as several trait modalities influenced by Ammonium and Phosphate, while for N the feeding modes filter suspension and sub-surface deposit feeder were influenced by Chl *a* and salinity (Figure 4.8g-h).

4.4. Discussion

4.4.1 Patterns of taxonomic and functional metrics

Spatial and temporal patterns of benthic communities, based on taxonomic and functional metrics, elucidated variation in benthic macrofauna diversity and functional traits, suggesting differences in ecosystem functioning across habitats and seasons. The theory proposed by various researchers states that greater taxonomic biodiversity will increase the number of expressed traits, resulting in greater functional diversity, and therefore greater effects on ecosystem functioning (Tilman et al. 1996; Loreau et al. 2002; Reiss et al. 2009). However, correlations between taxonomic and functional metrics have yielded highly variable results, often mediated by environmental context and habitat heterogeneity (Hewitt et al. 2008; Strong et al. 2015; Thrush et al. 2017; Kokarev et al. 2017). In this study, we identified positive relationships between taxonomic and functional metrics, and ascertained that habitats with greater number of taxa and diversity (H’) also showed high Functional Diversity FD (as FRic, FEve and FR), as previously reported in other marine and estuarine systems (e.g. Wong and Dowd 2015; Hajializadeh et al. 2020; Delfan et al. 2021; Shojaei et al. 2021).

Yet, we also found that taxonomic and functional diversity of benthic communities were site-dependent and varied across the two studied seasons, similar to findings reported in other studies (e.g. Wong and Dowd 2015; Gladstone-Gallagher et al. 2017; Gammal et al. 2019). The differences of FD (i.e. FRich, FEve, FR) across sites and seasons could be determined by several factors: i) abundance, diversity and taxa, and ii) specific environmental conditions and benthic habitat characteristics (e.g. sediment organic matter, grain size, sorting), as described

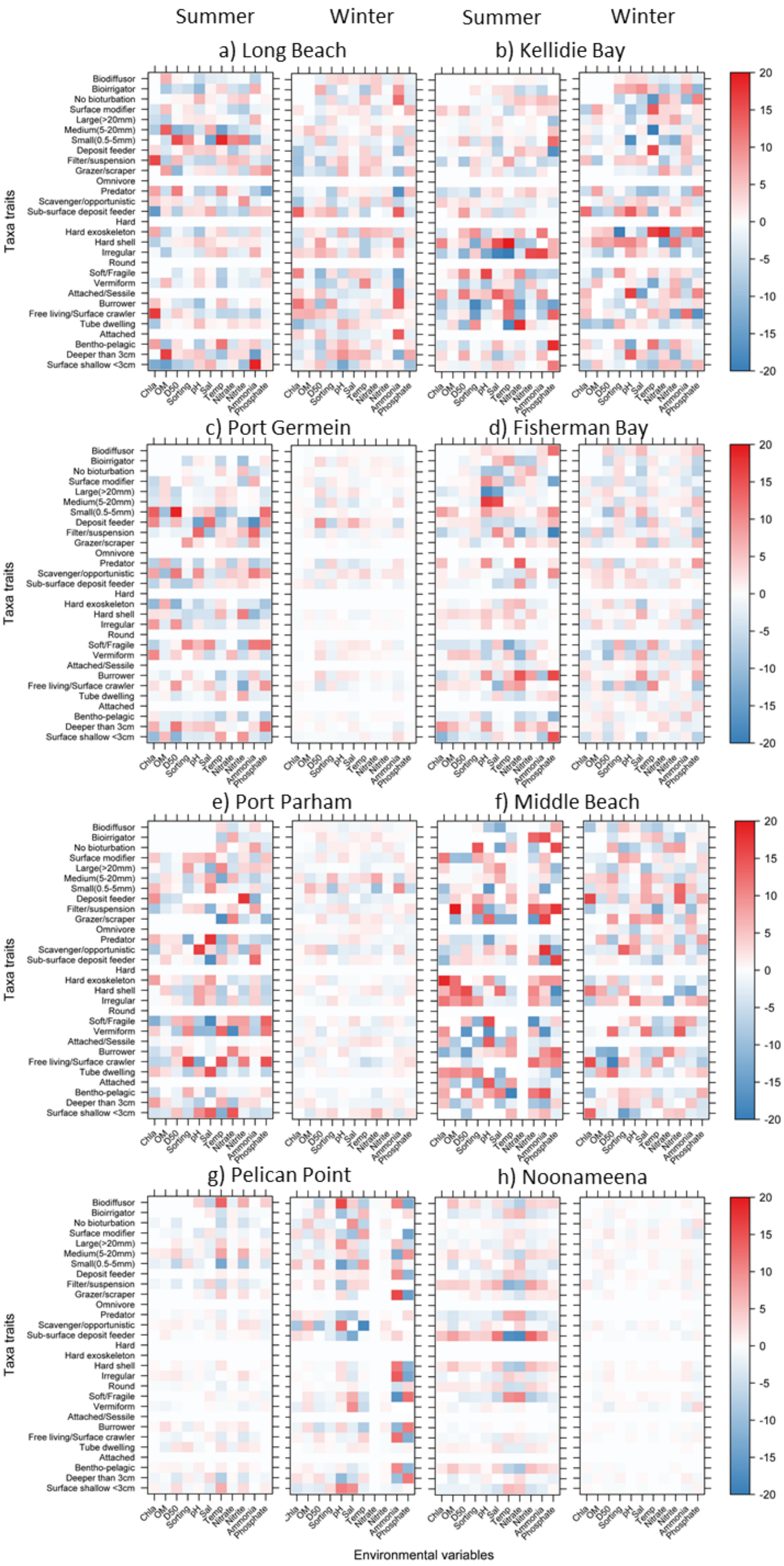


Figure 4.8. Level plot for the fourth corner interaction (taxa abundance, traits, and environmental conditions) using NB-GLLVM showing the interactions by site and seasons. The colour scale indicates significant interactions and magnitudes of the point estimates.

in previous studies (e.g. Hewitt et al. 2008; Shojaei et al. 2015; Henseler et al. 2019; Cappelatii et al. 2020). FRic and FR were greater across all the sites in summer compared to winter, suggesting that the expression of traits was greater in summer. The lower FD in winter could be explained by a temporary decrease of benthic taxa (e.g. bivalves, crustaceans, polychaetes) with specific functional traits modalities or redundant taxa (Loreau et al. 2002), similar to seasonal patterns in cold temperate ecosystems in the Northern hemisphere (e.g. Kröncke et al. 2013; Shojaei et al. 2021).

The two sites at the Coorong lagoon showed a distinctive pattern compared to other habitats, with a low number of taxa but greater FR (ratio FD/H'), indicating low functional redundancy. The low number of taxa could be explained by the habitat characteristics and environmental conditions of the Coorong (e.g. high salinity, eutrophication) (Dittmann et al. 2015; Mosley et al. 2020). Low functional redundancy arising from few taxa occupying the available functional space with few common traits shared, can indicate vulnerability to future functioning loss, as suggested by van der Linden et al. (2012) and Gammal et al. (2020). In this case, 14 taxa accounted for the low functional redundancy across PP and N, and were dominated by the polychaete *Capitella sp*. and the insect larvae Chironomidae, which shared traits related to opportunistic behaviours in disturbed habitats (e.g. free living, scavenger, deposit feeder, surface shallow sediment position).

Functional traits and their modalities also varied across sites and seasons, as a result of changes in the benthic macrofauna. Such spatial and temporal differences in functional traits resulting from environmental conditions and habitat complexity are not uncommon in mudflats (e.g. Wong and Dowd 2015; Gusmao et al. 2016; Henseler et al. 2019; Hajializadeh et al. 2020; Mestdagh et al. 2020). The multivariate (PCO) analysis for both taxonomic and functional trait composition showed a separation based on the site and season. However, the grouping based on traits was less evident, indicating different patterns of alignment between the two metrics. The functional traits and their modalities were thus more homogenous than the taxonomic composition across sites and seasons.

For example, the taxonomic composition of the Coorong lagoon was differentiated from the other habitats, but the multivariate structure of the functional traits in this habitat was similar to the other habitats. Such patterns could result from functional redundancy, when different taxa share few common traits, or new taxa added until all traits are represented, or a combination of both (Schulze and Mooney 1993; Loreau et al. 2002; van der Linden et al. 2012; Gammal et al. 2020).

4.4.2 Linkages between benthic macrofauna, functional traits and environmental conditions

In this study, the relationships between benthic macrofauna, functional traits and environmental conditions varied across sites and seasons, potentially indicating that, depending on the benthic composition and trait expression, some ecosystem functioning derived from these relationships may be different across habitats. In the absence of direct measurements, insights into ecosystem functioning can be inferred from knowledge of the linkages between taxa, traits and environmental conditions (Wong and Dowd 2015; Lam-Gordillo et al. 2020a; Delfan et al. 2021). In our study, the trait modalities bioirrigator, surface modifier (‘Bioturbator’ trait), burrower, free-living (‘Living habit’), deeper than 3 cm and bentho-pelagic (‘Sediment position’) were commonly expressed. These trait modalities showed strong relationships with the sediment characteristics (D50, sorting) at each habitat, showing that muddy to sandy sediments were most suitable for burrowers and free-living organisms (Liu et al. 2019), which increases sediment oxygenation and nutrient cycling from benthic macrofauna activities (Lam-Gordillo et al. 2020a; Delfan et al. 2021).

The trait ‘feeding mode’ was related with environmental conditions in most of the cases across sites and seasons, as it is fundamental for the structural complexity and trophic status of benthic ecosystems (Pearson and Rosenberg 1978). In our study, the trait modality of deposit feeder was expressed more in summer. Deposit feeders are generally dominant in muddy sediments (Rhoads and Young 1970; Hajializadeh et al. 2020), and the sediment grain size (D50 and sorting) was smaller in summer compared to winter. The deposit feeders and grazer trait modalities were also expressed most at sites where high concentrations of Chl *a* were found, as they feed on microphytobenthos (e.g. Wong and Dowd 2015; Daggers et al. 2020). The relationship of different feeding mode modalities with sediment conditions and primary productivity could also indicate differentiation in the use of resources, food availability, and prey accessibility across sites and seasons (Norkko et al. 2013; Weigel et al. 2016; Sivadas et al. 2020). The traits for ‘body size’ and ‘morphology’ also varied across sites and seasons, but the trait modalities large body size and irregular body shape were important at almost all sites. Body size is a relevant trait for assessing ecosystem functioning that can be correlated with other traits and provide insight to processes such as nutrient cycling, sediment reworking and energy fluxes (Norkko et al. 2013; Hillman et al. 2020). Large individuals related most to environmental conditions at the studied habitats, however, small and medium body size were the trait modalities most expressed at the lagoon habitats, probably as a result of the large-scale fluctuations in salinity and eutrophic conditions in the Coorong (Dittmann et al. 2015; Mosley et al. 2020).

Environmental conditions correlated most with benthic macrofauna-traits were chlorophyll *a*, organic matter, sediment grain size (D50 and sorting) and concentrations of ammonium. Functional diversity (i.e. FRic, FEve, FR) was also correlated with the environmental conditions Chlorophyll *a*, sediment grain size (D50), sediment organic matter content, temperature, ammonium, and nitrite, supporting the pattern found with the linkages between taxa-traits and environmental conditions. The findings from both perspectives (i.e. correlation between taxa-traits, and environment conditions, and functional diversity), suggest that across the surveyed sites the ecosystem functioning mostly occurring includes nutrient cycling, productivity, and sediment stability and transport (Norkko et al. 2013; Wong and Dowd 2015, Hajializadeh et al. 2020; Lam-Gordillo et al. 2020a; Delfan et al. 2021).

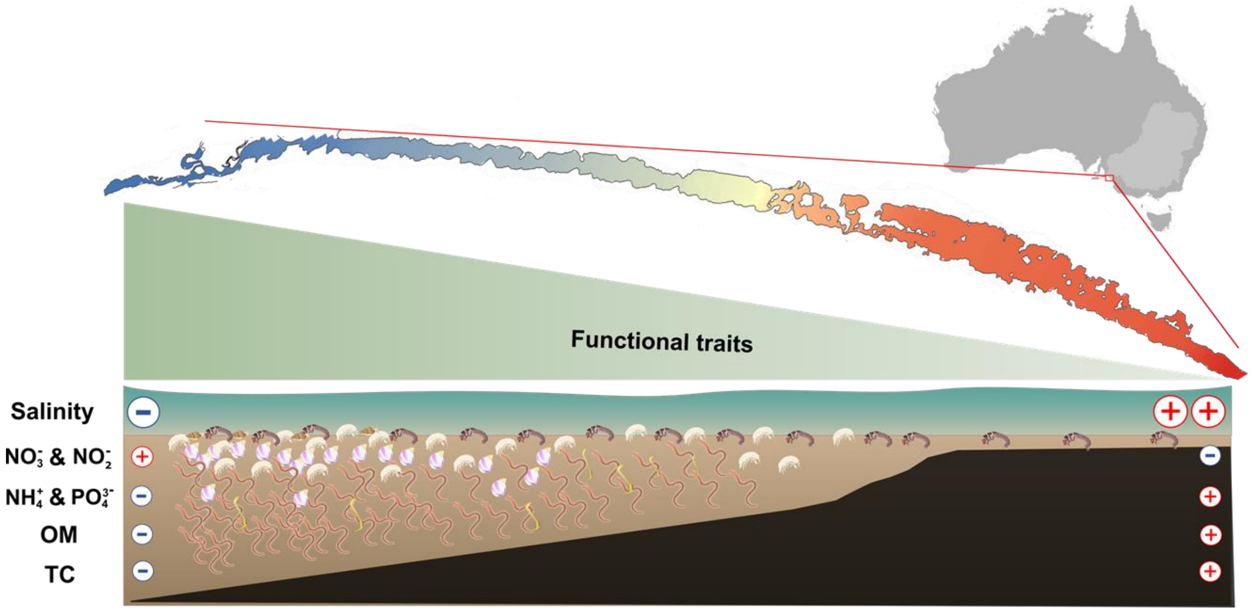
4.3 Implications of functional diversity for conservation and management

Across the south Australian coast, different patterns in benthic taxa, functional traits and functional diversity were identified, as a result of site-dependent environmental conditions and habitat characteristics. In addition, anthropogenic activities are also shaping the benthic communities and their trait expression. The lagoon showed the lowest functional redundancy compared to other habitats, indicating that the functional traits expressed were less common, and only few taxa occupied the available functional space. It has been proposed that the greater the number of taxa and traits expressed in an ecosystem (i.e. functionality), the greater probability of taxa and traits to persist and maintain ecosystem functioning (van der Linden et al. 2012; Kokarev et al. 2017; Murillo et al. 2019). Our findings could thus indicate that the lagoon is vulnerable to further loss of benthic taxa and structural changes (i.e. ecosystem functioning loss) caused by anthropogenic or natural environmental changes. In contrast, benthic communities in the coastal embayment showed high functional richness and redundancy, suggesting that these sites are more resilient and are more likely to maintain their ecosystem functioning if an event of change (i.e. taxa loss) occurs.

4.5. Conclusion

This study identified spatial and temporal patterns of benthic communities, based on both taxonomic and functional metrics. Functional diversity and expression of functional traits were site-dependent and different across habitats, which could be explained by the benthic community at each site, the influence of environmental conditions and habitat complexity. Correlations between benthic macrofauna, functional traits and environmental conditions were mostly driven by deposit feeders with large and irregular body organisms, performing bioirrigation and burrowing deep into the sediment. Thus, ecosystem functioning would be most affected by the loss of taxa displaying these traits. Our findings corroborate that using both taxonomic and functional metrics is complementary for conservation and management seeking to maintain biodiversity with the implicit understanding that ecosystem functioning will also be maintained. The outcomes presented here advance the understanding of the relationship between benthic taxa, functional traits and environmental conditions in tidal flats. Understanding those relationships will further enable us to predict how ecosystem functioning changes with biodiversity loss, and could potentially help to improve management to ensure healthy functioning of intertidal benthic ecosystems.

Chapter 5. Loss of benthic macrofauna functional traits correlates with changes in sediment biogeochemistry along an extreme salinity gradient in the Coorong lagoon, Australia



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Author contributions

Orlando Lam Gordillo: Conceived the ideas and developed the outline for the manuscript, designed the methodology, collected the data, analysed the data, prepared the figures and tables, wrote the manuscript and corresponding author.

Sabine Dittmann – primary supervisor: Guidance on the project development, acquisition of funding, discussion of project ideas, contribution to drafting manuscript, and critical refinement.

Luke Mosley: Discussion of project ideas, acquisition of funding, and contribution to drafting manuscript.

Stuart Simpson: Discussion of project ideas and contribution to drafting manuscript.

David Welsh: Discussion of project ideas and contribution to drafting manuscript.

Abstract

Estuarine ecosystems are considered hotspots for productivity, biogeochemical cycling and biodiversity, however, their functions and services are threatened by several anthropogenic pressures. We investigated how abundance and diversity of benthic macrofauna, and their functional traits, correlate to sediment biogeochemistry and nutrient concentrations throughout an estuarine-to-hypersaline lagoon. Benthic communities and functional traits were significantly different across the sites analysed, with higher abundance and more traits expressed in the estuarine region. The results revealed that the benthic trait differences correlated with sediment biogeochemistry and nutrient concentrations in the system. The estuarine regions were dominated by high abundance of large burrowing and bioturbating macrofauna, promoting nutrient cycling and organic matter mineralization, while these organisms were absent in the hypersaline lagoon, favouring accumulation of organic matter and nutrients in the sediment. The results highlight the importance of preserving healthy benthic communities to maintain ecosystem functioning and mitigate the potential impacts of eutrophication in estuarine ecosystems.

Keywords: Biological traits, eutrophication, macroinvertebrates, nutrient cycling, hypersaline, Australia.

5.1. Introduction

Coastal soft sediment habitats are some of the most productive ecosystems worldwide, with multiple contributions to ecosystem services such as food production, protection, recreation, carbon sequestration, and nutrient cycling (Cai 2001; Snelgrove et al. 2014; Douglas et al. 2019; Hillman et al. 2020). These ecosystems, especially estuaries, are considered hotspots for biogeochemical cycling, biodiversity, and productivity (Thrush et al. 2006; Douglas et al. 2019; Rodil et al. 2020). Benthic invertebrates play a key role in modifying sediment biogeochemistry and nutrient fluxes by actively dispersing, recycling and changing the sediments (Welsh 2003; Thrush et al. 2006; Belley and Snelgrove 2016), thus driving the functioning of coastal and estuarine sediments (Kauppi et al. 2018, Wrede et al. 2019; Mestdagh et al. 2020). However, estuarine ecosystems around the world are subjected to anthropogenic pressures such as coastal development, eutrophication, increased sediment loads, pollution, and climate change (Lotze et al. 2006; Chariton et al. 2010; Dittmann et al. 2015; Passeri et al. 2015), that may influence environmental conditions, and which can threaten benthic communities and consequently the ecosystem functioning and services they provide (Wetz and Yoskowitz 2013; Caswell et al. 2018; Potter et al. 2021).

The functioning of estuarine sediments encompasses complex relationships of biological, chemical, and physical processes at different spatial and temporal scales (Waldbusser and Marinelli 2006; Villnäs et al. 2019) that are often difficult to depict. The contribution of benthic invertebrates to sediment ecosystem services is influenced by abiotic and biotic factors which strongly interact. Abiotic factors include water and sediment conditions (e.g. water temperature, salinity, dissolved oxygen, sediment particle size, organic matter, nutrient concentrations), that in turn structure the biotic factors, i.e. microbial to macrofauna communities (Reise 1985; Honkoop et al. 2006; Chariton et al. 2010).

Benthic communities influence estuarine sediment properties, subject to their abundance and composition, but mainly according to the behavioural, morphological, and physiological characteristics, here defined as functional traits, of each species (Bremner 2008; Beauchard et al. 2017). Benthic macrofauna functional traits are directly and indirectly related to several ecosystem functions, including carbon sequestration, nutrient cycling, oxygen consumption and sediment transport (Snelgrove et al. 2014; Lam-Gordillo et al. 2020a). For example, macrofauna can increase organic matter (OM) inputs to sediments through biodeposition (Graf and Rosenberg, 1997) and mix this OM into deeper strata via bioturbation (Kristensen 2000; Welsh 2003). Burrow construction and the irrigation of these burrows by their occupants, increases the surface area of contact between the sediment and water column, promoting solute exchange which creates mosaics of oxidised (redox) zones within the sediments (Nielsen et al. 2004; Robertson et al. 2009; Stief 2013). These redox change zones, and in some cases the fauna themselves, can then act as substrates for colonisation by specific functional groups of bacteria such as nitrifying and denitrifying bacteria (Welsh and Castadelli 2004; Stief 2013; Welsh et al. 2015), which are ultimately responsible of organic matter decomposition and nutrient cycling (Welsh 2003; Wyness et al. 2021). Sediment nutrient cycling is critical to maintain functioning of estuarine ecosystems, mitigating nutrient over-enrichment, i.e. eutrophication.

Benthic macrofauna are also considered powerful bio-indicators of environmental change, as their functional traits (e.g. long-life spans, limited mobility) can be affected by environmental conditions (Tweedley et al. 2012; Veríssimo et al. 2012). Changes in abundance, diversity and functional traits are commonly reported as responses to changes in the environmental conditions, particularly disturbances that affect sediment biogeochemistry and structure (Veríssimo et al. 2012; Borja et al. 2015). For example, when an estuary becomes eutrophic, the abundance of macrobenthic fauna increases but diversity decreases (Tweedley et al. 2012). Macrobenthic fauna also respond to salinity changes, with the abundance and diversity of macrobenthic fauna decreasing from estuarine to hypersaline conditions (Dittmann et al. 2015).

While changes in macrobenthic communities and their functional traits across estuarine gradients have been extensively studied in the northern temperate regions and tropical estuaries (e.g. Cloern 2001; Villnäs et al. 2019; Medeiros et al. 2021), there is a little understanding on how these changes influence sediment biogeochemistry and nutrient cycling in systems with extreme salinity gradients (from estuarine to hypersaline conditions). The lack of understanding is even more evident in estuarine lagoons in arid or semi-arid climates, which are threatened by hydrological and climatic shifts, due to their generally higher evaporation rates and lower freshwater inflow, water extraction for irrigation, and climate change (Cloern et al. 2016; Tweedley et al. 2019; Mosley et al. 2020). The Coorong is an estuarine lagoon system and listed Ramsar site (Coorong and Lakes Alexandrina and Albert Ramsar Wetland), located at the terminus of the largest river system of Australia, the Murray-Darling Basin. It provides an ideal case study site as it is characterized by an extreme salinity gradient (Mosley et al. 2020) that strongly influences the abundance and distribution of benthic fauna (Dittmann et al. 2015; Dittmann et al. 2018). The Coorong has been experiencing increased frequency and severity of pressures, such as eutrophication, hypersalinity, drought (due to water abstraction for agriculture in the catchment and climate change), leading to a decline in its ecological health over recent decades (Dittmann et al. 2015; Mosley et al. 2020).

The ongoing pressures in the Coorong challenge the benthic communities role in mitigating eutrophication, by limiting their survival, abundance and distribution. This estuarine lagoon system thus presents an important example for understanding the interactions between salinisation, benthic macrofauna and sediment biogeochemical processes. The aim of this study was to investigate how benthic macrofaunal communities and their functional traits change across an extreme salinity (freshwater to several times seawater concentrations) gradient, and whether there are corresponding patterns in sediment biogeochemistry and nutrient concentrations. We hypothesised that (1) benthic macrofauna, sediment biogeochemistry and nutrient concentrations will be different across the system, due to the strong salinity gradient, and that (2) pore water nutrient concentrations and sediment biogeochemistry will be correlated with benthic macrofauna, especially those with functional traits that enhance nutrient cycling and sediment redox status. It is hoped the results can be used to help identify management interventions required to improve the health of the Coorong and other estuarine-lagoon systems experiencing increased salinisation and eutrophication.

5.2. Methods

5.2.1 Study area

The Coorong is located in South Australia, at the end of Murray-Darlin Basin, the largest river catchment in Australia (Figure 5.1). The Coorong covers three regions: the Murray Estuary, North Lagoon, and South Lagoon, which are connected via a narrow channel (<100 m). The Murray Estuary consists of several channels on either side of the river mouth opening to the Southern Ocean (Mosley et al. 2018). The region is microtidal, and water level in the lagoons are determined mainly by evaporation, wind, and water release over the river Murray barrages rather than by tides (Mosley et al. 2018). A strong salinity gradient characterises the Coorong with a corresponding eutrophication gradient increasing towards the hypersaline South Lagoon (Mosley et al. 2020). Seven sites across this system were selected and surveyed in spring 2020: Sites were ordered from North to South, which also reflected the increasing salinity gradient: Murray Estuary: Hunters Creek (HC) and Pelican Point (PP); North Lagoon: Long Point (LP) and Noonameena (NM); South Lagoon: Hells Gate (HG) Jack Point (JP) and Salt Creek (SC) (Figure 5.1). All sites were surveyed when the mudflats were exposed and accessible from shore (Appendix D Table S1).

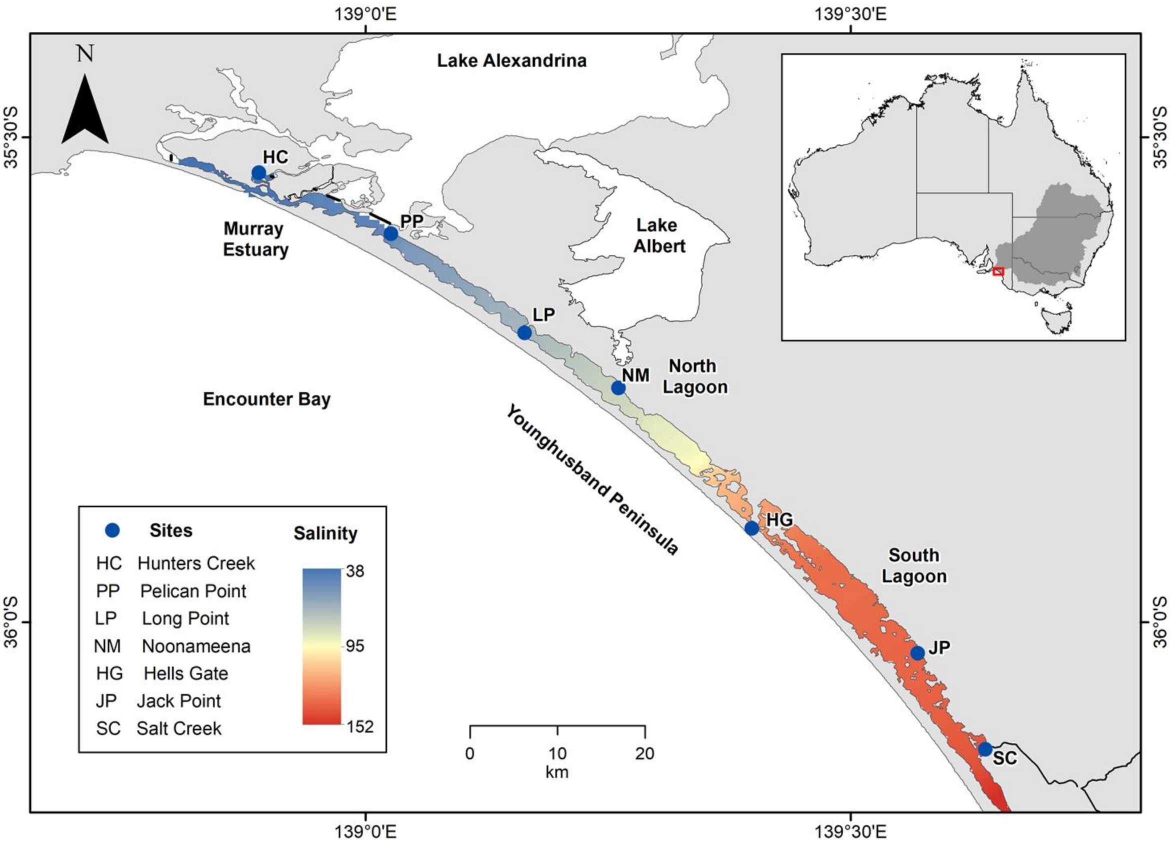


Figure 5.1. Location of the sampling sites and salinity gradient across the Coorong. The inset indicates the catchment of the Murray-Darling River system in Australia and the red square the area shown in the main figure. Murray Estuary: HC and PP; North Lagoon: LP and NM; South Lagoon: HG, JP, and SC. Salinity data were generated using the 1-dimensional Coorong Hydrodynamic Model (Jöhnk and Webster, 2014), using historical data for boundary conditions and validated against recorded salinity at sensors (available from water.data.sa.gov.au).

5.2.2 Data collection

5.2.2.1 Biological data

Sediment samples for benthic macrofauna were taken using a handheld PVC cylindrical corer (83.3 cm^2 surface area) with five replicates randomly taken within an area of 5 m^2 per site. (Appendix D Table S1). Samples were sieved through a 500 µm mesh size in the field and preserved in ethanol (70%) until further processing. In the laboratory, samples were sorted, and all organisms identified to the lowest possible taxonomic level and counted (Appendix D Table S2).

2.2.2 Environmental variables

At each sampling site, environmental variables known to influence benthic communities in the Coorong were measured (Dittmann et al. 2015; Dittmann et al. 2018). Five replicate samples for each environmental variable were taken at each site within the same area (5 m^2) where the sediment samples for benthic macro fauna were collected. Water temperature (°C), salinity, and pH were measured in the overlying water during the macrofauna sampling using a Hannah HI98194 multiparameter meter and a refractometer (for salinities above 80). Sediment samples were taken using a cut off 10 mL syringe (surface area 1.8 cm^2 and 10 cm depth) to analyse OM content, sediment grain size, and chlorophyll-*a*, and using a cut-off 60 mL syringe (surface area 6.6 cm^2 and 10 cm depth) to analyse sediment nutrients. In addition, sediment pore water was collected using Rhizon samplers with a 0.2 um pore size (Seeberg-Elverfeldt et al. 2005) for analysing nutrients. Porewater nutrient and sediment samples were immediately stored in portable freezers and frozen to -20ºC until further analysis.

Sediment OM content (OM%) was determined by a partial combustion method; firstly by drying the sediment samples to constant weight using an Ohaus MB45 Moisture Balance (controlling the temperature profile at 80 ºC), then when constant weight was achieved, sediment samples were combusted in a furnace at 450°C for 5 h, and OM content determined by gravimetry. Grain size was determined by laser diffraction using a particle size analyser (Malvern Mastersizer 2000). Average values for grain size fractions for each site were entered into the GRADISTAT program v8.0 (Blott and Pye 2001) to obtain the median (D50 µm) and sorting coefficient (σG). Chlorophyll-a (g m^{-3}), as a proxy of microphytobenthos, was determined after extraction in 99% ethanol using a spectrophotometer (Thermo Scientific, Spectronic 200) and following protocols from Ritchie (2008). Sediment pH, conductivity, total phosphorus as well as total carbon and total nitrogen concentrations by LECO analysis were determined by the NATA accredited Environmental Analysis Laboratory at Southern Cross University, following strict quality control and assurance procedures. Porewater nutrient concentrations (mg L^{-1}) of nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+) and phosphate (PO_4^{3-}) were determined using a Skalar SAN ++ SFA segmented flow analyser. Replicates were within 10% and recoveries for spiked samples were within 75–100% of expected values.

5.2.2.3 Organic matter degradation

Five Rapid Organic Matter Assessment (ROMA) plates were deployed at four sampling sites in the estuary and North Lagoon region (HC, PP, LP, NM) 11 days prior to the sampling, following a design by O’Meara et al. (2017). The ROMA plates have vertically-aligned columns of substrate-filled holes, and during the deployment period the consumption of the substrate within the holes has been found to be influenced by differences in redox conditions in marine sediments and vertical distributions of fauna (Hewitt et al. 1996; Thrush et al. 1996; Lohrer et al. 2010). The holes in the ROMA plates were initially filled with a substrate comprising a 0.029 g C/ml mixture of food grade agar, microcrystalline cellulose (CAS 9004-34-6; Thermofisher), and powdered bran. Ratios of these substrates were adapted from bait lamina recipes and optimized for estuarine ecosystems (O’Meara et al. 2017). After 11 days, ROMA plates were retrieved from the sediment and carbon consumption was measured by the change in agar volume in each hole on the ROMA plate following O’Meara et al. (2017). ROMA plates could not be used in the South Lagoon as the mixed substrate was not stable in salinities >80.

2.3 Selection of functional traits and trait information

To assess the relationship between benthic macrofauna functional traits and sediment biogeochemistry and nutrient concentrations, a set of six functional traits and 29 trait-modalities were selected (Table 5.1). The functional traits selected describe behavioural, morphological, and physiological attributes of the organisms, and are closely related to ecosystem functioning, such as nutrient cycling and sediment transport (Lam-Gordillo et al. 2020a). Trait information was obtained from the South Australia Macrobenthic Trait (SAMT) database (Lam-Gordillo et al. 2020b). The SAMT database applied a fuzzy coding procedure assigning scores from 0 to 1, with 0 being no affinity and 1 being high affinity to a trait (for details see Lam-Gordillo et al. 2020b).

5.2.4 Data analysis

5.2.4.1 Environmental data analysis

To test for differences in environmental variables between sites, univariate PERMutational ANalysis Of VAriance (PERMANOVA) and multiple pair-wise tests were conducted, using Euclidean distance and 9999 permutations for the single variables in PRIMER v7 with PERMANOVA+ add on software (Anderson et al. 2008). Environmental data were normalised prior to multivariate analysis (Clarke et al. 2014) and tested for collinearity. As no redundant environmental variables were identified, all variables were included in the analyses. Principal Component Analyses (PCA) were performed to explore spatial patterns in environmental conditions using the package "vegan" (Oksanen et al. 2019) in R software (R Core Team, 2018).

Table 5.1. List of the functional traits and traits-modalities selected based on their effect on nutrient cycling and sediment transport (Lam-Gordillo et al. 2020a). Acronyms are used in Figure 5.6.

Trait	Trait modalities	Acronym
Bioturbator	Biodiffusor	Bdiff
	Bioirrigator	Birri
	No bioturbation	Nbio
	Surface modifier	Sumo
Body size	Large (>20mm)	Lar
	Medium (5-20mm)	Med
	Small (0.5-5mm)	Sma
Feeding mode	Deposit feeder	Defe
	Filter/suspension	Fisus
	Grazer/scraper	Graz
	Omnivore	On
	Predator	Pred

	Scavenger/opportunist	Scav
	Sub-surface deposit feeder	Ssdf
Morphology	Hard	Hard
	Hard exoskeleton	Hexos
	Hard shell	Hshell
	Irregular	Irre
	Round	Rou
	Soft / Fragile	Fraso
	Vermiform	Verm
Living habit	Attached/Sessile	Att/S
	Burrower	Burr
	Free living / Surface crawler	Free
	Tube dwelling	Tudw
Sediment position	Attached	Att
	Bentho-pelagic	Bepel
	Deeper than 3cm	Deep
	Surface shallow <3cm	Sursh

5.2.4.2 Biological data analysis

Benthic macrofauna data were analysed for diversity (as species richness) and abundance (individuals per m^{-2}). Functional traits were analysed as community-level weighted means of trait values (CWM). CWM trait values were calculated using the package “FD” (Laliberté et al. 2014). Taxa abundance and CWM data were fourth root transformed prior to analyses. To assess community structure differences between sites, Principal Component Analysis (PCA) were performed for the benthic macrofauna and functional trait data with the package “vegan” (Oksanen et al. 2019). CWM and PCA were performed in R software (R Core Team, 2018). Differences across sites in species richness, abundance, community structure, and OM degradation (also testing for differences across depths) were analysed using PERMANOVA. For univariate tests for the single variables, the tests were based on Euclidean distance similarity and 9999 permutations. In addition, multiple pair-wise tests were conducted if the fixed factor (sites) was significant to identify which groupings contributed to differences from PERMANOVA main tests (Anderson et al. 2008).

To evaluate the relationship between benthic macrofauna and environmental conditions (porewater nitrate, nitrite, ammonium, phosphate and sediment OM, total carbon, total nitrogen, and total phosphorus), non-parametric multiple regressions were performed with the DISTLM routine, using Euclidean distances, 9999 permutations, and the macrobenthic fauna as predictor variables (McArdle and Anderson, 2001). PERMANOVAs, pair-wise tests, and DISTLM analyses were carried out using PRIMER v7 with PERMANOVA+ add on.

To assess relationships between benthic macrofauna, their functional traits, and sediment biogeochemistry and porewater nutrient concentrations (fourth corner analysis), several generalized linear latent variable models (GLLVMs) were performed with the R package “gllvm” (Niku et al. 2020). GLLVMs were constructed using the six most abundant taxa across sites, and a negative binomial distribution as the best fit model (lowest Akaike information criterion – AIC; Appendix D Table S3) (Niku et al. 2019). Level plots were performed for visualizing the interactions between taxa-traits and environmental conditions obtained with the GLLVMs using the R package “lattice” (Sarkar 2008).

5.3. Results

5.3.1 Environmental variables

The environmental variables were characterised by a strong spatial differentiation between sites in the Murray Estuary, North Lagoon and South Lagoon. Significant differences in environmental variables were found across sites (PERMANOVA $p<0.01$; Table 5.2; Figure 5.2; Appendix D Table S4). Extreme hypersaline conditions (salinity >80) were recorded at sites in the South Lagoon compared to the other sites (Figure 5.2a), while pH was more alkaline at PP, LP and NM compared to the other sites ($p<0.01$; Figure 5.2b; Appendix D Table S4). Sediment chlorophyll *a* content, as a proxy for microphytobenthic biomass, showed higher concentrations at two sites (HC and LP), while the other five sites were more homogeneous (Figure 5.2c). Sediment OM content was higher at sites in the South Lagoon (HG, JP, and SC) and lower in the North Lagoon (LP and NM) (Figure 5.2d). Sediment grain size was coarser and poorly sorted in the South Lagoon sites compared to the other sites (Figure 5.2e-f).

Table 5.2. Test results from univariate one-way fixed factor PERMANOVA to compare the environmental conditions and nutrient concentrations across sites. Significant *P* values are highlighted in bold.

Source	df	SS	MS	Pseudo-*F*	*P*(perm)
Chlorophyll *a* (mg.m^{-3})					
Site	6	30.027	5.004	11.132	**0.0001**
Residual	28	12.588	0.449		
Total	34	42.615			
Organic matter (%)					
Site	6	20.250	3.375	37.402	**0.0001**
Residual	28	2.530	0.090		
Total	34	22.800			
Median grain size (D50)					
Site	6	218000.000	36340.000	63.495	**0.0001**
Residual	28	16025.000	572.330		
Total	34	234000.000			
Sorting (σG)					
Site	6	5.219	0.869	1.484	0.1651
Residual	28	16.403	0.585		
Total	34	21.622			
pH					
Site	6	1.630	0.271	4.161	**0.0002**
Residual	28	1.820	0.065		
Total	34	3.450			
Salinity					
Site	6	43544.000	7257.300	2691.400	**0.0001**
Residual	28	75.500	2.696		
Total	34	43619.000			
Nitrate (mg.L^{-1})					
Site	6	0.655	0.109	6.734	**0.0001**
Residual	28	0.454	0.016		
Total	34	1.110			
Nitrite (mg.L^{-1})					
Site	6	0.085	0.014	1.503	**0.007**
Residual	28	0.266	0.009		
Total	34	0.352			
Ammonium (mg.L^{-1})					
Site	6	5.537	0.922	2.075	0.0439
Residual	28	12.454	0.444		
Total	34	17.991			
Phosphate (mg.L^{-1})					

Site	6	0.229	0.038	2.282	0.0182
Residual	28	0.468	0.016		
Total	34	0.697			
Total Nitrogen (% TN)					
Site	6	0.018	0.003	21.839	**0.0001**
Residual	14	0.002	0.001		
Total	20	0.020			
Total Carbon (% TC)					
Site	6	10860.000	181.000	285.180	**0.0001**
Residual	14	8.880	0.634		
Total	20	1094.900			
Carbon/Nitrogen (TC/NT)					
Site	6	734000.000	122000.000	102.520	**0.0001**
Residual	14	16706.000	1193.300		
Total	20	751000.000			
Total Phosphorus (mg /kg)					
Site	6	276000.000	45965.000	48.728	**0.0001**
Residual	14	13206.000	943.300		
Total	20	289000.000			

Porewater nitrate concentrations were greater at the Murray Estuary sites, decreasing towards the South Lagoon (Figure 5.2g). Although concentrations of nitrite followed a similar pattern as nitrate, nitrite concentrations were lower (Figure 5.2h). Porewater ammonium concentrations were higher at JP, SC in the South Lagoon and LP in the North Lagoon, with PP and LP significantly different compared to the other sites (p<0.01; Figure 5.2i; Appendix D Table S4). In contrast, porewater phosphate concentrations were similar across all sites (Figure 5.2j). Sediment total nutrient concentrations also varied significantly across sites (p<0.01; Table 5.2; Figure 5.2k-n). Total nitrogen, total carbon and carbon/nitrogen ratio followed the same pattern, with the highest concentrations recorded at sites in the South Lagoon (HG, JP, and SC), and decreasing concentrations from sites in the Murray Estuary towards the sites at the North Lagoon (Figure 5.2k-m). Concentrations of total phosphorus were highest at HC, decreasing towards NM, but increasing again at the South Lagoon sites (Figure 5.2n).

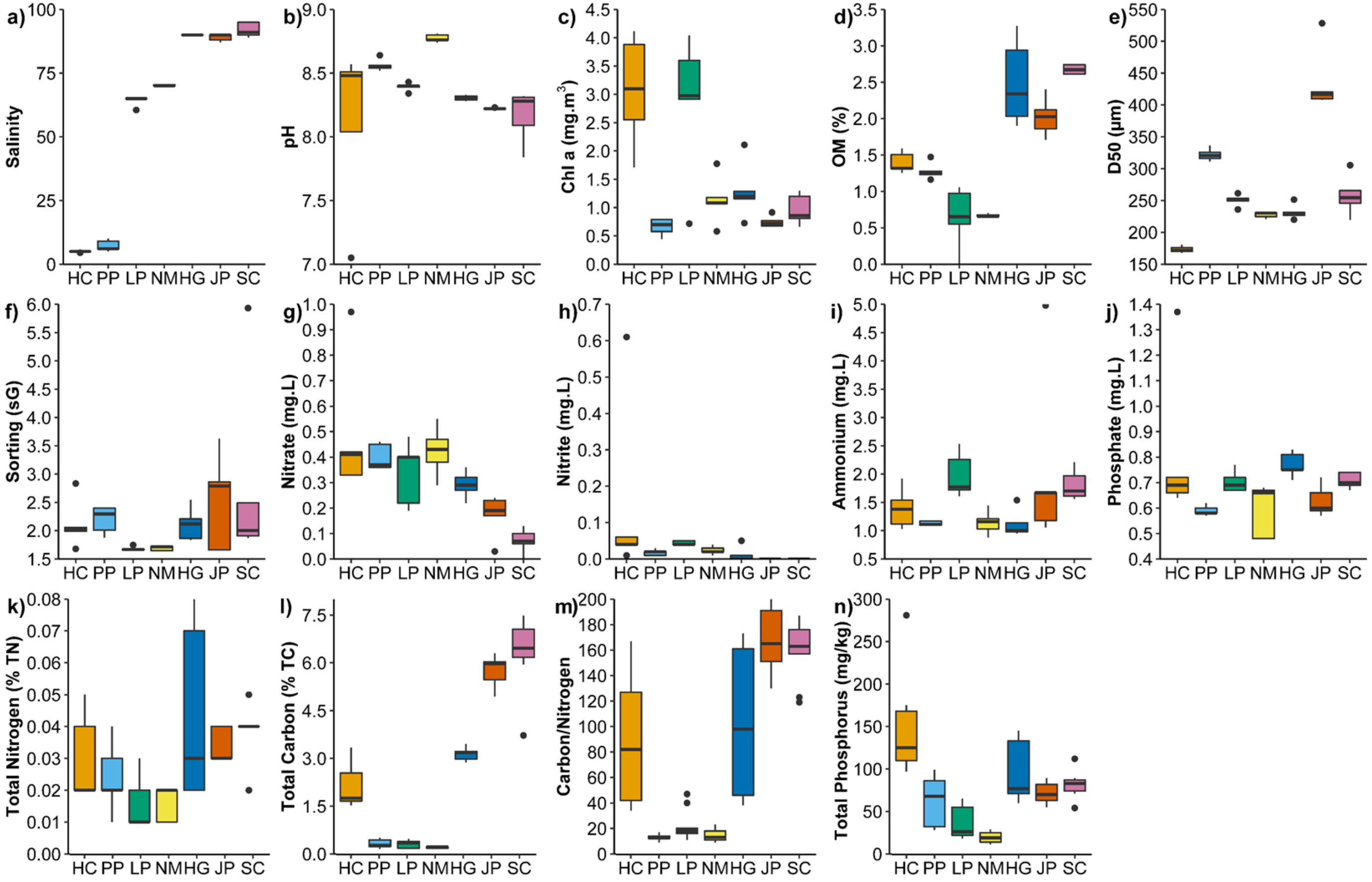


Figure 5.2. Boxplots of the environmental variables recorded in the Coorong across sampling sites. Water column (n=5) (a) salinity and (b) pH. Sediment (n=5) (c) chlorophyll *a*, (d) organic matter content (OM), (e) mean grain size (D50), and (f) sorting coefficient. Pore water (n=5) concentrations of (g) nitrate, (h) nitrite, (i) ammonium, and (j) phosphate. Sediment (n=3) total concentrations of (k) nitrogen, (l) carbon, (m) carbon/nitrogen, and (n) phosphorus. HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

The PCA analyses revealed distinct spatial variation of the Coorong porewater nutrient concentrations and water column variables, as well as sediment variables with 58.4% and 82.8% of variability explained by the first two axes respectively (Figure 5.3). Based on porewater nutrient concentrations, and sediment and water column variables, sites in the South Lagoon were separated from the other sites by salinity, organic matter content, sediment grain size and ammonium.

Although less evident, sites in the Murray Estuary and North Lagoon were also differentiated, mainly by high concentrations of chlorophyll *a* at HC, and the more alkaline pH recorded at NM. Yet, large amount of variation was unexplained (Figure 5.3a). Based on sediment variables, sites were separated according to their region: Murray Estuary (HC and PP), North Lagoon (LP and NM), and South Lagoon (HG, JP, and SC), with conductivity and total carbon as the main drivers (Figure 5.3b).

5.3.2 Macrobenthic fauna composition

In total, 17 taxa were recorded across seven sites in the Coorong. The taxa richness recorded between sites was significantly different (PERMANOVA $p<0.01$; Table 5.3), with significantly higher taxa richness at HC, PP, LP and NM compared to the three sites in the South Lagoon which contained almost no benthic macrofauna ($p<0.01$; Appendix D Figure S1a). In terms of overall lagoonal benthic macrofauna abundance, Crustacea was the taxon with the greatest abundance (62.5%), followed by Bivalvia (21.1%) and Annelida (9.3%) (Figure 4a).

The total abundance of macrofauna individuals was significantly different across sites (PERMANOVA $p<0.01$; Table 5.3). Individual densities at HC PP, and LP were >100,000 ind.m^2, and significantly higher compared to the other four sites, NM with less than 30,000 ind.m^2, and HG, LP, and SC with less than 3,000 ind.m^2 ($p<0.01$; Figure 5.4b; Appendix D Figure S1b).

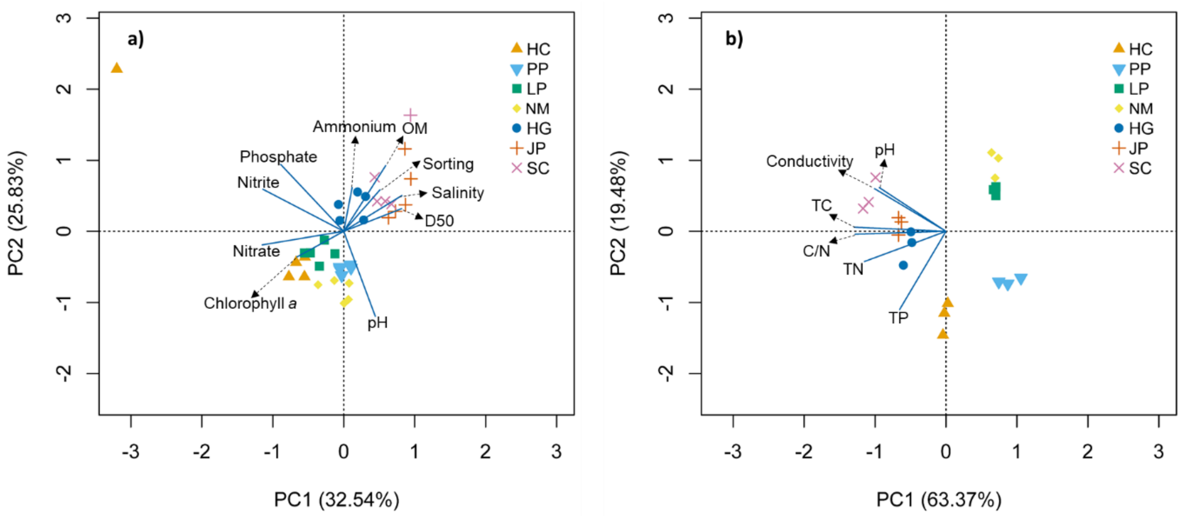


Figure 5.3. Principal Component Analysis (PCA) plots for the environmental conditions measured across the seven sampling sites in the Coorong. a) Porewater nutrients and water quality variables; n=5, b) sediment variables; n=3. Black arrows point out origins of the labels to avoid overlaps. HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

Table 5.3. Test results from univariate one-way fixed factor PERMANOVA to compare number of taxa (richness) and abundance of macrobenthic fauna across sampling sites. Significant *P* values are highlighted in bold.

Source	df	SS	MS	Pseudo-*F*	*P*(perm)
Number of taxa (Richness)					
Site	6	197.09	32.848	52.258	**0.0001**
Residual	28	17.60	0.628		
Total	34	214.69			
Abundance (ind.m^{2})					
Site	6	2.19E+11	3.65E+10	42.178	**0.0001**
Residual	28	2.42E+10	8.66E+08		
Total	34	2.43E+11			

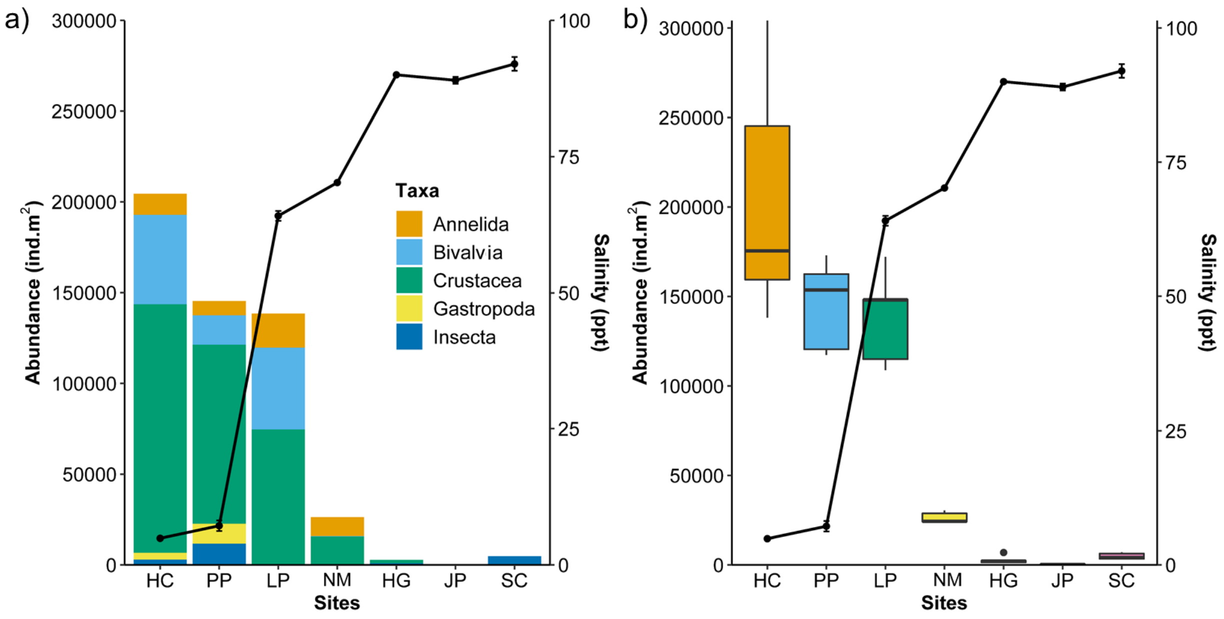


Figure 5.4. Mean (n=5) total abundance of benthic macrofauna (a) stacked bar graph by taxa and (b) box plot of all taxa pooled across each of the seven sampling sites in the Coorong. Black line shows the salinity at each sampling site. Error bars for salinity show the standard error (SE). HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

5.3.3 Functional traits composition

The functional traits and their modalities (as CWM) varied significantly across all sites in the Coorong (Table 5.4). In general, sites in the Murray Estuary (HC and PP) and North Lagoon (LP and NM) were more similar to each other compared to the sites in the South Lagoon (HG, JP, and SC) (Figure 5.5). In pairwise comparisons, significant differences in CWM trait modalities across sites were also identified (PERMANOVA $p<0.01$; Appendix D Figure S2-S7). The expression of several functional trait modalities was similar across sites in the Murray Estuary and North Lagoon. In contrast, some trait modalities were absent at sites in the South Lagoon. For example, ‘biodiffussor’, bioirrigator’ and ‘surface modifier’ were significantly higher at sites in the Murray Estuary and North Lagoon, but almost non-existent at sites in the South Lagoon, where ‘no bioturbator’ was the main trait expressed ($p<0.01$; Figure 5.5a; Appendix Figure S2). ‘Large’ body size was only recorded in Murray estuary and North Lagoon sites, while ‘medium’ body size was significantly higher at JP and SC sites in the South Lagoon compared to the other sites ($p<0.01$; Figure 5.5b; Appendix D Figure S3).

Table 5.4. Summary of the test results from univariate one-way fixed factor PERMANOVA to compare functional trait modalities across sampling sites. NC: No computed. Significant *P* values are highlighted in bold.

Trait	Trait modality	Pseudo-F	P value	Permutations
Bioturbator	Biodiffusor	42.568	**0.0001**	9946
	Bioirrigator	195.570	**0.0001**	9955
	No bioturbation	3375.40	**0.0001**	9913
	Surface modifier	282.060	**0.0001**	9945
Body size	Large (>20mm)	105.030	**0.0001**	9946
	Medium (5-20mm)	15.744	**0.0001**	9952
	Small (0.5-5mm)	12.620	**0.0001**	9943
Feeding mode	Deposit feeder	95.299	**0.0001**	9960
	Filter/suspension	17.619	**0.0001**	9946
	Grazer/scraper	11.973	**0.0001**	9941
	Omnivore	NC	NC	NC
	Predator	1.088	0.3735	9945
	Scavenger/opportunist	26.874	**0.0001**	9939
	Sub-surface deposit feeder	319.350	**0.0001**	9949
Living habit	Attached/sessile	NC	NC	NC
	Burrower	614.040	**0.0001**	9948
	Free living / Surface crawler	724.460	**0.0001**	9952
	Tube dwelling	38.939	**0.0001**	9943
Morphology	Hard	NC	NC	NC
	Hard exoskeleton	NC	NC	NC
	Hard shell	9.853	**0.0001**	9933
	Irregular	299.160	**0.0001**	9947
	Round	10.034	**0.0001**	9951
	Fragile/Soft	9.196	**0.0001**	9945
	Vermiform	47.164	**0.0001**	9948
Sediment position	Attached	NC	NC	NC
	Bentho-pelagic	1116.200	**0.0001**	9951
	Deeper than 3cm	52.144	**0.0001**	9949
	Surface shallow <3cm	1447.000	**0.0001**	9947

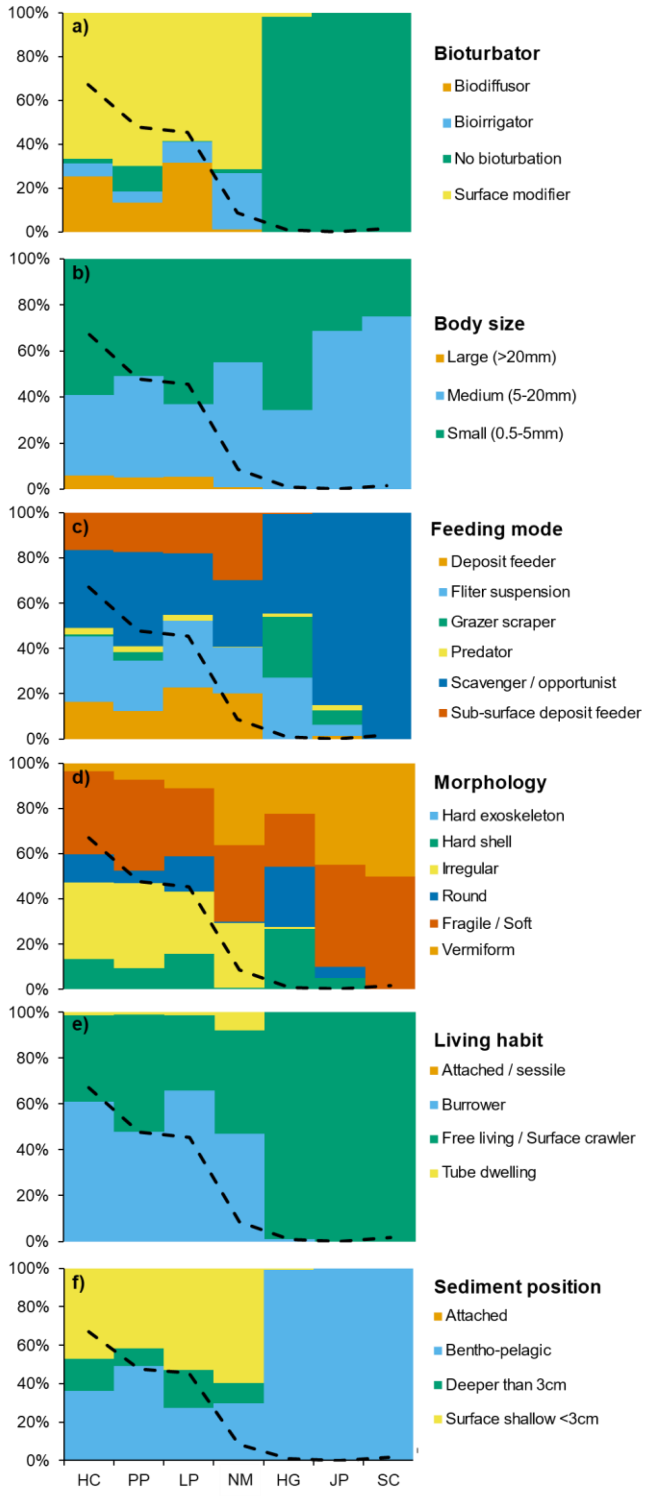


Figure 5.5. Community-weighted means (CWM) of functional trait-modalities expression. Scale represents the percentage contribution to CWM recorded in the Coorong across sampling sites. Black dotted line shows the relative abundance to the maximum abundance recorded. HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

In terms of feeding mode, sites in the South Lagoon were mainly dominated by 'scavengers/opportunistic', however HG, JP, and SC were not significantly different to the other sites (*p*<0.01; Figure 5.5c; Appendix D Figure S4). 'Irregular' and 'vermiform' modalities were significantly different across the majority of the sites, while the other morphological trait modalities were more similar across sites. (*p*<0.01; Figure 5.5d; Appendix Figure S5). The functional trait modalities 'burrower' and 'tube dwelling' were significantly higher at sites in the Murray Estuary and North Lagoon compared to the sites at the South Lagoon, while 'free living/surface crawler' was the only trait modality recorded at sites in the South Lagoon (*p*<0.01; Figure 5.5e; Appendix Figure S6). Sediment position showed a similar pattern to living habit, with the modalities 'deeper than 3 cm' and 'surface shallow (<3 cm)' significantly higher at sites in the Murray Mouth and North Lagoon compared to the sites in the South Lagoon, while 'bentho-pelagic' was the unique modality recorded at the South Lagoon sites (*p*<0.01; Figure 5.5f; Appendix Figure S7).

Across the entire Coorong, the macrobenthic functional trait modalities which were most expressed, in terms of community-level weighted means (CWM), were scavenger-opportunistic (Feeding Mode; contribution: 51.8%), medium size (5-20 mm) (Body Size; contribution: 48.9%), free living (Living Habit; contribution: 66.5%), no bioturbator (Bioturbation; contribution: 44.9%), bentho-pelagic (Sediment Position; contribution: 63.1%), and 'fragile-soft' Morphology with a contribution of 37.0% (Table 5.5).

Table 5.5. Total CWM contribution of functional traits and their modalities across sampling sites. Highest contribution shown in bold.

Trait	Trait modality	CWM trait contribution
Bioturbator	Biodiffusor	10.19
	Bioirrigator	6.63
	No bioturbation	**44.86**
	Surface modifier	38.31
Body size	Large (>20mm)	2.51
	Medium (5-20mm)	**48.95**
	Small (0.5-5mm)	48.55
Feeding mode	Deposit feeder	10.36

	Filter/suspension	19.03
	Grazer/scraper	5.39
	Omnivore	0.00
	Predator	1.78
	Scavenger/opportunist	**51.77**
	Sub-surface deposit feeder	11.68
Living habit	Attached/sessile	0.00
	Burrower	31.76
	Free living / Surface crawler	**66.55**
	Tube dwelling	1.69
Morphology	Hard	0.00
	Hard exoskeleton	0.00
	Hard shell	10.11
	Irregular	18.36
	Round	9.43
	Fragile/Soft	**37.01**
	Vermiform	25.10
Sediment position	Attached	0.00
	Bentho-pelagic	**63.08**
	Deeper than 3cm	8.07
	Surface shallow <3cm	28.84

5.3.4 Macrobenthic and functional traits structure

Significant community differences were identified across sites for both taxa and functional traits (PERMANOVA $p<0.01$, Table 5.6). The PCA analysis revealed different structures across sites with 49.4% of the variability explained by the first two axes in taxa composition, and 83.3% of the variability explained by the first two axes in trait composition (Figure 5.6). Based on taxa, sites were separated according to region Murray Estuary (HC and PP), North Lagoon (LP and NM), and South Lagoon (HG, JP, and SC). Sites in the South Lagoon were grouped together by a dominance of benthic insect larvae, North Lagoon sites LP and NM grouped mainly by Capitellidae, and Murray Estuary sites HC and PP by the snails *S. fragilis* and Hydrobiidae (Figure 5.6a). The majority of the sites were significantly different to each other, except HG to JP, and JP to SC ($p<0.01$; Appendix D Figure S8a). Although less evident, a separation between sites was also identified based on functional traits, HC, PP and

LP were significantly more similar to each other, while sites in the South Lagoon were differentiated from the other sites by the trait modalities ‘no bioturbation’, ‘free living’, ‘bentho-pelagic’, ‘scavenger’ and ‘grazer’ (Figure 5.6b; Appendix D Figure S8b).

Table 5.6. Test results from univariate one-way fixed factor PERMANOVA to compare macrobenthic community structure based on taxa and functional traits across sampling sites. Significant *P* values are highlighted in bold.

Source	df	SS	MS	Pseudo-*F*	*P*(perm)
Community Taxa					
Site	6	69634.0	11606.00	29.59	**0.0001**
Residual	28	10982.0	392.23		
Total	34	80617.0			
Traits					
Site	6	42000.0	6990.00	19.50	**0.0001**
Residual	28	10000.0	358.61		
Total	34	52000.0			

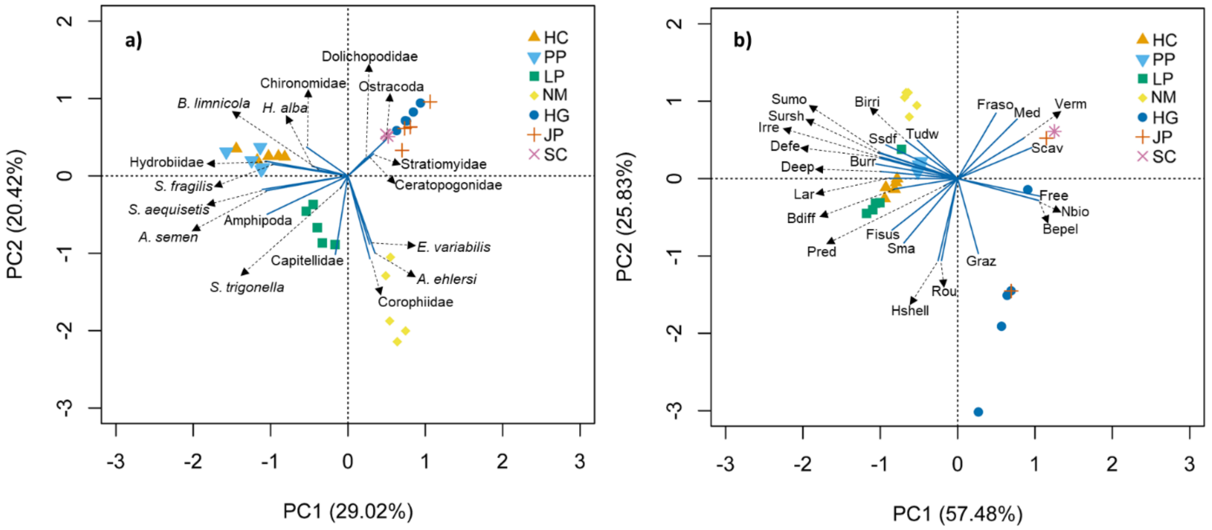


Figure 5.6. Principal Component Analysis (PCA) plots for benthic communities based on the taxonomic (a) and trait (b) composition across sampling sites. Black arrows point out origins of the labels to avoid overlap. HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek. Labels (acronyms) in panel b) are defined in Table 5.1.

3.5 Relationships between macrobenthic fauna functional traits and porewater nutrient concentrations, sediment biogeochemistry and organic matter degradation

DISTLM analyses revealed relationships between benthic macrofauna, mainly Capitellidae, *S. aequisetis, A. semen, H. alba,* and Amphipoda, and the concentrations of porewater nutrients and sediment variables (Table 5.7; Figure 5.7). Porewater concentration of nitrate was correlated with the abundance of *S. aequisetis, A. semen,* and Amphipoda (Table 5.7), showing low concentrations of nitrate when low abundance of macrobenthic fauna was recorded (Figure 5.7a). Concentrations of nitrite in porewater followed a similar pattern to nitrate, being greater when high abundance of macrobenthic fauna was recorded (Figure 5.7b), suggesting that the concentrations of nitrite were also influenced by *S. aequisetis, A. semen, H. alba,* and Amphipoda (Table 5.7). Porewater ammonium and phosphate concentrations were not significantly correlated to the benthic macrofauna (p>0.01). However, for ammonium an opposite pattern compared to nitrate and nitrite was identified with concentrations increasing from sites in the Murray Estuary towards sites in the South Lagoon (Figure 5.7c), while phosphate concentrations were very similar across all sites (Figure 5.7d). Sediment OM content showed an inverse relationship with the abundance of the benthic macrofauna (Table 5.7). OM was lower when the abundance of benthic macrofauna increased (Figure 5.7e). Total carbon was significantly correlated with Capitellidae, *S. aequisetis, A. semen,* and Amphipoda (Table 5.7), with sediment total carbon decreasing with increasing abundance of benthic macrofauna (Figure 5.7f). Sediment total nitrogen also showed a significant correlation of lower concentration at higher abundances of macrobenthic fauna (Capitellidae, *E. variabilis,* Corophiidae and Amphipoda) (Figure 5.7g). Sediment total phosphorus content was also correlated to the abundance of benthic macrofauna (Table 5.7), being highest at both high and low macrobenthic fauna abundances and lowest at intermediate abundances (Figure 5.7h).

Significant relationships were identified between the benthic macrofauna, their functional traits, and porewater nutrient and sediment variables (Figure 5.8). Across all seven sites surveyed, we identified stronger relationships between functional traits and porewater nutrients than with sediment variables and functional traits relationships. Sites at the Murray Estuary (HC and PP) showed strong correlation of various functional traits to nitrate, nitrite, sediment OM, and total phosphorus contents. For example, the trait modalities ‘bioirrigator’, ‘deposit feeder’, ‘scavenger’, ‘sub-surface deposit feeder’, and ‘surface shallow <3 cm’ were correlated to porewater nitrite concentration and sediment OM content (Figure 5.8a-b).

Table 5.7. Result of DISTLM forward analysis. Only significant ($p<0.01$) results are shown.

Variable	R^2	SS (trace)	Pseudo-*F*	P-value	Proportion
All	0.63				
Capitellidae		43.306	4.817	0.0004	0.127
Simplisetia aequisetis		64.435	7.716	0.0001	0.190
Arthritica semen		64.258	7.690	0.0001	0.189
Hiatula alba		45.445	5.091	0.0046	0.134
Amphipoda		81.150	10.346	0.0001	0.239
Nitrate	0.68				
Simplisetia aequisetis		0.312	12.929	0.0008	0.282
Arthritica semen		0.294	11.896	0.0009	0.265
Amphipoda		0.428	20.748	0.0001	0.386
Nitrate	0.44				
Simplisetia aequisetis		0.036	3.772	0.0004	0.103
Arthritica semen		0.038	3.963	0.0004	0.107
Hiatula alba		0.124	17.911	0.0093	0.352
Amphipoda		0.030	3.042	0.0031	0.084
Organic matter	0.92				
Capitellidae		14.473	57.516	0.0001	0.635
Euchone variabilis		4.969	9.209	0.0035	0.218
Simplisetia aequisetis		7.522	16.273	0.0006	0.330
Arthritica semen		7.916	17.577	0.0003	0.348
Amphipoda		13.367	46.875	0.0001	0.587
Corophiidae		7.775	17.102	0.0003	0.341
Ostracoda		4.813	8.842	0.0039	0.211
Total Carbon	0.97				
Capitellidae		657.270	28.535	0.0002	0.600
Simplisetia aequisetis		434.750	12.512	0.0021	0.397
Arthritica semen		418.660	11.763	0.0041	0.382
Amphipoda		741.680	39.895	0.0001	0.677
Total Nitrogen	0.97				
Capitellidae		0.015	64.905	0.0001	0.774
Euchone variabilis		0.006	8.027	0.0086	0.297
Amphipoda		0.009	14.935	0.0014	0.440
Corophiidae		0.008	11.736	0.0015	0.382
Total Phosphorus	0.98				
Capitellidae		183400.000	33.001	0.0001	0.635
Euchone variabilis		89584.000	8.535	0.0096	0.310
Hiatula alba		127250.000	14.948	0.0052	0.440
Corophiidae		109220.000	11.543	0.0043	0.378

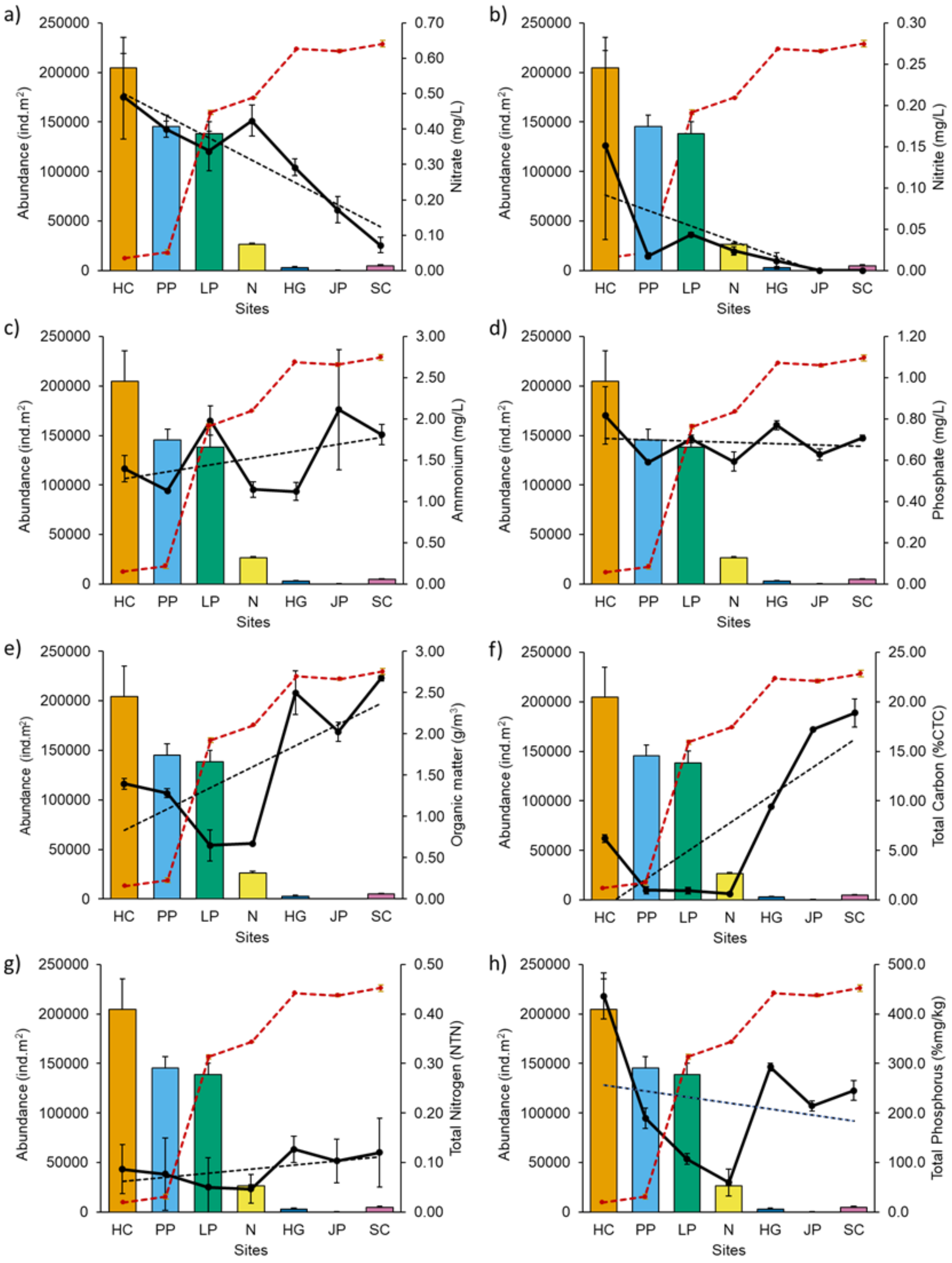


Figure 5.7. Bar graphs showing the mean total abundance of benthic macrofauna in relation to (a-d) pore water nutrient concentrations, and (e-h) sediment variables across sampling sites. Error bars show the standard error (SE). Dotted lines show the trend line of each variable. For reference the red dotted lines show the relative salinity pattern, but the scale is not shown (refer Figs. 1 and 2). HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

At sites in the North Lagoon (LP and NM), trait modalities of bioturbator, body size and sediment position were the most correlated to porewater nitrite concentration, and sediment OM, chlorophyll-*a*, total carbon and total nitrogen contents (Figure 5.8c-d). Sites in the South Lagoon (HG, JP, and SC) showed fewer and lower correlations between functional traits, porewater nutrient concentrations and sediment conditions. The trait modalities 'no bioturbation', 'medium' body size, 'free living' and 'bentho-pelagic' were the most correlated to porewater phosphate, and sediment OM and chlorophyll-*a* content (Figure 5.8e-g).

Sediment OM degradation rates at the Murray Estuary and North Lagoon sites, determined using ROMA plates, differed significantly across sites and depths within sites (Table 5.8). Sites at the Murray Estuary (HC and PP) showed higher OM degradation rates compared to sites in the North Lagoon (LP and NM) (Figure 5.9). Degradation rates in HC were significantly higher in the 1-3 cm depth horizon compared to other depths ($p < 0.01$; Appendix D Table S5). At PP, degradation rates followed a similar pattern to those at HC, but the 4-7 cm depth horizon was also significantly different to the 16-19 cm horizon ($p < 0.01$; Appendix D Table S5). LP and NM showed similar OM degradation rates across depths ($p > 0.01$; Appendix D Table S5). Similar degradation rates were found at HC compared to PP, and LP compared to NM ($p > 0.01$; Appendix D Table S6). The OM degradation rates at sites in the Murray Estuary were significantly different compared to sites in the North Lagoon in the 1-3 cm depth horizon ($p < 0.01$; Appendix D Table S6). Significant differences were also found at HC and PP compared to LP in the 4-7 cm depth horizon, and at PP compared to LP and NM in the 16-19 cm depth horizon ($p < 0.01$; Appendix D Table S6).

Table 5.8. Test results of univariate one-way fixed factor PERMANOVA comparing organic matter degradation rates determined using ROMA plates across the four sampling sites in the Murray Estuary (Hunters Creek, Pelican Point) and North Lagoon (Long Point, Noonameena). Significant *P* values are highlighted in bold.

Source	df	SS	MS	Pseudo-*F*	P(perm)
Site	3	0.033	0.011	14.878	**0.0001**
Depth	4	0.055	0.014	18.832	**0.0001**
Site × Depth	12	0.043	0.003	4.847	**0.0001**
Residual	80	0.059	0.001		
Total	99	0.190			

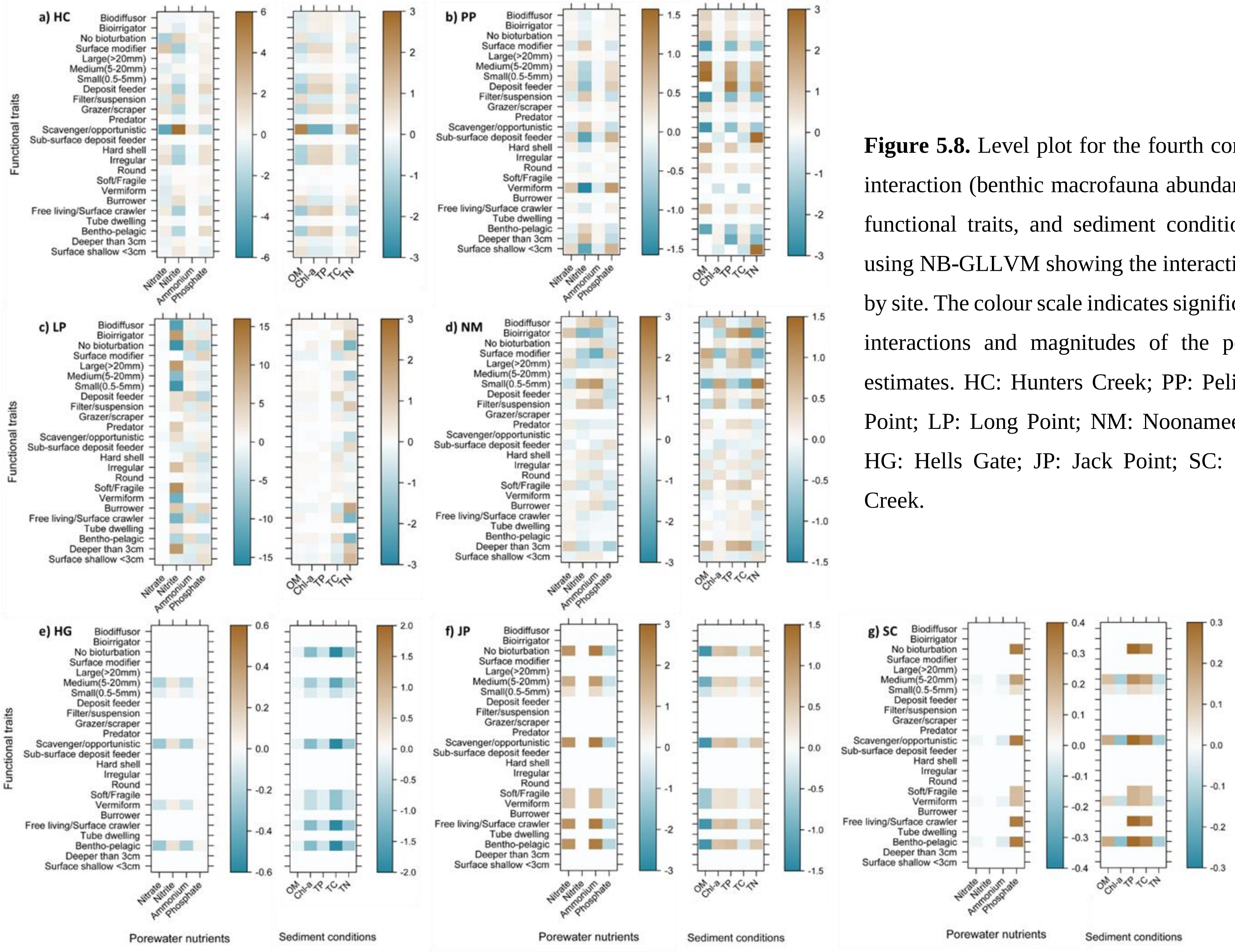


Figure 5.8. Level plot for the fourth corner interaction (benthic macrofauna abundance, functional traits, and sediment conditions) using NB-GLLVM showing the interactions by site. The colour scale indicates significant interactions and magnitudes of the point estimates. HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

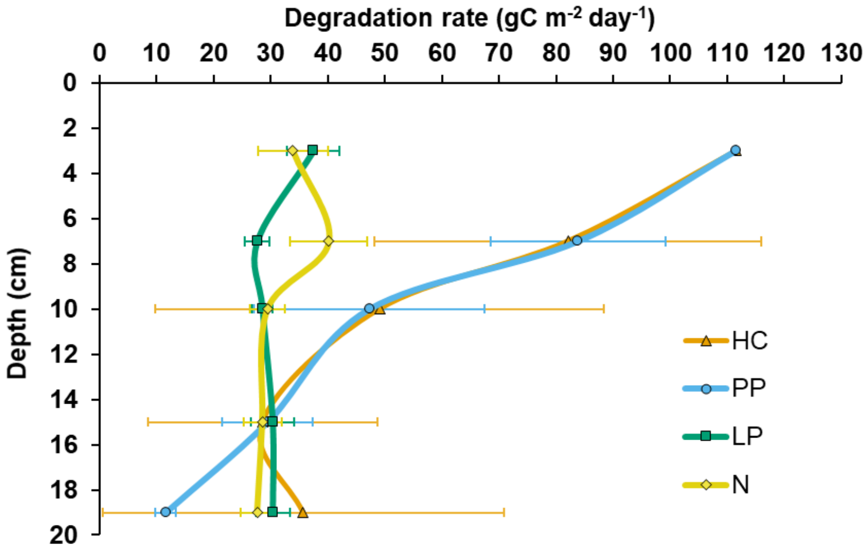


Figure 5.9. Organic matter degradation rate across depths and sites in the Coorong, based on Rapid Organic Matter Assessment (ROMA) plates. Data points indicate mean values (n = 5) and error bars show the standard error (SE) HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena.

5.4. Discussion

In this study, we analysed benthic macrofauna communities, their functional traits, and the relationships between these biotic components, porewater dissolved and sediment total nutrients in the Coorong lagoon system along a salinity gradient from estuarine-to-hypersaline conditions. Our results revealed significantly different benthic communities and functional traits across the sampling sites mainly mediated by the extreme salinity gradient. Macrobenthic functional trait relationships with dissolved and solid phase nutrients suggested variation in sediment biogeochemistry and nutrient concentrations correlated with these biotic components, that in turn could enhance different ecosystem functioning across this system.

In accordance with our first hypothesis, we found that the extreme salinity gradient in the system strongly influenced the benthic macrofauna, delimitating their presence/absence, community structure, and therefore expression of functional traits, consistent with previous studies in the system (Dittmann et al. 2015; 2018). Despite the differences in macrobenthic communities and functional traits found across the entire system and between regions, communities and traits were similar within each of the regions. Benthic macrofauna community richness and abundance were higher within the Murray Estuary region (sites HC and PP), where salinity was typically brackish to marine due to freshwater inputs from the River Murray-Lower Lakes. Abundance decreased in the North Lagoon (sites LP and NM; salinity 50-70), and the lowest benthic macrofauna richness and abundances were found at the South Lagoon sites (HG, JP, and SC), where hypersaline (89-92) conditions were recorded. This pattern of decreasing benthic macrofauna, in terms of both abundance and richness, was attributed to the salinity tolerance of the organisms that inhabit the system, with bivalves, crustaceans, gastropods, and polychaetes occurring at salinities <60 ppt, while only insect larvae were found in hypersaline conditions in the South lagoon (Dittmann et al. 2015; Remailli et al. 2018).

Functional traits were site-dependent, and attributed to changes in both benthic macrofauna and habitat conditions; a finding commonly reported in other systems (e.g. Douglas et al. 2019; Gammal et al. 2019; Henseler et al. 2019; Villnäs et al. 2019). The differences identified in functional traits followed a similar pattern as the taxonomic composition, with higher expression of trait modalities at the Murray Estuary sites, and the lowest recorded in the South Lagoon sites. However, the multivariate structure of the functional trait composition showed similarities in trait expression at HC, PP and LP, NM distinct from trait compositions in from other sites, and the South Lagoon sites grouping together, indicating that the functional traits at the study sites were more homogenous than the taxonomic composition, similar to findings reported in other studies (e.g. Wong and Dowd 2015; Henseler et al. 2019; Lam-Gordillo et al. 2021).

Sediment biogeochemistry and porewater nutrients changed across the system, showing significant differences between sites and regions, which concurred with the extreme salinity gradient. We found indications that these differences were correlated with the benthic macrofauna (abundance, community structure) and their functional traits, as frequently described in other studies (e.g. Braeckman et al. 2014; Villnäs et al. 2019; Bon et al. 2021). For example, sites in the Murray Estuary and North Lagoon regions showed the highest porewater concentrations of nitrate and nitrite, which coincided with the highest abundance of benthic macrofauna dominated by burrowing and bioturbating taxa, particularly the polychaete *Simplisetia aequisetis*. This implies that these macrobenthic organisms could influence sediment nutrient cycling, which aligned with our second prediction. Benthic macrofauna have been shown to increase rates of total dissolved inorganic nitrogen export from the sediment to the overlying water (see Stief 2013 for review), which would decrease porewater ammonium concentrations due to increased ammonium loss. Macrofauna can also stimulate rates of bacterial nitrification, a biological sink for ammonium and source of nitrite and nitrate, and rates of denitrification, which is a sink for nitrate and a source or sink for nitrite, favouring benthic nitrogen loss as gaseous end-products via coupled nitrification-denitrification (Welsh 2003; Stief 2013; Norkko et al. 2019; Wyness et al. 2021). This is proposed to occur by promoting sediment oxygenation, which is correlated to the trait ‘bioturbation’, i.e. as the burrow wall sediments increase the volume of oxic sediments, where nitrification can occur, the total surface area of oxic-anoxic interfaces increases and denitrification is enhanced by up to several fold (Kristensen 2000; Welsh 2003; Stief 2013). Thus, the presence of active nitrification within the sediments lining macrofaunal burrows would tend to increase average porewater nitrite and nitrate concentrations, as these solutes would accumulate within the oxic sediment layer and this effect would increase with increasing macrofauna abundance, as the relative volume of burrow wall sediments increased (Welsh 2003; Stief 2013). In the Coorong, the presence of macrofauna burrows in the Murray Estuary and North Lagoon sediments favoured lower porewater ammonium concentrations due to increased rates of conversion of ammonium to nitrite and nitrate via nitrification, and the diffusion of porewater ammonium in and outside the burrow by bioirrigation (Welsh 2003; Stief 2013). These results align with a long-term mesocosm experiment using the Thalassinidean shrimp (*Trypaea australiensis*), which reported a decrease in sediment ammonium content compared to the sediment control, as well as stimulated nitrification rates and ammonium effluxes to the water column (Jordan et al. 2009).

At sites in the South Lagoon, the absence of burrowing and bioturbating macrofauna, and thereby oxic burrow wall sediments where nitrification could occur, resulted in lower average pore water nitrate and nitrate concentrations, and is likely to have contributed to the higher porewater concentrations of ammonium recorded at these sites. The absence of faunal burrows would favour accumulation of ammonium in the sediment porewater due to decreased conversion of ammonium to nitrite and nitrate, and decreased ammonium efflux to the water column, as diffusive exchange between the sediment and overlying water would be limited to the sediment surface (Welsh 2003; Stief 2013). However, no significant correlation between ammonium, phosphate and the macrobenthic abundance was found, which could be explained by other processes occurring in the lagoon, such as aquatic plants uptake (*Ruppia sp.*), eutrophication, and high sulfate reduction (Mosley et al. 2020).

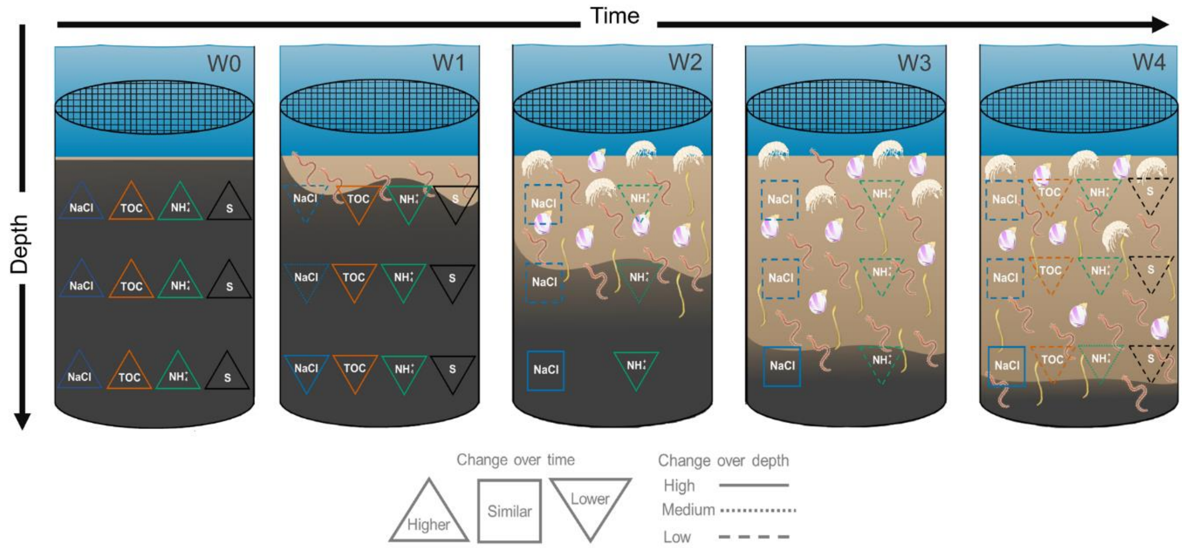
In the Coorong sediments, the modern OM deposited and degraded was consistent with an algal (phytoplankton-derived) source based on C and N isotope and ^{13}C NMR techniques (Krull et al. 2008). Differences in sediment OM content and total carbon (% TC) also corresponded with differences in the benthic macrofauna, with a general increase in sediment OM and total carbon with decreasing benthic macrofauna abundance. Lower sediment OM contents were found in the Murray Estuary and North Lagoon, correlated with benthic macrofauna performing bioturbating and burrowing activities (e.g. *A. semen*, *Capitella sp.*, *S. aequisetis*), but were also in concordance with the high expression of the functional trait modalities 'deposit feeder', 'filter suspension' and 'sub-surface deposit feeder'. It has been suggested that high abundance of biodiffuser and biorrigator fauna traits in combination with other feeding modes enhance microbial activities which are ultimately responsible for OM remineralisation, therefore promoting nutrient cycling (Welsh 2003; Braeckman et al. 2014; Villnäs et al. 2019; Bon et al. 2021). For example, organisms which inhabit burrows are proposed to influence OM degradation rates by increasing oxygen transfer to the sediment and the overall volume of oxic sediment by irrigating their burrows with the overlying water (Kristensen 2000; Welsh 2003). Bioturbation by organisms can influence OM degradation rates by physically transporting organic particles between sediment redox zones, resulting in decomposition occurring under alternating oxic-anoxic conditions (Aller 1994). However, this could be also correlated to a eutrophication gradient, with lower OM content in water and consequently lower OM loads to the sediment, as previously suggested in another system (Grebmeier et al. 1988).

In contrast, higher sediment OM and total carbon contents were recorded at sites in the South Lagoon, which is consistent with the low abundance and low taxonomic and functional trait diversity present in this region. The macrobenthic communities at sites in the South Lagoon consisted of low abundances of primarily of small sized insect larvae with free living/surface crawler living habit. Thus, these communities would only have limited interaction with the sediment and little, if any, influence on oxygen availability in the deeper sediments. Thus, aerobic sediment zones were largely limited to the sediment surface and dependent upon diffusion of oxygen from the overlying water. Consequently, the bulk of the sediment OM would be permanently buried in anoxic sediment layers, where OM mineralisation rates are low (Kristensen 2000) favouring OM accumulation. The findings suggesting that sediment OM content correlated with macrofauna communities by stimulating OM mineralisation rates was also supported by our *in situ* determinations of OM degradation rates using the ROMA plates technique at the Murray Estuary and North Lagoon sites, indicating that higher organic matter degradation rates in surface sediments occurred when bioturbating and burrowing macrobenthic abundance is greater. Laboratory and/or field transplantation experiments would be beneficial to better establish causal links between macrobenthic fauna, organic matter and nutrient cycling processes in the Coorong.

5.5. Conclusion

Changes in benthic macrofauna abundance and functional trait composition across sites and regions were mainly determined by the extreme salinity gradient in the Coorong, and corresponded with changes in the sediment biogeochemistry. Differences in nutrient and organic matter patterns across the system were highly correlated with changes in macroinvertebrate diversity, abundance and functional traits. The high abundance and diversity of benthic macrofauna in the Murray Estuary and North Lagoon regions correlated with lower sediment concentrations of total nitrogen and total carbon, higher concentrations of oxidised nitrogen species (nitrate and nitrite) in porewater, and higher carbon mineralisation rates. In contrast, in the hypersaline South Lagoon larger bioturbating macrobenthic organisms were absent, and the loss of these organisms appeared to result in reduced nutrient and organic matter processing, which could favour eutrophication conditions. This limited ecosystem functioning has likely had serious implications for management and conservation as the Coorong is now experiencing major issues with persistent and large-scale algal blooms. Further process-based research (e.g. using mesocosms and/or *in situ* experiments) would be beneficial to confirm the links between benthic ecosystem function and sediment quality along the Coorong. The research highlights the importance of preserving benthic communities for improving resilience to eutrophication issues, and to ensure healthy functioning of estuarine benthic ecosystems.

Chapter 6. Restoration of benthic macrofauna promotes biogeochemical remediation of hostile sediments; an *in situ* transplantation experiment in a eutrophic estuarine-hypersaline lagoon system



This chapter has been submitted to the journal Science of the Total Environment, and is currently under review.

Author contributions

Orlando Lam Gordillo: Conceived the ideas and developed the outline for the manuscript, designed the methodology, collected the data, analysed the data, prepared the figures and tables, wrote the manuscript and corresponding author.

Sabine Dittmann – primary supervisor: Guidance on the project development, acquisition of funding, discussion of project ideas, and contribution to drafting manuscript and critical refinement.

Jianyin Huang: Support performing the DGT/DET techniques, discussion of project ideas, and contribution to drafting manuscript.

Andrea Barcelo: Support collecting the data, discussion of project ideas, and contribution to drafting manuscript.

Jordan Kent: Support collecting the data, discussion of project ideas, and contribution to drafting manuscript.

Luke Mosley: Discussion of project ideas, acquisition of funding, and contribution to drafting manuscript.

Stuart Simpson: Discussion of project ideas and contribution to drafting manuscript.

David Welsh: Discussion of project ideas and contribution to drafting manuscript.

Abstract

Estuarine ecosystems have very high ecological and economic value, and also act as a buffer for coastal oceans by processing nutrient inputs from terrestrial sources. However, ongoing pressures from increased urbanisation and agriculture, overlaid by climate change, has reduced inflows and increased nutrient loads that challenge the health and buffering capacity of these ecosystems. This study aimed to investigate whether restoring the bioturbating activity of *Simplisetia aequisetis* (Polychaeta: Nereididae) and other macrofauna could improve biogeochemical conditions in 'hostile' (i.e. hypersaline, sulfide-rich) sediments. To achieve this aim, we conducted an *in situ* experiment in the Coorong estuarine-lagoon ecosystem, translocating hostile hypersaline sediments, devoid of bioturbating macrofauna, to a 'healthy' (lower salinity) location where macrobenthic fauna naturally occur, and manipulating the *S. aequisetis* density in the sediments. Porewater, solid-phase, and diffusive equilibrium and diffusive gradient in thin-films (DET/DGT) measurements showed that bioturbation by macrobenthic fauna significantly influenced sediment biogeochemistry and remediated hostile conditions in sediment within a short time (four weeks) irrespective of *S. aequisetis* density. Bioturbation promoted sediment oxygenation, while salinity and the concentrations of total organic carbon and porewater sulfide, ammonium, and phosphate all decreased over time at all sediment depths. This research highlights the importance of macrobenthic communities and their functional traits for improving sediment conditions, promoting resilience to eutrophication, providing a nature-based remediation option, and in general ensuring healthy functioning of estuarine ecosystems.

Keywords: Eutrophication, macroinvertebrates, nutrient cycling, sulfide, Murray-Darling Basin, Australia.

6.1. Introduction

Coastal and estuarine ecosystems provide a wide range of important values (e.g. ecology, fishing, tourism) and services, including biogeochemical functions, such as nutrient cycling (Thrush et al. 2013, Snelgrove et al. 2014, Belley and Snelgrove 2016). These ecosystems act as buffer areas for coastal seas, mitigating nutrient, sediment and organic matter loads received from terrestrial sources (Villnäs et al. 2019, Ehrnsten et al. 2020, O'Meara et al. 2020). However, the excessive production and accumulation of organic matter, i.e. eutrophication, has become a major environmental issue in coastal and estuarine ecosystems worldwide (Nixon 1995, 2006). This is a consequence of increasing inputs of nutrients (e.g. from fertilisers) and organic matter from anthropogenic activities along with hydrological and climate drivers (Nixon 1995, Beusen et al. 2016, Cloern et al. 2016, Malone and Newton 2020). Eutrophication promotes excessive algal growth, that in turn results in reduction of dissolved oxygen, increased sediment reduction and toxicity, and loss of benthic organisms (Nixon 2009, Hale et al. 2016, le Moal et al. 2019). Eutrophication, climate change and other anthropogenic pressures, may eventually lead to exceedance of the buffering potential of coastal and estuarine ecosystems, which results in potentially severe impacts to ecosystem functioning and a decrease in the health of entire ecosystems (Cloern 2001, de Witt et al. 2001, Grall and Chauvaud 2002, Douglas et al. 2019, Villnäs et al. 2019).

Marine macrobenthic organisms are crucial for alleviating high nutrient and sediment organic matter loads in coastal and estuarine ecosystems (Snelgrove et al. 2014, Thrush et al. 2017, Wrede et al. 2019). Benthic macrofauna actively disperse, mix, and modify the sediment via bioturbation and promote oxygen and nutrient exchange with the water column by bioventilation and bioirrigation processes, promoting solute movements and microbial activities which are ultimately responsible for organic matter mineralisation and nutrient cycling (Welsh 2003, Lohrer et al. 2004, Kristensen et al. 2012, Stief 2013, Remaili et al. 2018, Wyness et al. 2021). Yet, the influence of benthic macrofauna activities on sediment biogeochemical cycling is not fixed and depends on species type, density, functional traits (e.g. size, behaviour, living habit), their interaction with the environment, and tolerance to environmental conditions (e.g. ammonia, salinity, sulfide) (Waldbusser and Marinelli 2006, Kauppi et al. 2018, Thomas et al. 2020, Wrede et al. 2019, O'Meara et al. 2020).

Importantly, benthic macrofauna (e.g. polychaetes, bivalves, crustaceans) and their activities have been shown to increase sediment oxygenation and the overall volume of oxic sediments (Mermillod-Blondin et al. 2004, Braeckman et al. 2010, Volkenborn et al. 2012, Bosch et al. 2015, Kauppi et al. 2018). The construction and intermittent irrigation of burrows increases the surface area of contact between the sediment and water column, promoting solute exchanges and creating shifting mosaics of redox zonation within the sediments (Nielsen et al. 2004, Robertson et al. 2009, Volkenborn et al. 2012, Stief 2013, Remaili et al. 2017). The close juxtaposition of these redox zones enhances nutrient cycling by providing the conditions and substrates for specific functional groups of bacteria responsible for nitrification and denitrification processes (Welsh 2003, Mermillod-Blondin and Rosenber 2006, Stief 2013, Bosch et al. 2015). Additionally, the animals themselves can be colonised by nitrifying and denitrifying bacteria and these populations can significantly contribute to overall sediment rates of nitrification and denitrification (Welsh and Castadelli 2004, Heisterkamp et al. 2013, Welsh et al. 2015).

Nitrification and denitrification are important processes for mitigating nitrogen loading (e.g. eutrophic conditions), as the first transforms bioavailable ammonium to nitrate and nitrite, which can subsequently be reduced and eliminated as nitrogen gas (Seitzinger 1988). However, whilst denitrification mitigates against eutrophication, the competing nitrate reduction process of dissimilatory nitrate reduction to ammonium (DNRA) promotes eutrophication as it recycles and retains nitrate and nitrite within the system by reducing them to ammonium (Burgin and Hamilton 2007, Chen et al. 2021). High organic matter loads and sediment reduction associated with eutrophication favour DNRA over denitrification due to the high availability of organic and inorganic electron donors (Nizzoli et al. 2006, Seitzinger 1988, Burgin and Hamilton 2007). Unbalanced shifts in this coupled (nitrification-denitrification) process can result in increased macroalgae growth, anoxia, and eutrophication (Pérez-Ruzafa et al. 2019), with severe repercussions for the functioning and health of coastal and estuarine ecosystems (e.g. Mosley et al. 2020, Lam-Gordillo et al. 2022). Sediment oxygenation also promotes the chemical and biological oxidation of reduced compounds such as the sulfide produced by bacterial sulfate reduction, mitigating the build-up sulfide in the porewater, which can be toxic to benthic invertebrates and aquatic plants (de Witt et al. 2001, Azzoni et al. 2001, Pedersen and Kristensen, 2015).

The Coorong is the estuarine-lagoon system at the end of Australia's largest river system, the Murray-Darling Basin, which is characterised by a strong salinity gradient (Mosley et al. 2018). This system is ecologically, environmentally, and economically important at local, national and international scale (Ramsar-listed site). Over recent decades, this estuarine lagoon-system has experienced extreme changes and declining ecological health (Kingsford et al. 2011, Mosley et al. 2018, Mosley et al. 2020). The combination of low river inputs, reduced flushing, the arid climate, and climate change has contributed to increasingly hypersaline conditions in the lagoon, which has exacerbated hypereutrophication in some regions of this system (Mosley et al. 2020, Lam-Gordillo et al. 2022). In the Coorong, the structure of macrobenthic communities is strongly modulated by the salinity gradient (brackish to hypersaline), resulting in extended areas with complete loss of bioturbating macrofauna, and thus reduced ecosystem functioning (Dittmann et al. 2015, Dittmann et al. 2018, Lam-Gordillo et al. 2022).

Although the effects of bioturbating macrofauna on coastal and estuarine sediments are becoming better understood (e.g. Kauppi et al. 2018, Casado-Coy et al. 2020, Thomas et al. 2020), there is limited knowledge on the consequences of their loss, or on the potential for their restoration to remediate hostile conditions. The extreme range in sediment characteristics and macrofaunal functional trait distribution in the Coorong (Lam-Gordillo et al. 2022) provide an important opportunity for understanding the influence of bioturbating macrofauna on biogeochemical processes and their capability to reduce nutrient loads in sediments.

In this study we aimed to investigate whether the restoration of bioturbating activity by the polychaete *Simplisetia aequisetis* (Nereididae), could improve biogeochemical conditions in 'hostile' (i.e. hypersaline, eutrophic, sulfide-rich) sediments of the Coorong. We used an *in situ* experimental approach to investigate the short-term effects of different densities of *S. aequisetis* on sediment biogeochemistry across two distinct sedimentary sources, the marine North (non-hostile) and hypersaline South (hostile) lagoon. It was hypothesised that (1) hostile conditions will be reduced (e.g. lowered concentrations of sulfide, ammonium, phosphate, organic matter) in sediments with higher than lower density of *S. aequisetis*, and that (2) the hostile conditions will be remediated over time, due to bioturbating organisms oxygenating the sediment, promoting oxidation of sulfide and reduced iron(II). Outcomes from the study can help to support ecological options for remediating adverse sediment conditions to improve the ecological health and sustainability of estuarine lagoon systems.

6.2. Methods

6.2.1 Study area

The *in situ* experiment was conducted in the Coorong (Figure 6.1). The Coorong is an estuarine to hypersaline lagoon that encloses three regions: the Murray Mouth (salinity range 2-36), North Lagoon (salinity range 40-75), and South Lagoon (salinity range 80-120). This ecosystem is characterised by a strong salinity gradient with decreasing ecological health due to declining inflows, eutrophication, human-made barrages, and hypersalinization (Dittmann et al. 2018, Mosley et al. 2020, Lam-Gordillo et al. 2022).

6.2.2 Experimental design and set-up

To investigate whether the bioturbating activity of the polychaete *Simplisetia aequisetis* can improve biogeochemical conditions in hostile sediments, a manipulative *in situ* experiment was conducted in autumn (April-May) 2021 (Appendix E Figure S1a). The location of Long Point in the Coorong North Lagoon was selected as the experimental site as salinities are low enough (mean salinity 28) for benthic macrofauna to occur (Lam-Gordillo et al. 2022, Figure 1). The *in situ* experiment design allowed for the analysis of three main factors (Appendix E Figure S1b): Sediment source; Density of deep burrowing macrobenthic fauna; and Time. These three factors resulted in 108 core units for measurements, 96 experimental units (2 Sources × 4 Densities × 4 Times × 3 Replicates) and 12 control units (1 Source x 1 Density × 4 Times × 4 Time × 3 Replicates) (Appendix E Figure S1b).

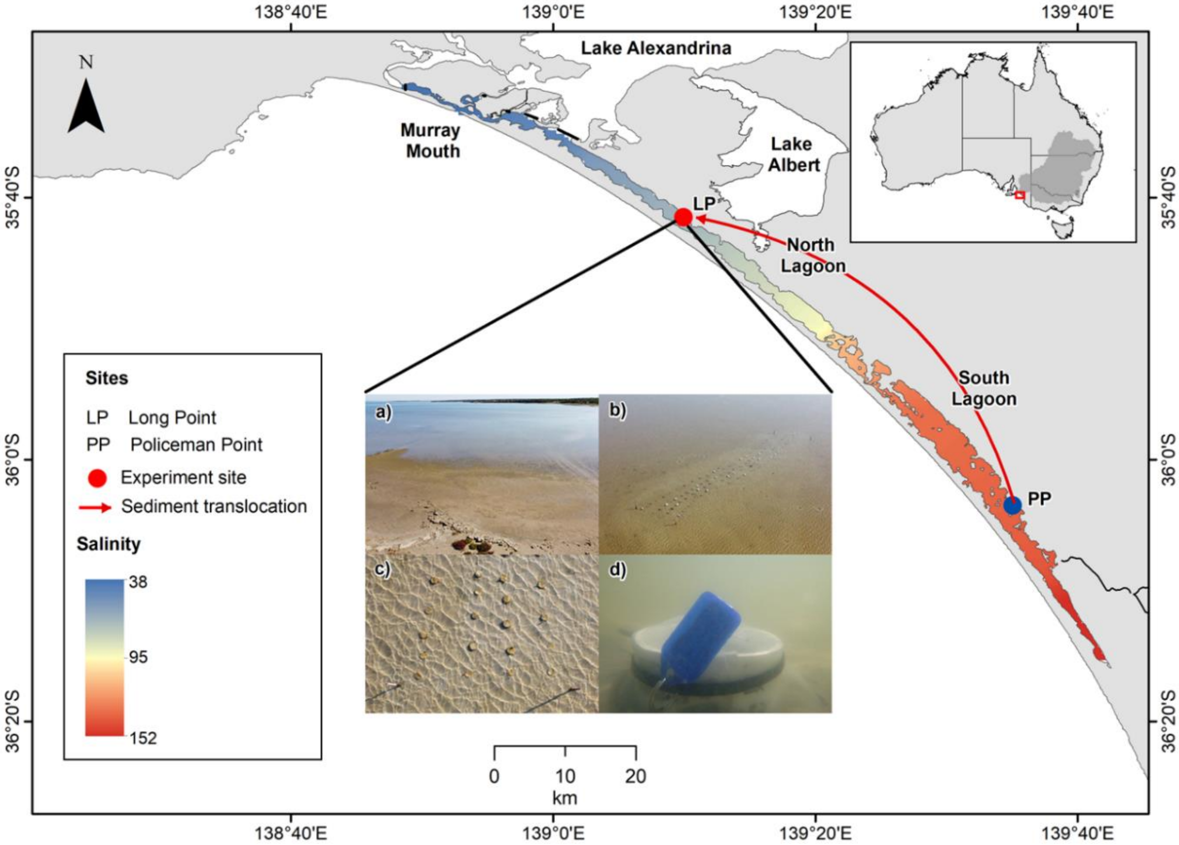


Figure 6.1. Location of the experimental site and salinity gradient across the Coorong system. The inset indicates the catchment of the Murray-Darling River system in Australia. The sediment was sourced from LP: Long Point and PP: Policeman Point. a) Mudflat at the experimental site (LP). b-c) Aerial view of the complete grid of experimental units deployed at LP. d) Illustration of experimental unit in the sediment under water. Salinity data were generated using the 1-dimensional Coorong Hydrodynamic Model (Jöhnk and Webster, 2014), with historical data for boundary conditions and validated against recorded salinity at sensors (available from water.data.sa.gov.au).

Sediment sources comprised (a) hypersaline (mean salinity 131, compared to seawater salinity of 35) and sulfide-rich sediment from the South Lagoon (Policeman Point: PP), and (b) marine – brackish sediment from LP. 48 sediment cores at each sediment source, i.e. experimental units, were hand collected using PVC tubes (83 cm^2 surface area) to 20 cm depths. Sediments were defaunated (through freezing over one week), thawed, and randomly translocated (with experimental units spaced at least 1 m apart) into sediments in the lower intertidal zone of the mudflat at LP in the North Lagoon. (c) Natural and undisturbed sediment at LP, which was not subjected to any experimental manipulation, served as control (LPc).

The density of deep burrowing macrobenthic fauna was modified using polychaete *S. aequisetis* individuals of 4-6 cm length. *S. aequisetis* were collected from Pelican Point in the Murray Mouth where they are very abundant, with a mean natural density of 90 individuals per core (10,802 ind.m^2) (Dittmann et al. 2021). As the density of bioturbators can affect sediment porewater nutrient concentrations and biogeochemistry (Lam-Gordillo et al. 2022), four levels of density were used based on the natural (minimum) density of *S. aequisetis* recorded at LP (5 individuals per core, 600 ind.m^2; Ye et al. 2020), simulating four Coorong scenarios from low densities during drought to higher densities after longer periods with high freshwater inflow: 0× – azoic sediments (no organisms); 0.5× (3 organisms) – half the natural density; 1× (5 organisms) – natural density; and 2× (10 organisms) – twice the natural density. *S. aequisetis* were added accordingly to the densities of each experimental unit five days after the sediment translocation (sediment settlement period).

The factor time was also measured after adding bioturbators, where nutrient concentrations and sediment biogeochemical changes were assessed over four weeks (Week 1-4), with weekly analyses of three randomly chosen (replicate) experimental units per treatment. All the PVC cores (experimental units) were open at the bottom and top ends, with only a 0.5 mm mesh size cover, to retain the experimentally-introduced *S. aequisetis* organisms and allow the natural flux of water and suspended matter (Appendix E Figures S1-S2). Other smaller sized benthic macrofauna (<0.5 mm), that were naturally present in the sediment at the LP site, were also able to recolonise the defaunated LP and translocated PP sediment. The density of these was also measured as described below.

6.2.3 Data collection

Each of the 108 experimental units (27 experimental units each week) were analysed for pore water salinity, porewater nutrients, sediment grain size, and macrobenthic fauna over the length of the experiment (Appendix E Table S1). Sediment total organic carbon and nitrogen content, and porewater sulfide, iron(II), ammonium, nitrate, and phosphate concentrations were measured before the addition of *S. aequisetis* (Week 0), Week 1 and Week 4 (Appendix E Table

S1). In addition, three core units per sediment source were sampled for porewater salinity and nutrients, sediment total organic carbon and nitrogen, and macrobenthic fauna immediately after collection to define the natural conditions of the sediment sources.

Upon retrieval of each experimental unit, samples for porewater salinity and nutrients (ammonium, nitrate, nitrite and phosphate) were collected using Rhizon samplers (Seeberg-Elverfeldt 2005) within three depth horizons (0-2 cm, 2-10 cm, 10-20 cm). Salinity was measured *in situ* using a refractometer (IWAKI, Japan, range 0-200), and samples for porewater nutrient concentrations were immediately stored in portable freezers and frozen to -20ºC until further laboratory analysis. Sediment from each experimental unit was collected using a cut-off 60 mL syringe (surface area 6.6 cm^2) pushed into the sediment of each unit, the collected sediment was extruded and divided into three depth horizons (0-2 cm, 2-10 cm, 10-20 cm) and samples for sediment grain size, sediment total organic carbon and nitrogen were collected. Any *S. aequisetis* present in these sediment samples were added into the macrofauna samples. Sediment samples were also stored frozen at -20°C until further laboratory analysis. For benthic macrofauna, the remaining sediment was sieved through 500 µm mesh size in the field and placed in plastic bags until further laboratory processing.

DGT (Diffusive Gradients in Thin-films) and DET (Diffusive Equilibration in Thin-films) techniques were used as they are well-established *in situ* passive samplers for obtaining high resolution porewater profiles of solutes concentrations (Pagès et al. 2012, Huang et al. 2016, Kankanamge et al. 2017, Huang et al. 2019). DET-DGT probes were applied for sulfide (S) and iron(II) (Fe II) measurements, while DET probes were used for nutrient measurements (ammonium, phosphate, and nitrate). Gel preparation for DET-DGT and DET techniques were conducted following the protocols described by Robertson et al. (2008), Bennett et al. (2012), Pagès et al. (2012) and Huang et al. (2016). The DET-DGT and DET probes were assembled (See Pagès et al. 2012, Huang et al. 2016 for details) and deployed *in situ* inside three replicate experimental unit on the day before retrieving the experimental units for other porewater and sediment analyses (described above). The probes were carefully inserted into the sediment and deployed for approximately 7.5 h under natural light conditions, with 2-3 cm of the probe exposed to the overlaying water above the sediment and 12-13 cm under the sediment surface. At the end of the deployments, DET-DGT and DET probes were retrieved from the sediment.

DET-DGT probes for iron(II) and sulphide were rinsed to remove any sediment residue, the gel layers within the probes were collected and immediately processed as described by Robertson et al. (2008) and Bennett et al. (2012), scanned using a portable colour scanner, and the image processed using GIMP software v.2.10.22 and MATLAB to generate two-dimensional concentration distributions following the protocols described by Robertson et al. (2008). To generate individual depth profiles of iron(II) and sulfide, concentrations in the two-dimensional distributions were laterally averaged across the width of the distribution for each 1-mm depth interval, as described by Pagès et al. (2012). DET probes for porewater dissolved nutrients were also rinsed to remove any sediment, the gel layers were collected and immediately sliced into 1 cm intervals. DET gel slices was transferred into a 5-mL plastic vials and frozen until further processing (See Appendix E Figure S2 for details of the experimental design setting and measurement process).

6.2.4 Laboratory analyses

Following sieving of the experimental and control units, benthic macrofauna samples were sorted live in the laboratory, all organisms were identified to the lowest possible taxonomic level and counted.

Porewater nutrient concentrations (µmol/L) of nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+) and phosphate (PO_4^{3-}) in Rhizon collected samples were determined using a Skalar SAN ++ SFA segmented flow analyser. Replicates were within 10% and recoveries for spiked samples were within 75–100% of expected values. Sediment grain size was determined by laser diffraction using a particle size analyser (Malvern Mastersizer 2000). Average values for grain size fractions for each site were entered into the GRADISTAT program v8.0 (Blott and Pye 2001) to obtain the median (D50 µm) and sorting coefficient (σG), and percentage of fine sand (%FS). Sediment total organic carbon (TOC), and nitrogen (TN) were determined by high temperature dry combustion (LECO instrument) at the National Association of Testing Authorities, Australia (NATA) accredited Environmental Analysis Laboratory at Southern Cross University, following strict quality control and assurance procedures. The DET gel layers were eluted in 3 mL 0.1 mol/L HCl for 24 h, then neutralised by addition 0.28-0.3 mL 1 mol/L NaOH before analysis. The DET eluents were analysed for (µmol/L) ammonium (NH_4^+), phosphate (PO_4^{3-}), and nitrate (NO_3^-) using a Seal AA3 segmented flow analyser (Seal

Analytical, USA). Replicates were within 10% and recoveries for spiked samples were within 93–110% of expected values.

6.2.5 Data analysis

To test for differences in macrobenthic fauna density and fixed treatment factors (sediment source, added *S. aequisetis* density, depth, and time), univariate PERMutational ANalysis Of VAriance (PERMANOVA) tests were conducted, using Euclidean distance for the single variables and 9999 permutations in PRIMER v7 with PERMANOVA add on software (Anderson et al. 2008). In addition, multiple pair-wise tests with Monte-Carlo test (MC) and 9999 permutations were conducted if the fixed factors were significant to identify which groupings contributed to differences from PERMANOVA main tests. To evaluate the direct influence of *S. aequisetis* and other benthic macrofauna (predictor variables) on porewater nutrients and sediment biogeochemical characteristics, a series of non-parametric multiple regressions were performed with the DISTLM routine, using Euclidean distances, 9999 permutations (McArdle and Anderson, 2001). To test for significant differences between the sediment source, *S. aequisetis* density, depth, and week, and their influence on sulfide, iron(II) and nutrient (DET-DGT measured) concentrations, multiple Generalised Additive Models (GAM) were performed using the packages “mgcv” (Wood 2011) and “ggplot2” (Wickham 2016) in R software (R Core Team 2018). GAMs were constructed using the method “REML” and formula “y ~ s(x, bs = "cs")+ε” to best fit the observations (Wood 2017).

6.3. Results

6.3.1 Pre-experiment sediment biogeochemistry and macrobenthic fauna

Sediment from Long Point (LP) was classified as a moderately sorted medium sand (Table S2). Five macrobenthic taxa were recorded: Amphipoda, *Arthritica semen*, *Capitella sp.*, Chironomidae and *Simplisetia aequisetia*. The macrofauna mean total abundance was 6667 ind.m^2 (55 individuals per core), with the highest mean total abundance within the 0-2 cm sediment horizon (Appendix E Table S2). The mean TOC concentration at LP was on average 0.21%, with the highest concentration recorded in the 0-2 cm sediment horizon, while TN concentration in sediment was low (mean 0.02 %TN) and relatively homogenous across the three sediment depth horizons (Appendix E Table S2). Porewater salinity was 22.1, and concentrations of nitrate and nitrite were lower (0.32 and 2.17 µmol/L respectively) than concentrations of ammonium and dissolved phosphorus, 1.0 and 2.42 µmol/L respectively (Appendix E Table S3). ‘Hostile’ sediment from the South Lagoon at Policeman Point (PP) was characterised by moderately well sorted fine sand (Appendix E Table S2). No macrofauna were recorded, mainly due to the high porewater salinity recorded (>160). TOC followed a similar pattern as in LP, with an average content of 0.19%, recording the highest concentration in the top sediment horizon. TN was also hardly detected (<0.1%) at PP, and homogenous across the three sediment depths (Appendix E Table S2). Porewater concentrations of nitrate (1.94 µmol/L), nitrite (3.04 µmol/L), ammonium (154 µmol/L) and phosphate (6.53 µmol/L) were higher than the concentrations recorded in sediments from Long Point (Appendix E Table S3).

6.3.2 Simplisetia aequisetis and other macrobenthic fauna recovered after the experiment

Once the hostile (i.e., hypersaline, sulfide-rich) sediment in the experimental units from PP were translocated into the lower salinity site at LP, macrobenthic fauna rapidly colonized the sediment. Significant differences were found in the abundance of *S. aequisetis* added across the treatments 0×, 0.5×, 1×, and 2× ($p<0.05$; Figure 6.2; Appendix E Table S4). The recovery rate of *S. aequisetis* which had been added to the experimental units ranged from 48% to >100%. In some experimental units, the density of *S. aequisetis* exceeded the number of polychaetes added to the treatment due to colonisation by local *S. aequisetis* (Table 6.1; Figure 6.2a). Other taxa also found to have colonised experimental units were *Arthritica semen*, Amphipoda, *Capitella sp.*, and small sized *S. aequisetis* (hereafter referred as ‘*S. aequisetis* (s)’; length <2 cm) (Table 1), yet the macrobenthic abundance (all taxa included) was significantly different across the treatments ($p<0.05$; Figure 6.2b; Appendix E Table S5). The macrobenthic community found in the control units (undisturbed sediment from LP) were characterised by the same four macrobenthic taxa, with significantly higher abundance compared to the experimental units ($p<0.05$; Figure 6.2b).

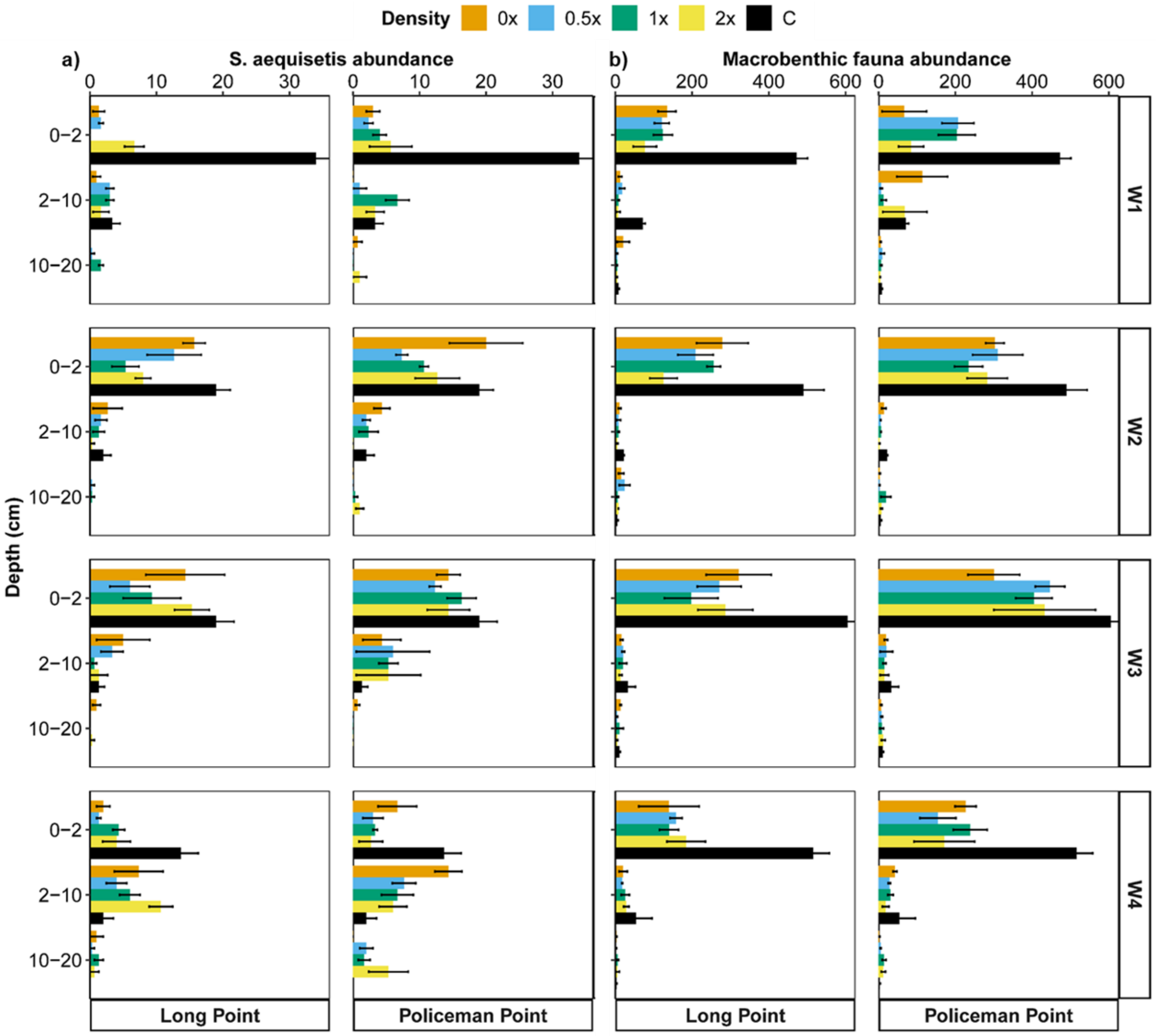


Figure 6.2. Bar graph showing a) *S. aequisetis* mean abundance and b) macrobenthic fauna mean abundance across depth horizons and weeks. W1 = Week 1, W2 = Week 2, W3 = Week 3, W4 = Week 4. 0× = no *S. aequisetis* added, 0.5×= 3 *S. aequisetis*, 1×= 5 *S. aequisetis*, and 2×= 10 *S. aequisetis* added, C= Control. Data are mean values and ± error standard (n=3).

6.3.3 Salinity and sediment characterization

After an initial period of sediment equilibrium (five days), porewater salinity in PP experimental units decreased from >160 to an average of 25, which enabled the rapid colonisation of macrobenthic fauna. Porewater salinity in the experimental units (both LP and PP) during the extension of the *in situ* experiment ranged from 17-34. Porewater salinity was not significantly different between LP and PP experiment units, and control units ($p>0.05$; Figure 6.3a; Appendix E Table S6). Significant differences in porewater salinity were found between measurement events ($p<0.05$; Appendix E Table S6), as porewater salinity was lower at the start of the experiment (Week 1), and gradually increased towards the end of the experiment (Week 4). Significant differences were also found across depth horizons ($p<0.05$; Appendix E Table S6), with lower porewater salinity recorded in the upper depth horizon (0-2 cm), and higher concentrations in the deepest 10-20 cm depth horizon (Figure 6.3a).

Sediment grain size (D50) differed significantly with time, depth, and sediment sources ($p<0.05$; Appendix E Table S6). Sediment grain size was characterised by fine sand, and slightly larger grain size in Week 1 than in Week 3 (Figure 6.3b). In the LP experimental units, sediment grain size increased from the 0-2 cm to 10-20 cm depth horizon, while larger sediment grain size was found between the 2-10 cm depth in PP experimental units (Figure 6.3b). Sediment sorting coefficient was significantly different between sediment sources ($p<0.05$; Appendix E Table S6), with moderately sorted sediments in LP experimental units, and very well sorted sediments in PP experimental units (Figure 6.3c). The percentage content of fine sand differed significantly with time, depth, and sediment source ($p<0.05$; Appendix E Table S6). Fine sand content was higher in the upper horizon (0-2 cm) for both LP and PP experimental units, and lower between the 10-20 cm depth in LP, and in the 2-10 cm depth horizon in PP experimental units (Figure 6.3d). Sediment characteristics (grain size, sorting coefficient, fine sand content) in the experimental units were similar to the control units (Figure 6.3b-d).

Table 6.1. Number of *S. aequisetis* added to each sediment source, and recovery of *S. aequisetis* and other macrobenthic fauna during each weekly sampling of the experiment. *S. aequisetis* (s) = Juvenile *S. aequisetis*; smaller individuals than those added to the experimental units. Recovery was calculated using the mean + standard error values (n = 3).

	Long Point				**Policeman Point**				**Control**
	0x	**0.5x**	**1x**	**2x**	**0x**	**0.5x**	**1x**	**2x**	
Simpisetia aequisetis added (ind.core)	0	3	5	10	0	3	5	10	Undisturbed sediment
Week 1									
Simpisetia aequisetis recovered (ind.core)	0.78 ± 0.63	1.67 + 0.76	1.56 + 0.82	2.78 + 1.97	1.22 ± 0.99	1.11 + 0.84	3.56 + 1.96	3.33 + 2.14	12.44 ± 9.4
Recovery (%)	+1	81%	48%	48%	+2	65%	110%	55%	NA
Abundance of other taxa found (ind.core)									
Arthritica semen	8.67 ± 7.70	11.56 + 9.03	15.33 + 13.57	13.56 + 14.38	7.00 ± 6.24	20.89 + 17.18	27.78 + 25.99	24.00 + 19.62	56.11 ± 75.08
Amphipoda									
Capitella sp.	0.56 ± 0.96	1.89 + 1.99	0.78 + 1.56	1.22 + 2.86	1.11 ± 0.84	0.67 + 0.96	0.44 + 1.59	0.33 + 2.41	73.89 ± 43.30
Simplisetia aequisetis (s)	24.78 ± 21.61	14.33 + 10.14	14.67 + 12.74	3.89 + 3.30	35.78 ± 32.00	20.56 + 22.22	20.67 + 20.38	12.89 + 12.93	15.00 ± 12.00
Week 2									
Simpisetia aequisetis recovered (ind.core)	6.11 + 4.41	4.89 + 3.97	2.33 + 1.73	2.78 + 2.34	8.11 + 5.97	3.11 + 1.97	4.44 + 2.86	4.56 + 3.91	7.00 + 5.4
Recovery (%)	+11	295%	81%	51%	+14	169%	146%	85%	NA
Abundance of new taxa found (ind.core)									
Arthritica semen	9.67 + 5.24	15.33 + 11.33	7.78 + 6.07	7.44 + 5.54	10.78 + 12.46	10.00 + 10.63	9.33 + 6.41	3.44 + 3.71	53.89 + 67.03
Amphipoda									
Capitella sp.	2.89 + 6.86	2.00 + 4.15	3.67 + 2.29	1.33 + 2.63	2.78 + 5.25	0.67 + 1.58	0.89 + 2.79	4.67 + 3.42	49.11 + 38.76
Simplisetia aequisetis (s)	64.78 + 58.36	38.33 + 36.49	52.22 + 44.24	15.33 + 12.88	65.00 + 57.67	59.56 + 56.52	50.78 + 45.77	57.56 + 54.44	28.67 + 24.26

Week 3									
Simpisetia aequisetis recovered (ind.core)	6.78 + 4.96	3.11 + 2.28	3.33 + 3.39	5.67 + 4.44	6.44 + 3.92	6.11 + 4.16	7.22 + 4.37	6.56 + 4.64	6.78 + 5.5
Recovery (%)	+12	180%	134%	101%	+10	342%	232%	112%	NA
Abundance of new taxa found (ind.core)									
Arthritica semen	13.22 + 14.00	4.00 + 2.25	5.33 + 4.13	4.00 + 4.04	13.67 + 12.91	18.00 + 18.11	11.89 + 12.18	18.78 + 26.30	69.89 + 62.57
Capitella sp.	7.11 + 6.98	4.89 + 3.43	3.56 + 3.06	2.89 + 5.32	4.33 + 3.75	2.00 + 4.84	1.89 + 4.06	7.56 + 4.87	44.67 + 36.15
Simplisetia aequisetis (s)	66.78 + 65.83	47.67 + 46.14	31.22 + 34.07	54.00 + 51.68	49.22 + 52.58	74.11 + 63.30	61.00 + 57.35	78.00 + 81.12	30.56 + 25.15
Week 4									
Simpisetia aequisetis recovered (ind.core)	3.44 + 2.60	1.89 + 1.24	3.89 + 1.51	5.11 + 2.91	7.00 + 4.00	4.22 + 1.97	3.89 + 1.81	4.67 + 2.20	5.22 + 4.0
Recovery (%)	+6	104%	108%	80%	+11	206%	114%	69%	NA
Abundance of new taxa found (ind.core)									
Arthritica semen	3.33 + 3.42	8.11 + 8.57	5.78 + 7.12	7.33 + 5.97	14.56 + 13.81	13.44 + 14.66	16.56 + 15.50	3.33 + 2.89	43.44 + 86.50
Amphipoda									
Capitella sp.	2.22 + 3.50	2.44 + 1.85	4.11 + 3.05	4.11 + 5.85	5.33 + 4.73	4.67 + 1.89	7.00 + 1.91	3.56 + 2.22	66.11 + 49.93
Simplisetia aequisetis (s)	34.89 + 37.70	32.78 + 27.16	28.56 + 23.37	47.00 + 39.55	51.44 + 38.26	24.44 + 21.57	48.78 + 39.65	30.56 + 27.67	29.33 + 25.23

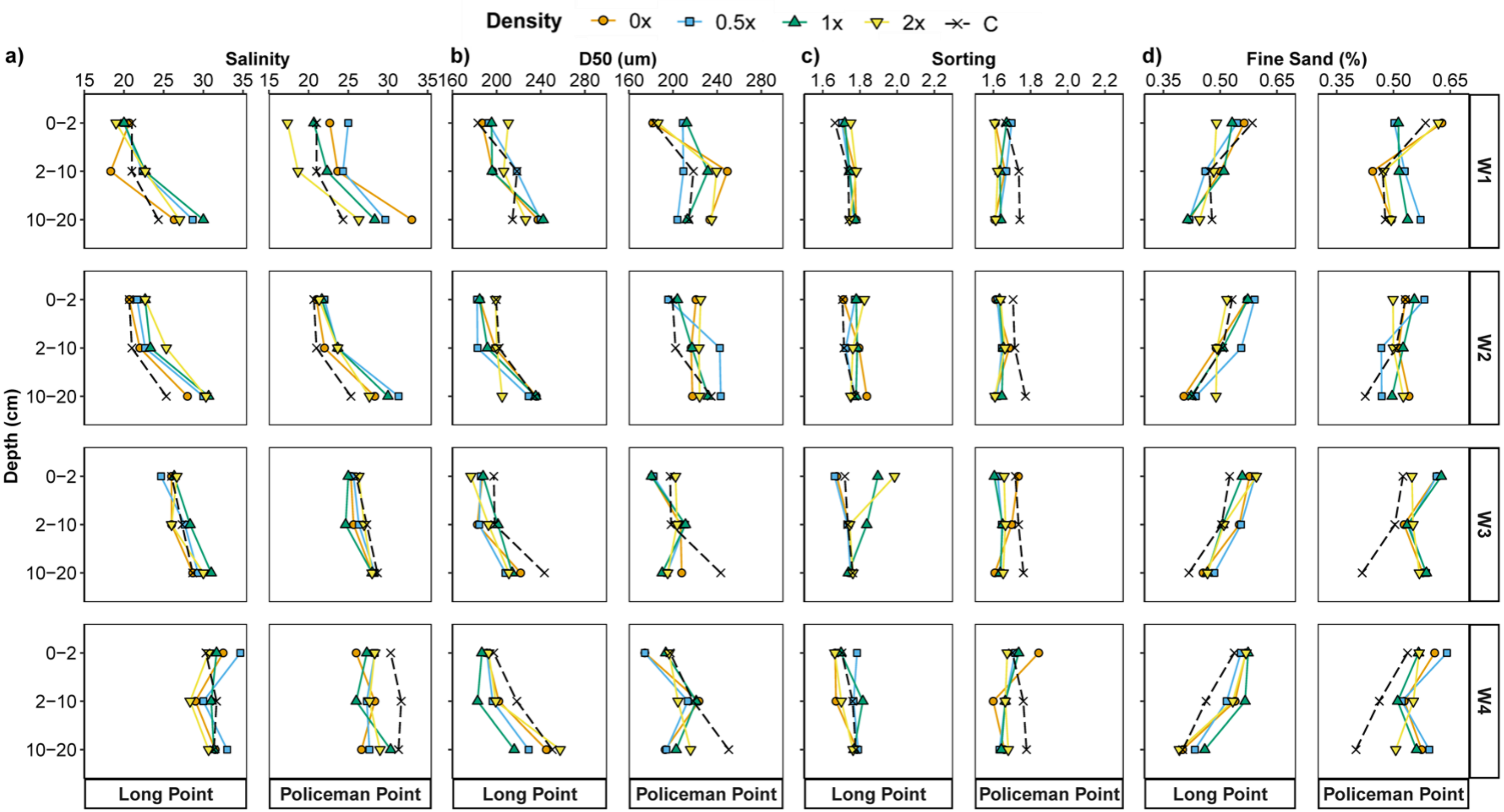


Figure 6.3. Depth profiles of a) sediment porewater salinity, b) median sediment grain size (D50 um), c) sediment sorting coefficient, and d) sediment fine sand content (%) across weeks. W1 = Week 1, W2 = Week 2, W3 = Week 3, W4 = Week 4. 0× = no *S. aequisetis* added, 0.5× = 3 *S. aequisetis*, 1× = 5 *S. aequisetis*, and 2× = 10 *S. aequisetis* added, C= Control. Data are mean values (n=3).

6.3.4 Influence of Simplisetia aequisetis and other macrobenthic fauna on sediment biogeochemistry and nutrients concentrations

The experimentally-introduced polychaete *S. aequisetis* and other colonising macrobenthic fauna (amphipods, *S. aequisetis* (s), *A. semen*, *Capitella sp.*) changed the sediment biogeochemistry over time (Table 6.2). *S. aequisetis*, amphipods, *S. aequisetis* (s), and *A. semen* significantly influenced the concentrations of TOC and TN in sediment, and the concentrations of ammonium, phosphate, nitrate and nitrite in sediment porewaters in Week 1 ($p<0.05$; Table 6.2). *S. aequisetis* was the taxa that explained most of the variation in sediment biogeochemistry ($p<0.05$; Table 6.2). In Week 2, changes in sediment biogeochemistry were explained only by *S. aequisetis* and *S. aequisetis* (s), while in Week 3 *S. aequisetis*, amphipods, *S. aequisetis* (s), and *Capitella sp.* accounted for most of the variation ($p<0.05$; Table 6.2). In Week 4, the majority of the taxa influenced changes in sediment biogeochemistry, whereby *S. aequisetis* (s) was the taxa that explained most of the variation ($p<0.05$; Table 6.2).

3.4.1 Sediment organic carbon and nitrogen concentrations

Changes of TOC concentrations in sediments were influenced by the presence of *S. aequisetis*, amphipods, *S. aequisetis* (s), *Capitella sp.* and *A. semen* ($p<0.05$; Table 6.3). Amphipods and *A. semen* were the taxa that accounted for most of the variation in TOC concentrations (Table 6.3). TOC concentrations in sediment ranged from 0.06 to 0.30 %. Sediment TOC concentration in the experimental units was higher than the initial concentration recorded in control units (mean values: LP = 0.19 %TOC, PP = 0.17 %TOC, and C = 0.14 %TOC). TOC concentrations in sediment were significantly higher in Week 1 (~0.13-0.28 %TOC) compared to Week 4, in which the TOC concentrations ware significantly lower (~0.06-0.24 %TOC) in both sediment sources ($p<0.05$; Figure 6.4a; Appendix E Table S7). TOC concentration was also significantly different between sediment depths ($p<0.05$; Appendix E Table S7), with higher contents in the upper depth horizon (0-2 cm), and lower concentration in the deepest 10-20 cm horizon (Figure 6.4a).

Table 6.2. Result of DistLM forward analysis for *S. aequisetis* and other macrofauna as predictor of the combined variables: total organic carbon and total nitrogen content, and porewater ammonium, phosphate, nitrate, and nitrite concentrations over time. Significant *P* values are in bold. *S. aequisetis* (s) = Juvenile *S. aequisetis*, smaller than those added in the experimental units. Proportion = variability explained.

Selected predictor	Response variable	Time	AIC	R^2	SS (trace)	Pseudo-*F*	P-value	Proportion
Amphipoda	Total organic carbon + total nitrogen + ammonium + phosphate + nitrate + nitrite	W1	125.9	0.106	24.600	4.290	**0.0014**	0.0577
Simplisetia aequisetis					24.722	4.313	**0.0022**	0.0580
Simplisetia aequisetis (s)					17.984	3.085	**0.0191**	0.0422
Capitella sp.					7.305	1.221	0.2491	0.0171
Arthritica semen					21.421	3.706	**0.0166**	0.0503
Amphipoda	Ammonium + phosphate + nitrate + nitrite	W2	99.3	0.047	9.484	2.418	0.0649	0.0334
Simplisetia aequisetis					13.446	3.479	**0.0387**	0.0473
Simplisetia aequisetis (s)					10.892	2.792	**0.0402**	0.0384
Capitella sp.					5.755	1.448	0.1399	0.0203
Arthritica semen					4.963	1.245	0.2254	0.0175
Amphipoda	Ammonium, phosphate, nitrate, nitrite	W3	94.0	0.139	26.333	7.154	**0.0001**	0.0927
Simplisetia aequisetis					29.884	8.232	**0.0001**	0.1052
Simplisetia aequisetis (s)					22.463	6.012	**0.0003**	0.0791
Capitella sp.					14.819	3.854	**0.0372**	0.0522
Arthritica semen					11.508	2.956	0.0521	0.0405
Amphipoda	Total organic carbon + total nitrogen + ammonium + phosphate + nitrate + nitrite	W4	118.3	0.195	63.353	12.229	**0.0001**	0.1487
Simplisetia aequisetis					8.415	1.411	0.2202	0.0198
Simplisetia aequisetis (s)					73.324	14.554	**0.0001**	0.1721
Capitella sp.					17.734	3.041	**0.0162**	0.0416
Arthritica semen					32.333	5.749	**0.0005**	0.0759

Changes in sediment TN concentrations were influenced by the presence of amphipods and *A. semen* ($p<0.05$; Table 6.3), with *A. semen* as the taxa that explained most of the variation in sediment TN concentrations in both experimental and control units (Table 6.3). Sediment TN was low (range 0.006-0.040 %TN), but higher in the experimental units than control units (mean values: LP = 0.022 %TN, PP = 0.018 %TN, and C = 0.016 %TN). TN concentration decreased significantly over time (Week 1: ~0.011-0.039 %TN, Week 4: ~0.006-0.025 %TN) in both LP and PP sediments ($p<0.05$; Figure 6.4b; Appendix E Table S7). Sediment TN concentration also varied significantly between depth horizons ($p<0.05$; Appendix E Table S7), following the same pattern as TOC, with higher concentrations in the upper horizon (0-2 cm), and lower concentration in the 10-20 cm depth horizon (Figure 6.4b).

Table 6.3. Result of DistLM forward analysis for *S. aequisetis* and other macrofauna as predictor of the individual variables: total organic carbon and total nitrogen content, and porewater ammonium, phosphate, nitrate, and nitrite concentrations over time. Significant *P* values are in bold. *S. aequisetis (s)* = Juvenile *S. aequisetis*, smaller than those added in the experimental units. Proportion = variability explained.

Selected predictor	Response variable	AIC	R^2	SS (trace)	Pseudo-*F*	P-value	Proportion
Simplisetia aequisetis	**Total Organic Carbon**	-826.1	0.0974	0.049	15.336	**0.0001**	0.0975
Amphipoda				0.117	43.294	**0.0001**	0.2337
S. aequisetis (s)				0.062	19.902	**0.0001**	0.1229
Capitella sp.				0.015	4.2654	**0.0369**	0.0292
Arthritica semen		-848.6	0.2594	0.072	23.979	**0.0001**	0.1445
Simplisetia aequisetis	**Total Nitrogen**	-1181.9	0.0215	0.001	3.132	0.0685	0.0216
Amphipoda				0.002	7.345	**0.0109**	0.0492
S. aequisetis (s)				0.000	1.844	0.1556	0.0128
Capitella sp.				0.000	0.678	0.2967	0.0048
Arthritica semen		-1187.4	0.0961	0.003	11.965	**0.0080**	0.0777
Simplisetia aequisetis	**Ammonium**	1199.8	0.0922	1318.000	32.690	**0.0001**	0.0922
Amphipoda				22.944	0.000	0.0665	0.0888
S. aequisetis (s)		1206.0	0.0915	1018.800	24.701	**0.0001**	0.0712
Capitella sp.				430.100	9.985	**0.0247**	0.0301
Arthritica semen				573.870	13.462	**0.0068**	0.0401

Simplisetia aequisetis	**Phosphate**	-334.9	0.0040	0.457	1.291	0.2555	0.0040
Amphipoda				0.365	1.032	0.3031	0.0032
S. aequisetis (s)		-331.7	0.0126	0.168	0.473	0.4862	0.0015
Capitella sp.				1.259	3.586	**0.0479**	0.0110
Arthritica semen				0.376	1.062	0.3010	0.0033
Simplisetia aequisetis	**Nitrate**	-1183.0	0.0001	0.001	0.037	0.8526	0.0001
Amphipoda				0.032	1.247	0.2616	0.0039
S. aequisetis (s)		-1190.1	0.03947	0.081	3.170	0.0750	0.0097
Capitella sp.				0.132	5.185	**0.0274**	0.0158
Arthritica semen				0.074	2.902	0.0762	0.0089
Simplisetia aequisetis	**Nitrite**	-539.4	0.00316	0.192	1.021	0.2749	0.0032
Amphipoda				0.020	0.105	0.7570	0.0003
S. aequisetis (s)		-532.8	0.0013	0.020	0.106	0.7706	0.0003
Capitella sp.				0.037	0.195	0.5982	0.0006
Arthritica semen				0.002	0.013	0.9105	0.0000

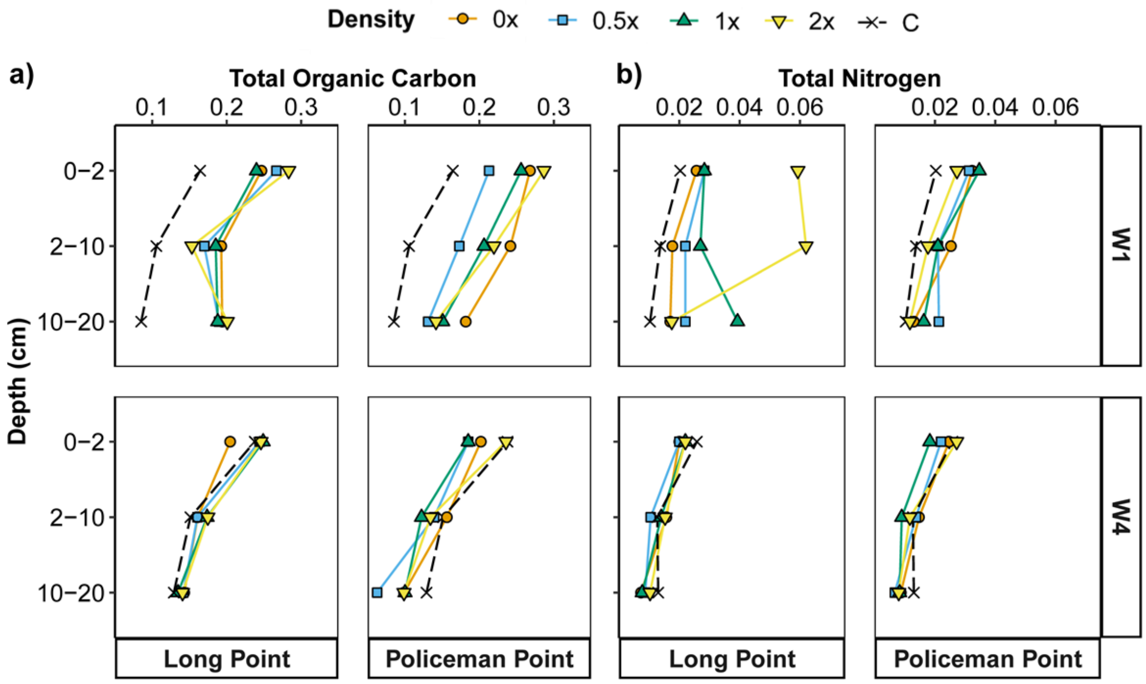


Figure 6.4. Depth profiles of sediment a) total organic carbon content, and b) total nitrogen content across weeks. W1= Week 1, W2 = Week 2, W3 = Week 3, W4 = Week 4. 0× = no *S. aequisetis* added, 0.5× = 3 *S. aequisetis*, 1× = 5 *S. aequisetis*, and 2× = 10 *S. aequisetis* added, C= Control. Data are mean values (n=3).

6.3.4.2 Porewater ammonium, phosphate, nitrate and nitrite

Changes of ammonium concentrations in porewater were influenced by the presence of *S. aequisetis*, amphipods, *S. aequisetis* (s), *Capitella sp.* and *A. semen* ($p<0.05$; Table 6.3). Yet, *S. aequisetis*, the polychaete added to the experimental units, accounted for most of the variation in ammonium concentrations (Table 6.3). Porewater ammonium concentrations in the experimental units were higher than in the control units (mean values: LP = 390 µmol/L, PP = 249 µmol/L, and C = 67.6 µmol/L). Concentrations of ammonium in porewater decreased significantly over time (Week 1: ~150-400 µmol/L, Week 4: ~0-160 µmol/L) in both LP and PP experimental units ($p<0.05$; Figure 6.5a; Appendix E Table S8). Porewater ammonium concentrations also differed significantly between depth horizons ($p<0.05$; Appendix E Table S8), with increasing concentrations from the shallowest 0-2 cm depth horizon to the deepest 10-20 cm depth horizon (Figure 6.5a). Porewater ammonium concentrations in LP and PP experimental units were significantly different, mainly due to the high concentrations recorded in Week 2 and Week 3 in LP experimental units ($p<0.05$; Figure 6.5a; Appendix Table S8).

Evidence of effects of *Capitella sp.* on porewater phosphate concentrations was identified ($p<0.05$; Table 6.3). Concentrations of porewater phosphate were significantly higher in LP (~4-20 µmol/L) compared to PP (~0-9 µmol/L) experimental units ($p<0.05$; Figure 6.5b; Appendix E Table S8). Significant differences were also identified across weeks and depth ($p<0.05$; Figure 6.5b; Appendix E Table S8). Concentrations of porewater phosphate were also higher in LP experimental units than the control units (mean = 9.48 and 2.43 µmol/L respectively), but similar in PP experimental units (2.32 µmol/L; Figure 5b). In both LP and PP sediments, the lowest concentrations of porewater phosphate occurred in the 10-20 cm depth horizon, while highest concentrations were found in the 2-10 cm and 0-2 cm depth horizons in LP and PP experimental units, respectively (Figure 6.5b).

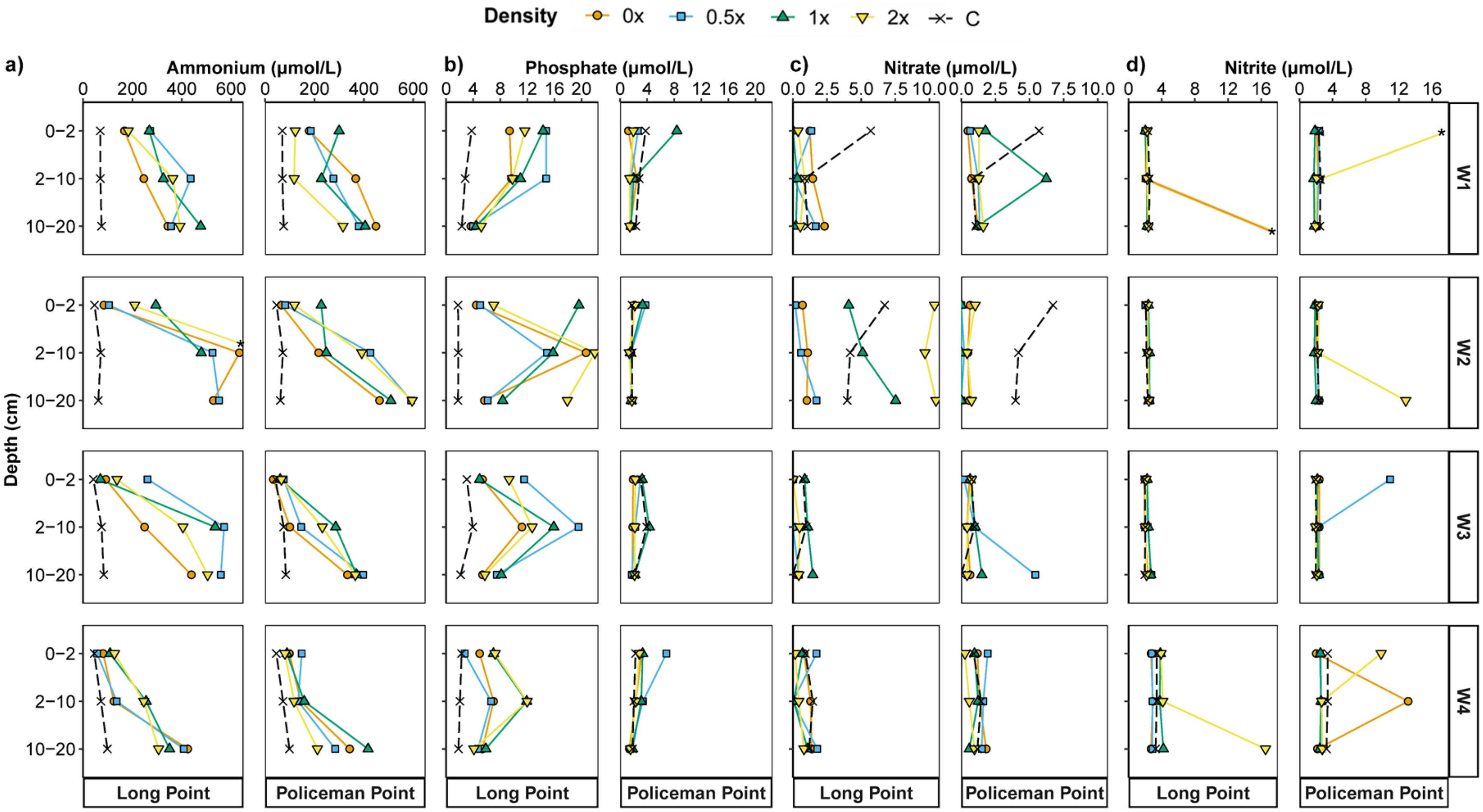


Figure 6.5. Depth profiles of porewater nutrient concentrations across weeks. a) Ammonium, b) phosphate, c) nitrate, d) nitrite. W1 = Week 1, W2 = Week 2, W3 = Week 3, W4 = Week 4. 0× = no *S. aequisetis* added, 0.5× = 3 *S. aequisetis*, 1× = 5 *S. aequisetis*, and 2× = 10 *S. aequisetis* added, C= Control. Data are mean values (n=3). *Outlier values not shown: Ammonium W2 LP= 1836.7 µmol/L; Nitrite W1 LP= 37.0 µmol/L, W1 PP= 40.6 µmol/L.

Initial concentrations of porewater nitrate in in both sediment sources ranged from 0-10.5 µmol/L, and were similar to concentrations recorded in the control units (Figure 6.5c). Significant differences however, were found between weeks, depths, and sediment sources ($p<0.05$; Appendix E Table S8), mainly due to the significantly higher concentrations of porewater nitrate found in the LP experimental units 1× and 2× in Week 2 ($p<0.05$; Figure 6.5c). Porewater nitrate concentrations were only influenced by *Capitella sp.* ($p<0.05$; Table 6.3). Concentrations of porewater nitrite in experimental units ranged from 0-17.4 µmol/L, and were similar to those in the control units (Figure 6.5d). Significant differences were not found between any factor ($p>0.05$; Appendix E Table S8), and direct effects of macrofauna on concentrations of nitrite in porewater were not detected (Table 6.3).

6.3.4.3 DGT/DET sulfide and iron

Sulfide concentrations in sediment porewater changed significantly across time and depth horizons ($p<0.001$; Table 6.4), and the influence of *S. aequisetis* and other macrofauna was evident (Figure 6.6a; Figure 6.7a). The initial two dimensional sulfide distributions showed near zero sulfide concentrations at the sediment surface, which increased with depth with the highest concentrations measured deeper sediments (Figure 6.6a). Concentrations of sulfide in LP (~10-150 µmol/L) and PP (~10-200 µmol/L) experimental units were higher than in the control units, where porewater sulfide concentrations were close to zero (Figure 6.6a; Figure 6.7a). Sulfide concentrations in LP and PP experimental units decreased over time, from ~10-200 µmol/L in Week 0, ~0-150 µmol/L in Week 1, to 0-100 µmol/L in Week 4 (Figure 6.6a; Figure 6.7a). Decreases in sulfide concentrations over time in the experimental units were the result of a uniform oxidation and no individual burrow structure were visible (Figure 6.6a). Significant differences in porewater sulfide concentrations were found across depths, sulfide concentrations decreased at shallower depth horizons (0-6 cm), and were more pronounced with depth, peaking between 8-12 cm (GAM $p<0.001$; Figure 6.7a). Shifts in sulfide concentrations across time and sediment depth were also identified, from ~150-200 µmol/L between 0-6 cm depth in Week 0 to ~0-25 µmol/L in the same horizon depth in Week 4, and between 6-12 cm depth sulfide decreased from ~100-150 µmol/L in Week 1 to ~50-100 µmol/L in Week 4 (GAM $p<0.001$; Figure 6.7a).

Iron(II) concentrations in sediment porewater were low in LP and PP experimental units (~0-3 µmol/L), and differed the control units (~0 µmol/L) (Figure 6.6b, Figure 6.7b; Appendix E Figure S3). Peaks of iron(II) concentrations were identified between 0-4 cm depth at LP I Week 1 and Week 2 (Figure 6.6b; Figure 6.7b). High variation in iron(II) concentrations were recorded across time and sediment depths in both LP and PP sediments (Appendix E Figure S3). Although significant differences in concentrations of iron were found across weeks and depth ($p<0.001$; Table 6.4), the model explained only 5% of the variation, as iron(II) concentrations in Week 0 and Week 4 in LP experimental units were significantly higher compared to any other experimental unit, due to the occurrence of "hotspots" of high iron(II) in some distributions (Figure 6.6b).

3.4.4 DET ammonium, phosphate and nitrite

The influence of *S. aequisetis* and other macrofauna on porewater profiles of ammonium concentrations was identified (GAM $p<0.001$; Figure 6.8a). Ammonium concentrations in sediment porewater varied significantly with time and sediment depth ($p<0.001$; Table 6.4). Concentrations of ammonium in LP (~10-1000 µmol/L) and PP (~10-250 µmol/L) experimental units were higher than in control units (Figure 6.8a). Porewater profiles of ammonium at LP showed peaks of high concentrations near the sediment surface in W0, decreasing at shallower depth horizons (0-6 cm), before increasing again in the deeper sediments (8-12 cm depth) (Figure 6.8a). Whereas, in PP and C sediments porewater ammonium concentrations showed more typical profiles with concentrations gradually increasing with depth. Ammonium concentrations also decreased over time, for example concentrations of ammonium decreased from ~10-1000 µmol/L in W0 to ~10-250 µmol/L in Week 4 in LP experimental units and LP profiles shifted to be more like those in the PP and C sediments, exhibiting gradually increasing concentration with depth (Figure 6.8a).

Concentrations of porewater phosphate were low across time and sediment depth in LP (~0-140 µmol/L) and PP (~0-20 µmol/L) experimental units, and similar to the control units in Week 1 and Week 4 (Figure 6.8b). Phosphate was significantly different across weeks and depth ($p<0.001$; Table 6.3), but the model only explained 8.61% of the variability. Phosphate concentration profiles showed similar trends to those of ammonium, with LP sediments exhibiting sub-surface peaks in W0, whereas, in Week 1 and Week 4 and in all three weeks in the PP and C treatments profiles were almost flat or showed gradual increase with sediment depth (Figure 6.8b).

Nitrate concentrations in porewater were barely detected, and similar between sediment sources (LP and PP experimental units) and control units (Appendix E Figure S4). Significant differences were not detected with time or sediment depth (p>0.001; Table 6.4), likely due to the low nitrate concentrations recorded.

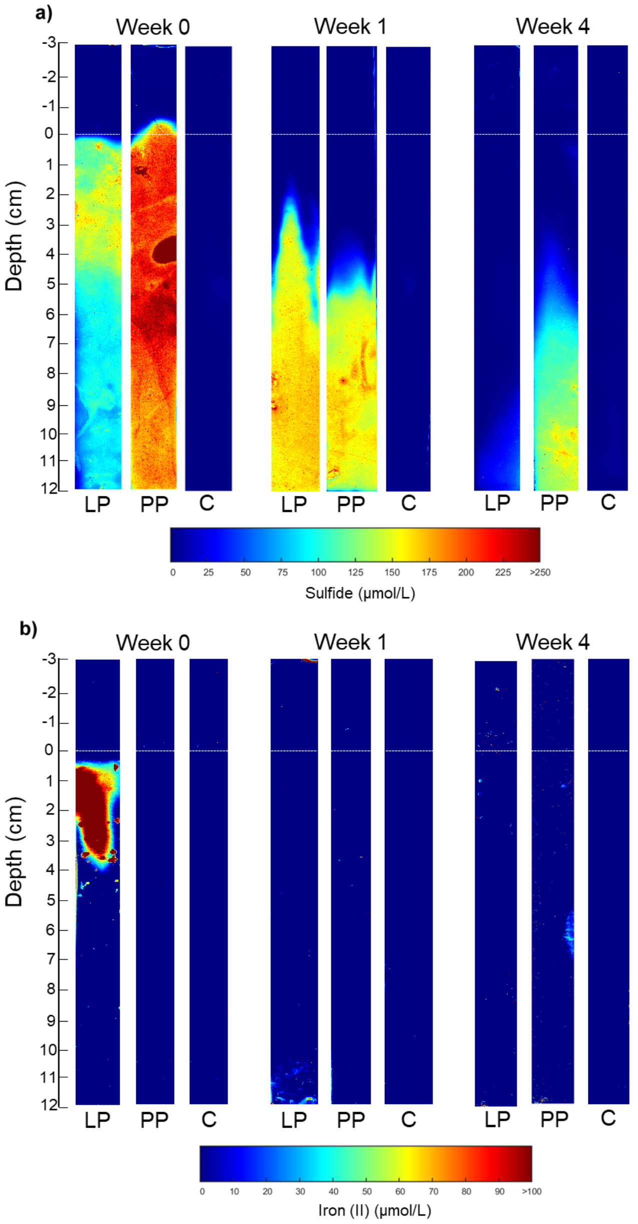


Figure 6.6. Typical examples of two dimensional sediment porewater concentration distributions of (a) colourimetric DGT measured sulfide and (b) colourimetric DET iron(II) in the experimental and control units in Week 0, Week 1, and Week 4. LP: Long Point; PP: Policeman Point; C: Control.

Table 6.4. Summary table of the results from the Generalized Additive Model (GAM) assessing porewater concentrations of a) sulfide, b) iron, c) ammonium, d) phosphate, and e) nitrate. W0 = Week 0, W1 = Week 1, W4 = Week 4.

Parametric coefficients:	Estimate	Std. Error	t value	Pr(>|t|)	Deviance explained	AIC
a) Sulfide						
Parametric coefficients						
Intercept (W0)	79.716	0.330	241.370	<0.001	48.80%	442260.0
W1	-26.985	0.469	-57.530	<0.001		
W4	-56.904	0.467	-121.770	<0.001		
Smooth terms						
Depth	edf = 8.711	Ref.df = 9	F = 2947.00	<0.001		
b) Iron						
Parametric coefficients						
Intercept (W0)	1.313	0.028	46.686	<0.001	5.00%	232187.4
W1	-0.922	0.040	-23.004	<0.001		
W4	-0.206	0.040	-5.171	<0.001		
Smooth terms						
Depth	edf = 8.793	Ref.df = 9	F = 190.90	<0.001		
c) Ammonium						
Parametric coefficients						
Intercept (W0)	225.210	9.058	24.864	<0.001	18.50%	1468413.0
W1	-102.357	12.202	-8.389	<0.001		
W4	-118.873	12.307	-9.659	<0.001		
Smooth terms						
Depth	edf = 4.467	Ref.df = 9	F = 15.76	<0.001		
d) Phosphate						
Parametric coefficients						
Intercept (W0)	14.487	0.944	15.35	<0.001	8.61%	10304.5
W1	-10.355	1.322	-7.831	<0.001		
W4	-7.126	1.335	-5.339	<0.001		
Smooth terms						
Depth	edf = 3.911	Ref.df = 9	F = 4.79	<0.001		

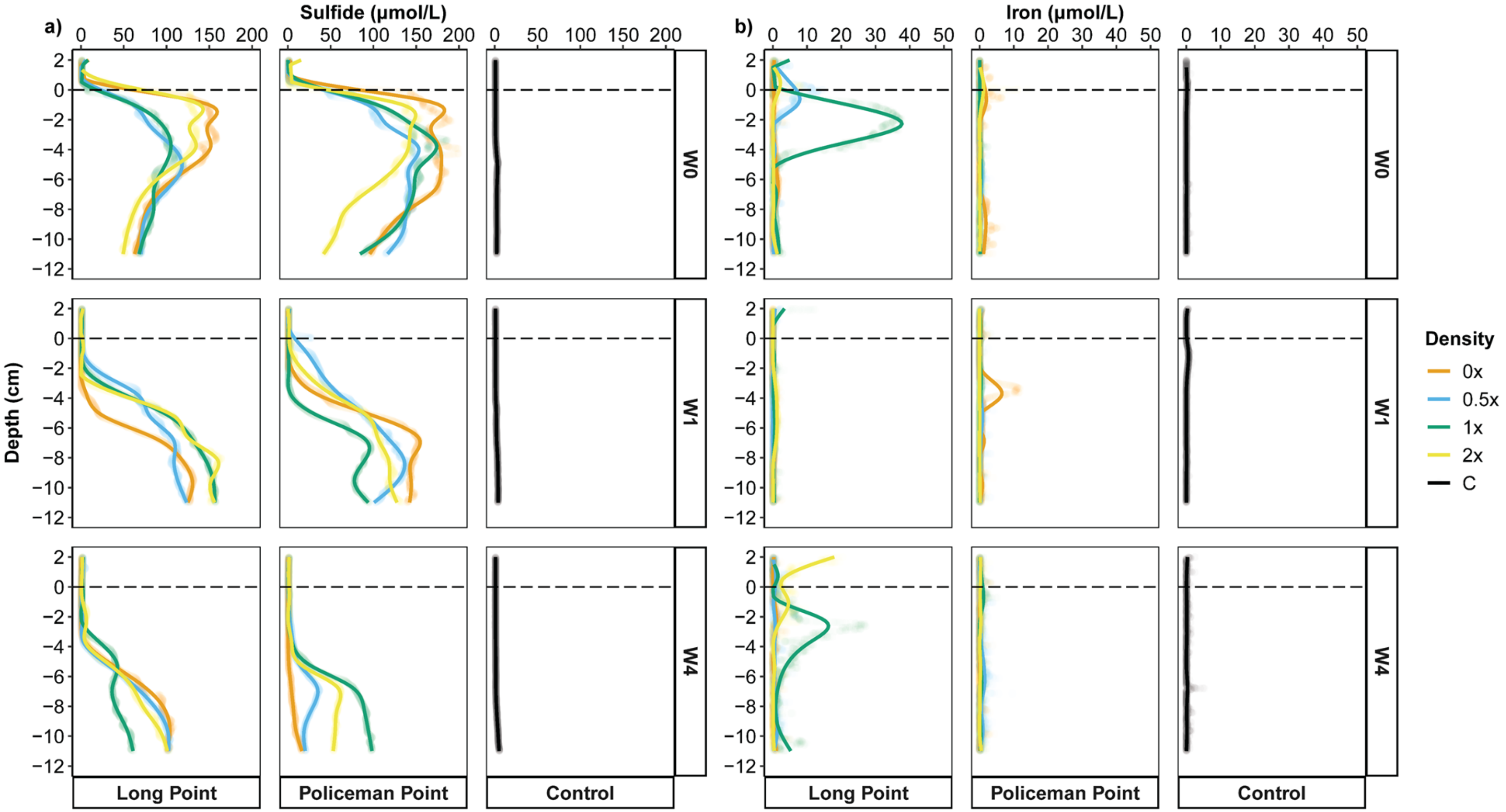


Figure 6.7. Generalized Additive Model (GAM) plots of sediment porewater concentrations profiles of a) sulfide and b) iron(II). Plots show significant differences in sulfide and iron(II) concentrations, and the influence of *S. aequisetis* and other macrofauna densities across weeks and depths. Colour shading represents the data values. W0 = Week 0, W1 = Week 1, W4 = Week 4. 0x = no *S. aequisetis* added, 0.5× = 3 *S. aequisetis*, 1× = 5 *S. aequisetis*, and 2× = 10 *S. aequisetis* added, C= Control. n=3.

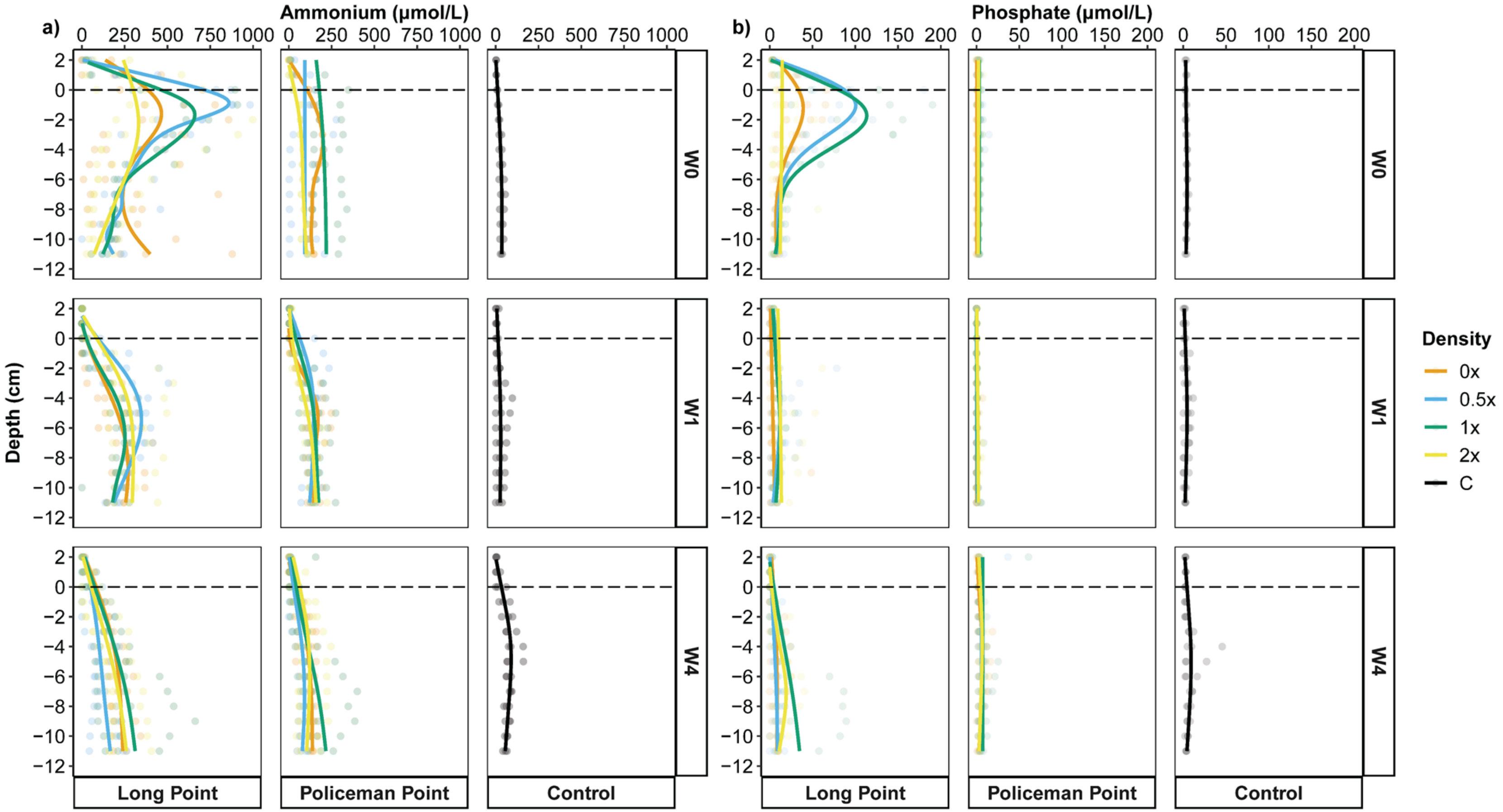


Figure 6.8. Generalized Additive Model (GAM) plots of sediment porewater concentrations for a) ammonium and b) phosphate . Plots show significantly differences in ammonium and phosphate concentrations, and the influence of *S. aequisetis* and other macrofauna densities across weeks and depths. Points coloured represents the data values. W0 = Week 0, W1 = Week 1, W4 = Week 4. 0× = no *S. aequisetis* added, 0.5× = 3 *S. aequisetis*, 1× = 5 *S. aequisetis*, and 2× = 10 *S. aequisetis* added, C= Control. n=3.

6.4. Discussion

In this study, we used an *in situ* experimental sediment translocation approach to test the short-term influence of bioturbating macrofauna on the biogeochemistry of hostile (i.e. hypersaline, sulfide-rich) sediment translocated to a less hostile environment. Our results showed that restoration of the bioturbation functions of benthic macrofauna, and in particular the polychaete *S. aequisetis*, modified the sediment biogeochemistry, promoting a healthier state (i.e., lower sulfide, ammonium and organic carbon concentrations) within a few weeks (following creation of suitable salinity conditions). This highlights that the preservation or restoration of benthic macrofauna communities is important to help prevent the formation of or to remediate hostile conditions in sediments.

6.4.1 Macrobenthic fauna recolonization

The findings of our *in situ* experiment showed that macrobenthic fauna colonised hypersaline and defaunated control sediments in a short period of time (one week). In the Coorong, macrobenthic communities are structured by the extreme salinity gradient, resulting in hypersaline regions without any bioturbating macrofauna (Dittmann et al. 2015, Dittmann et al. 2018, Lam-Gordillo et al. 2022). Evidence suggested that macrobenthic organisms inhabited these regions until prolonged periods of hypersalinity occurred (Cann and Lowers et al. 2018). In our experiment, colonisation of macrobenthic fauna was enabled by the translocation of sediment from a hypersaline site (PP) to a lower salinity site (LP). Porewater salinity in the experimental units rapidly decreased over time, likely promoted by the sandy sediments readily facilitating the exchange and dilution of porewater with surface water, reaching favourable salinity levels (<60) where many macrobenthic organisms can survive (Dittmann et al. 2015, Remaili et al. 2018, Lam-Gordillo et al. 2022). This allowed the sediment colonisation by macrobenthic fauna, promoting dilution of salinity in even deeper sediment horizons by burrowing and bioturbating activities (Lam-Gordillo et al. 2020).

6.4.2 Macrobenthic fauna effects on sediment biogeochemistry

Macrobenthic fauna have striking influences on sediment biogeochemistry, by actively mixing solid phases and modifying conditions with the sediment via their bioturbation, bioirrigation and bioventilation activities. These activities influence the distribution and mineralisation rates of organic matter, the exchange of solutes between the sediment and water column, and the distribution of redox zones within the sediment (Kristensen 2001, Welsh 2003, Wyness et al. 2021). The results from our *in-situ* experiment suggested that changes in sediment biogeochemistry and porewater nutrient concentrations were influenced by both *S. aequisetis* and other naturally colonising bioturbating macrofauna, which aligned with our first hypothesis. Our experiment showed that the hostile sediment conditions were reduced (i.e. decreases in ammonium, phosphate, TOC, sulfide, and iron concentrations), including in experimental units with no addition of *S. aequisetis* (0x - treatment) due to colonisation of the sediment by other macrobenthic fauna, despite the addition of mesh (500 µm) on both ends of the experimental units. Yet, the nutrient concentration pattern was idiosyncratic, and could be attributed to differences in abundance, composition and functional traits of the local communities, as previously reported in other experimental and field studies (e.g. Mermillod-Blondin et al. 2004, Braeckman et al. 2010, Kauppi et al. 2018, Casado-Coy et al. 2020, Kendzierska et al. 2020, Lam-Gordillo et al. 2021, 2022).

6.4.3 Bioturbation effects on sediment biogeochemistry over time

In accordance with our second hypothesis, our experiment showed that macrobenthic fauna remediated the hostile sediment conditions over time. The concentration of TOC and TN in sediment decreased within weeks, which could be correlated with the bioturbating activities by macrobenthic fauna. It has been suggested that biodiffuser and bioirrigator organisms, in combination with several feeding modes, promote microbial activities which are ultimately responsible for organic matter (i.e. TOC) mineralisation (Welsh 2003, Braeckman et al. 2014, Bon et al. 2021). For example, organisms such as *S. aequisetis* and amphipods that build and inhabit burrows, are proposed to influence organic matter degradation rates by increasing oxygen transfer to the sediment by irrigating their burrows with the overlying water (Kristensen 2000, Welsh 2003, Volkenborn et al. 2012). This results in a greater proportion of the organic matter being metabolised via aerobic pathways, which results in faster degradation rates as organic matter breakdown, especially older more recalcitrant organic matter fractions (See Kristensen 2000 for review). It has been suggested that organic matter mineralisation rates under the oscillating oxic/anoxic conditions that can occur in burrow wall sediments can be even faster than those that occur under fixed oxic or anoxic conditions (Aller 1994). This aligned with our results, showing that the TOC and TN concentrations recorded in Week 1 were reduced in Week 4, potentially due to the macrofauna bioturbation activities. It was also identified that the deepest horizon recorded the lowest content of TOC and TN concentrations, and the top horizon the highest TOC and TN concentrations, which could result from the growth of microphytobenthos and the biodeposition of organic matter by the fauna (Graf and Rosenberg 1997). Fauna can increase deposition of organic matter both directly by suspension feeding and the deposition of the captured organic matter as faeces and pseudofaeces, or indirectly by modifying the surface topography of the sediment, resulting in increased entrainment and deposition of suspended particles (See Graf and Rosenberg 1997 for review).

Based on the Rhizon-extracted porewater samples and DET measured concentration gradients, ammonium concentrations were higher before the addition of *S. aequisetis*, which could be explained by the lack of oxic (redox) zones and macrobenthic fauna in sediments from both experimental units (Welsh 2003, Stief 2013, Wyness et al. 2021). The absence of macrobenthic fauna (i.e. *S. aequisetis* in this experiment) and in general in Coorong South Lagoon and their activities (i.e., bioirrigation and bioventilation), favours accumulation of ammonium in the sediment porewater due limited exchange with the overlying water and the absence of oxic sediment zones where ammonium can be oxidised to nitrite and nitrate via nitrification (Welsh 2003, Stief 2013). Consequently, in defaunated sediments ammonium efflux to the water column is essentially limited to diffusive exchange between the sediment porewater and overlying water across the sediment surface. In contrast, the addition of *S. aequisetis* and colonization of the experimental units by other macrofauna over the course of the experiment, would be expected to promote the export of porewater from the sediment and thereby decrease porewater ammonium concentrations throughout the depth profile (Welsh 2003, Stief, 2013, Wyness et al. 2021). Macrobenthic fauna construct burrows increasing the surface area for diffusive exchange between porewater and water column by up to 500% (Welsh, 2000 and references therein). The periodic bioventilation of these burrows by their residents flushes ammonium accumulated in the burrow water to the water column and maintains steep ammonium concentration gradients in the burrow wall sediments that drive further diffusive fluxes to the burrow water (Kristensen 2000, Welsh 2003, Stief 2013). Moreover, in permeable sandy sediments, such as those in this study, the bioventilation of burrows can induce flow of water through the sediment itself (bioirrigation) and mass transport of sediment porewater and its solute load to the overlying water column (Kristensen 2000, Welsh 2003). Macrobenthic fauna also promote sediment oxygenation and the formation of oxic sediment zones around their burrows through the same burrow construction, bioirrigation and bioventilation activities (Robertson et al. 2009, Volkenborn et al. 2012, Stief 2013), which provides an increased volume of sediment where nitrification can occur. Increased rates of bacterial nitrification would also favour removal porewater ammonium by oxidising ammonium to nitrite and nitrate, resulting in lower porewater ammonium concentrations as previously observed in other studies (e.g. Jordan et al. 2009, Norkko et al. 2019, Wyness et al. 2021). Over time, as the colonisation process progressed, the zone of sediment influenced by the fauna increased, average porewater ammonium concentrations decreased and porewater ammonium depth profiles became increasingly flattened.

Although less evident, depth profiles of phosphate concentrations based on both Rhizon-collected porewater and DET samplers followed similar patterns to those of ammonium concentrations, with phosphate increasing with depth but in general decreasing over time. We found indications that the change on porewater phosphate concentrations over time were influenced by the bioturbation of benthic macrofauna, particularly *Capitella sp.*, a small, disturbance-tolerant polychaete. These results are consistent with those recorded for ammonium, as the effects of increased surface area of burrow walls, bioirrigation and bioventilation would influence exchanges of all porewater solutes with the overlying water, and with results of previous studies suggesting that the export of porewater phosphate concentrations to overlaying water is generally stimulated by the presence of benthic macrofauna (e.g. Mermillod-Blondin et al. 2004, Karlson et al. 2005, Kendzierska et al. 2020). Additionally, increased oxygenation and oxidation of the sediment would also influence sediment and porewater phosphate concentrations. Sediment oxidation would result in the rapid oxidation of porewater and solid phase iron(II) and the formation of iron(III) oxyhydroxides, which can efficiently adsorb and sequester phosphate from sediment porewaters, limiting its availability and mobility (de Witt et al. 2001, Azzoni et al. 2001).

In contrast to ammonium and phosphate, concentrations of oxidised nitrogen (nitrate and nitrite) based on extracted porewaters and DET profiles were low, although some changes in porewater nitrate concentrations were identified, e.g. increased concentrations in Week 2-Week 3 in both LP and PP and decreased concentrations in Week 4. The initial ‘low concentrations’ aligned with the highly anoxic and sulfide-rich sediment conditions, which would restrict the nitrification, as this is a strictly aerobic process (Welsh 2003, Nizzoli, et al. 2006, Hardison et al. 2015, Casado-Coy et al. 2020). Thus, the increased concentrations in Week 2-Week 3 may reflect the oxygenation of the sediment and the formation of oxic sediment zones where nitrification could proceed and the subsequent decrease may reflect the decreased availability of ammonium for nitrification and/or increased coupling between nitrification and nitrate reduction processes (denitrification and DNRA), However, whilst this scenario would be consistent with the general consensus that benthic macrofauna stimulate both rates of nitrification and coupled nitrate reduction processes (See Stief, 2013 for data compilation and review), further specific studies are required to evaluate to what extent this would occur if conditions in the South Lagoon were remediated to allow colonisation of the sediments by macrofauna.

Based on DET-DGT profiles and two-dimensional distributions, our results showed that porewater sulfide concentrations in PP sediments were high and increased with depth. The high concentrations of sulfide were consistent with highly anoxic sediment conditions. However, sulfide concentrations decreased over time following translocation, which can be explained by macrobenthic fauna functioning. Macrobenthic organisms, through their burrow construction, bioturbation, bioirrigation and bioventilation activities increase the transport of oxygen to the sediment and especially into deeper sediments, promoting aerobic respiration, and chemical and chemoautotrophic reoxidation of sulfide (e.g. Pagès et al. 2012, Casado-Coy et al. 2020, Kankanamge et al. 2020). The uniform and homogenous nature of changes in the two dimensional sulfide distributions over time also supports the hypothesis that bioventilation was a significant process in the permeable study sediments, as typically in impermeable fauna burrows are visible as distinct structures surrounded by halos of oxic and sub-oxic redox zones, as sediment oxidation is dependent upon the diffusion of oxygen from the burrow waters to the surrounding sediment (Robertson et al. 2008, 2009, Volkenborn et al. 2012, Kankanamge et al. 2020).

Porewater concentrations of dissolved iron(II) were typically low with only fairly rare “hotspots” present, which may be related to the decomposition of an animal killed by the freezing of LP sediments to kill any resident fauna present. Whilst these low iron(II) concentrations may reflect the generally low iron pools present in the Coorong sediments (Mosley et al. 2020), they are also consistent with the rapid changes in sediment redox status that occurred over the course of the experiment. As in the initially highly sulfidic PP sediments iron would principally be present as sulfide mineral phases such as iron monosulfide and pyrite (iron disulfide), which upon oxidation would have been converted to equally insoluble iron(III) oxyhydroxides.

Overall, the changes in iron(II) and sulfide distributions in the PP experimental units are consistent with the colonisation of these sediments by fauna having induced a rapid oxidation of the sediment, as porewater iron(II) and sulfide represent biogeochemical markers of anoxic and sub-oxic sediment zones, respectively. Thus in the PP experimental units the initial anoxic (sulfidic) sediments were progressively replaced by oxic (sulfide and iron(II) free) sediment zones.

6.4.4 Implications for estuarine lagoon systems

Estuarine lagoon ecosystems provide important ecosystem services, for example alleviating coastal eutrophication by acting as buffer areas for terrestrial nutrient loads (Villnäs et al. 2019, O’Meara et al. 2020). Yet, the buffer capacity of estuaries is constantly challenged by increased nutrient loads, algal blooms, and reduced freshwater inputs, threatening the healthy functioning of these ecosystems (Cloern 2001, Nixon 2009, Cloern et al. 2016). This study in the Coorong demonstrates that the preservation, and potentially promoting and/or re-introducing, macrobenthic fauna communities, and therefore their functions should improve sediment conditions by reducing concentrations of ammonium and sulfide, and promoting oxic conditions in the sediment, which enhances microbial activities ultimately responsible for organic matter mineralisation and nutrient cycling (Welsh 2003, O’Meara et al. 2020, Wyness et al. 2021). This was evident for concentrations of sulfide, ammonium, and phosphate in Coorong sediments, which were reduced over time by the macrobenthic fauna (e.g. *S. aequisetis)* activities of bioturbation, bioirrigation and bioventilation, promoting the remediation of the initially hostile sediment conditions and reducing sediment and organic matter build-up. Our research thus suggests that recolonisation of hostile sediments by macrobenthic fauna can occur when hypersalinity, or other inhibitory conditions preventing organism survival, are lowered sufficiently. Promoting or re-establishing healthy macrobenthic fauna communities will assist recovery and promote biogeochemical functioning in benthic ecosystems. Activities promoted by macrobenthic communities provide a nature-based option to management actions for improving estuarine lagoons with anoxic-eutrophic-hypersaline conditions. Reducing salinity in the South Lagoon of the Coorong sufficiently (<60). In combination with other mitigation and restoration activities, could allow recolonisation of the sediment by macrobenthic fauna, which in turn would improve sediment conditions and ecosystem functioning. However, larger scale mesocosm experiments, which also encompassed the water column and water column processes would be beneficial to illustrate the potential pros and cons of interventions to reduce the salinity in the South Lagoon and the response of macrobenthic fauna.

6.5. Conclusion

A pathway for benthic macrofauna facilitated remediation of hostile sediment conditions was elucidated from our *in situ* experiment. The short-term effects of bioturbating macrobenthic fauna, irrespective of the added *S. aequisetis* density, resulted in decreased concentrations of sulfide, ammonium, and phosphate in sediment porewater, and TOC in sediment, with the influence of macrobenthic fauna becoming more evident over time. Our results showed that the bioturbating fauna reduced concentrations of toxins like sulfide and ammonia, and helped to promote oxic conditions in sediment, which enhanced organic matter turnover and nutrient cycling rates that were previously limited the lack of macrobenthic organisms. This research highlights the importance of management actions that may promote the maintainence or re-establishment of benthic macrofauna communities for improving resilience to hostile conditions, assuring good functioning of estuarine benthic ecosystems, and allows managers to find nature-based solutions to conserve and improve the health of these important estuarine lagoon ecosystems.

Chapter 7. General Discussion

Marine soft sediments are considered one of the most productive habitats in the world. These ecosystems harbour a remarkable number of species and highly diversified macrobenthic communities involved in several ecosystem functions, processes, and services. Current anthropogenic pressures, such as climate change, habitat fragmentation, and pollution are the main drives of biodiversity loss, and for macrobenthic communities, such loss can modify the functioning of marine soft sediment ecosystems. In this thesis, I have investigated the functional ecology of marine macrobenthic communities, and their influence on ecosystem functioning. Several approaches and methodologies were considered to assess the functioning of marine macrobenthic fauna in soft sediments, including a global research weaving analysis (Chapter 2), functional traits classification derived from field surveys and literature (Chapter 3), regional empirical surveys measuring functional diversity across different habitats (Chapter 4), a local empirical study revealing changes in macrobenthic fauna, functional traits and their relationships with environmental conditions (Chapter 5), and an *in situ* manipulative experiment testing the functioning of macrobenthic fauna for sediment remediation (Chapter 6).

7.1 Overview of the main results

Investigating the relationship between macrobenthic biodiversity and ecosystem functioning in marine ecosystems has become topical in ecological research, motivated by the loss of biodiversity and its effects on ecosystem functions and services. The main aim of this PhD project was to understand the functional ecology of macrobenthic communities and investigate the relationship between ecosystem functioning and macrobenthic fauna using functional perspectives. To achieve this aim, I developed five interconnected data chapters (Figure 7.1) to provide a holistic understanding of the macrobenthic fauna – ecosystem functioning relationship using functional perspectives.

My review (Chapter 2; Lam-Gordillo et al. 2020a) applied a novel research weaving analysis which showed that the research topic of functional diversity and ecosystem functioning of marine macrobenthic fauna has been growing over the last decade, motivated by a need to understand how changes in macrobenthic communities influence the functioning and services of ecosystems. Despite the growing research field, several inconsistencies and knowledge gaps in terminology, methodology and metrics were identified. Therefore, I provided a global overview on the research topic for unifying the research field with a coherent terminology, methodology and metrics, and delivered a step-by-step framework towards a global consensus in ecosystem functioning and the use of functional approaches for marine macrobenthic fauna.

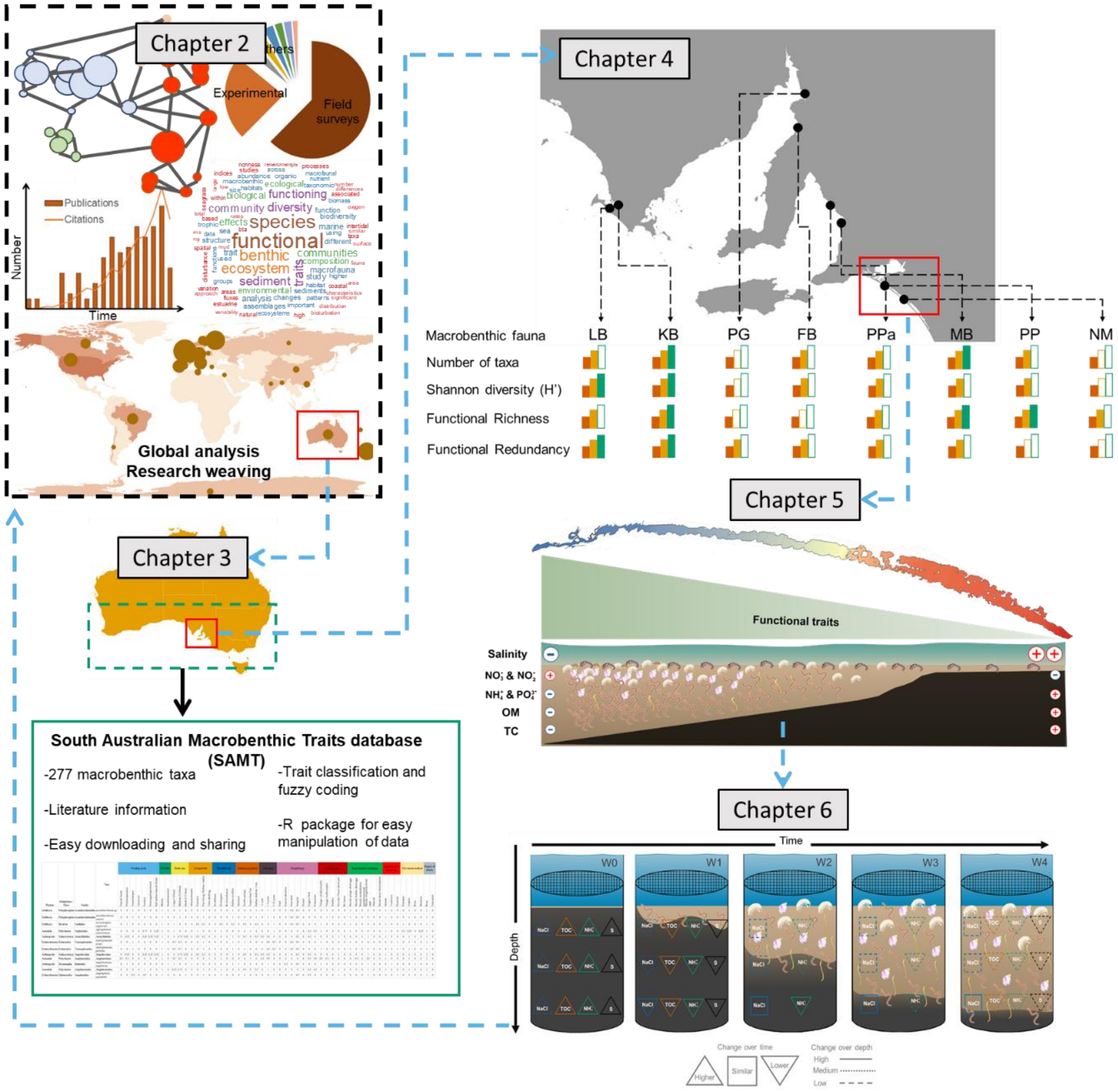


Figure 7.1. Summary of the main outcomes of the five data chapters included in this PhD thesis. Chapters are inter-linked and followed a structured sequenced, ranging from global (Chapter 2) to regional (Chapter 3 and 4) and local (Chapter 5 and 6) scale investigations.

The review presented in this PhD thesis also demonstrated the lack of macrobenthic functional trait information, especially for southern temperate soft sediments (Chapter 2; Lam-Gordillo et al. 2020a). To reduce the knowledge gap of macrobenthic traits, I collected macrobenthic trait information (e.g. life history, morphology, physiology, and behaviour) from different sources (e.g. literature: local, national, international, expert knowledge), developed and introduced the South Australian Macrobenthic Traits (SAMT) database (Chapter 3; Lam-Gordillo et al. 2020b). The SAMT database will assist functional assessments, providing a trait classification for more than 250 macrobenthic taxa. A fuzzy coding analysis was applied on these macrobenthic taxa to provide a standardised and comparable classification for future assessments. Furthermore, a step-by-step guide is provided detailing the use and functionality of the SAMT database, which enables functional assessments in temperate Australian waters (Chapter 3; Lam-Gordillo et al. 2020b) that can be used as baseline for other temperate waters around the world. In addition, a R package was developed and released for assistance in using and analysing the SAMT database, as well as future functional assessments.

My work further addressed the knowledge gaps identified (i.e. use of standardised terms, traits, and methods, and investigations in regions with no or little prior functional data) in the global analysis (Chapter 2; Lam-Gordillo et al. 2020a) and applied the outcomes from the SAMT database (Chapter 3; Lam-Gordillo et al. 2020b) to perform a holistic functional assessment across three different soft sediments habitats (coastal embayment, gulfs, and lagoon) along ~1,260 km of the South Australian temperate coastline (Chapter 4; Lam-Gordillo et al. 2021). The analysis of functional and taxonomic patterns demonstrated that changes in taxonomic diversity are positively corelated with changes in functional diversity (e.g. Functional richness, Functional redundancy), which are ultimately mediated by the intrinsic characteristics of each habitat (e.g. habitat geomorphology, salinity, sediment characteristics). Changes in the relationships between macrobenthic fauna, functional traits, and environmental conditions at each of the survey locations were also identified, suggesting different ecosystem functioning along the South Australian coastline (Chapter 4; Lam-Gordillo et al. 2021). The results presented in Chapter 4 contribute to the growing body of knowledge in the research field, supporting that functional and taxonomic patters are highly variable and subjected to environmental context (Gladstone-Gallagher et al., 2017; Thrush et al., 2017; Gammal et al., 2019). This holistic study provided new insight into links between macrobenthic fauna, functional traits, and environmental conditions, and possible derived ecosystem functioning, but also showed that complementary perspectives of taxonomic and functional metrics can be beneficial.

Furthermore, the functional assessment performed along the South Australian coastline identified habitats of particular concern for conservation and management, due to low functional diversity and functional redundancy compared to other habitats (Chapter 4; Lam-Gordillo et al. 2021). Based on these results, two further functional assessments were performed (Chapters 5-6) to gather a more detailed evaluation of the identified vulnerable ecosystem. A localised field study along a salinity gradient (estuarine-to-hypersaline) was performed to investigate the ecosystem functioning of this particular habitat using a functional perspective (Chapter 5; Lam-Gordillo et al. 2022), and an *in situ* experiment to investigate sediment remediation by macrobenthic functional diversification (Chapter 6).

My field study along the salinity gradient revealed that changes in macrobenthic communities and functional traits correlated with changes in sediment biogeochemistry (Chapter 5; Lam-Gordillo et al. 2022). It was also revealed that it was mostly bioturbating macrofauna, and the functional trait ‘bioturbation’, that influenced sediment biogeochemistry, promoting nutrient cycling and sediment remineralisation, while the absence of macrobenthic organisms and bioturbation in hypersaline locations favoured the accumulation of organic matter and nutrients in the sediment. Changes in macrobenthic fauna and functional traits, and their dependency to site-specific environmental conditions aligned with previous investigations in other regions around the world (e.g. Henseler et al., 2019; Villnäs et al., 2019). This study provides further evidence of the strong correlation between macrobenthic fauna, their functional traits and sediment biogeochemistry (e.g. Braeckman et al., 2014; Villnäs et al., 2019; Bon et al., 2021), highlighting the pivotal role of macrobenthic organism for maintaining healthy ecosystem functioning, and mitigating the potential impacts of eutrophication in estuarine ecosystems.

Based on the outcomes from chapter 5 which detected sediment conditions hostile to macrobenthic occurrence (Lam-Gordillo et al. 2022), I further investigated the potential sediment remediation by macrobenthic fauna in an *in situ* manipulative experiment (Chapter 6). This experimental investigation demonstrated that the bioturbating macrofauna influenced sediment biogeochemistry by reducing the concentrations of total organic carbon and porewater sulfide, ammonium, and phosphate (Chapter 6). More important, it was demonstrated that hostile (i.e. sulfide-rich) sediments can be remediated over time (i.e. four weeks) due to the bioturbating processes performed by macrobenthic fauna. The research carried out in chapter 6 highlighted how essential macrobenthic fauna and their functional traits are for improving sediment conditions, providing a nature-based remediation option, and in general ensuring healthy functioning of estuarine ecosystems.

The combination of the outcomes presented in each chapter in this PhD thesis demonstrated that the loss of macrobenthic biodiversity in soft-sediments, and their functional traits, can affect the functioning of the ecosystems and their services. I further provide timely information on the functional ecology of marine macrobenthic communities to assist in the understanding of ecosystem functioning of marine soft sediment habitats, and their implications for future management and conservation strategies.

7.2 Current status of marine macrobenthic functional traits across southern Australia

Functional traits have been increasingly used in ecological research aiming to assist the understanding of the relationship between biodiversity and ecosystem functioning (Hooper et al. 2005; Bremner et al. 2003, 2006; Weiss and Ray 2019; Thrush et al. 2021). In marine ecosystems, functional traits and trait-based approaches have gained momentum, linking macrobenthic communities to the functioning of ecosystems, as functional traits relate to changes in functions across ecosystems (Díaz and Cabido 2001; Bremner et al. 2003; 2006; Castro et al. 2019; Chapter 2, Lam-Gordillo et al. 2020a; Thrush et al. 2021).

Despite the relevance of functional traits and its applicability for functional assessments, trait information is not always available for macrobenthic organisms (Beauchard et al., 2017; Chapter 2, Lam-Gordillo et al. 2020a; Thrush et al. 2021). Trait databases have been created in the Northern hemisphere, specifically in Europe, for example the Biological Traits Information Catalogue (MarLIN 2006) and Polytratis (Faulwetter et al. 2014), and in Polar Oceans (Degen and Faulwetter 2019). However, the terminology was lacking standardization, making it difficult to compare across databases and regions. Other constraints in the use of functional traits include knowledge gaps in identification keys for many macrobenthic fauna, and thus functional traits assigned based on various taxonomic resolution (Chapter 2, Lam-Gordillo et al. 2020a).

In soft sediments of New Zealand, functional traits have been applied in a wide range of studies, for example describing the influence of functional traits on ecosystem functioning (e.g. Lohrer et al. 2004; Schenone and Thrush 2020; Hillman et al. 2021; Thomas et al. 2021) and multifunctionality (e.g. Siwicka et al. 2021), mapping (e.g. Schenone et al. 2021), relating to sediment biogeochemistry (e.g. O'meara et al. 2020), predicting ecosystem functioning and services at different spatial and temporal scales (e.g. Gladstone-Gallagher et al. 2019; Gammal et al. 2020; Hillman et al. 2020; Rullens et al. 2022), and theoretical studies (Siwicka et al. 2020). Yet, most of these studies focused on specific taxa (e.g. bivalves) and particular functional trait (e.g. bioturbation), lacking in an available standardized functional trait classification for the macrobenthic organisms that inhabit that region.

In contrast, research on macrobenthic functional traits in soft sediments of southern temperate Australia was scare or non-existence until the last couple of years (see review Chapter 2, Lam-Gordillo et al. 2020a). Although, previous studies in the region assessed specific functional traits of macrobenthic organisms (e.g. Morris and Keough 2003; Macleod et al. 2008; O'Brien et al. 2009; Tweedley et al. 2012; Banks et al. 2013; Tweedley et al. 2015), a functional perspective was absent in these assessments, and the macrobenthic ecosystem functioning for southern Australia was understudied (Chapter 2, Lam-Gordillo et al. 2020a). Thus, the South Australia Macrobenthic Traits (SAMT) database was introduced (Chapter 3, Lam-Gordillo et al. 2020b) to assist with a functional trait classification in southern temperate Australia waters. The SAMT database provided trait information for more than 250 macrobenthic taxa that inhabit southern temperate waters. The trait classification included results from fuzzy coding analysis and an expanded literature with trait information for each taxon. The SAMT database was designed with a standardized trait classification, allowing comparison across multiple taxa, geographical areas, and studies (Costello et al. 2015; Chapter 3, Lam-Gordillo et al. 2020b).

The SAMT database is to be continually updated and expanded adding more taxa, functional traits, ecosystems, and regions. The SAMT database aims to become the foundation to develop a trait database for southern temperate regions beyond Australia, similar to the databases created in Europe (MarLIN 2006; Faulwetter et al. 2014) and Polar Oceans (Degen and Faulwetter 2019), to assist functional perspectives in this region. With the introduction of the SAMT database, assessments using functional perspectives were enabled with localised information derived from southern temperate region. Since implementation, the SAMT database and all its resources (e.g. functional traits, fuzzy coding classification, R package) have been used to assess the relationship between macrobenthic fauna and ecosystem functioning in South Australia coastline facilitating the allocation of trait information and further functional analysis (e.g. Muller et al. 2021; Chapter 4, Lam-Gordillo et al. 2021; Chapter 5, Lam-Gordillo et al. 2022), which has provided a better understanding of the functioning of soft sediment ecosystems in temperate Australia.

The implementation and use of macrobenthic functional traits (e.g. SAMT database; Chapter 3, Lam-Gordillo et al. 2020b) has facilitated functional assessments along the southern Australian coast. However, outcomes from functional traits analyses require to be interpreted with caution, as these analyses inherited some limitations (Thrush et al. 2021). Such limitations include, for example, missing knowledge on taxonomic information (Chapter 2, Lam-Gordillo et al. 2020a) and the traits of organisms (Thrush et al. 2021), the functional traits available and selected to assess specific questions of a determined research (Thrush et al. 2021), and functional trait plasticity that could be expressed depending on the environmental conditions (Cesar and Frid 2012; Thrush et al. 2021).

7.3 Functional assessments on macrobenthic biodiversity and ecosystem functioning in southern Australia soft sediments

This PhD thesis provided the first assessments on macrobenthic biodiversity and ecosystem functioning in southern Australian soft sediments, thus contributing to the growing body of knowledge of this research field. Using functional perspectives, my study along the south Australian coastline revealed different spatial and temporal patterns of macrobenthic communities based on taxonomic and functional metrics (Chapter 4, Lam-Gordillo et al. 2021).

The variation in taxonomic and functional metrics recorded along the distinct surveyed locations in South Australia, identified differences in ecosystem functioning across habitats and seasons, providing new information on the functioning of these ecosystems (Chapter 4, Lam-Gordillo et al. 2021). Most of the sites analysed showed greater number of taxa and diversity (H') correlated with high functional diversity, as described in other marine ecosystems (e.g. Hajializadeh et al. 2020; Delfan et al. 2021; Shojaei et al. 2021). But mismatches in patterns between taxonomic and functional metrics also emerged, for which there is also evidence in other studies (e.g. Emmerson et al. 2001; Frid and Caswell 2015; Gladstone-Gallagher et al. 2017). A possible explanation for variability in correlations between taxonomic and functional metrics could be the specific environmental characteristics of each site, as described in previous studies (e.g. Hewitt et al. 2008; Strong et al. 2015; Kokarev et al. 2017; Thrush et al. 2017). The idiosyncratic pattern across sites was also evident for the relationship between macrobenthic fauna, their functional traits, and environmental conditions, showing site-dependent correlation patterns (Chapter 4, Lam-Gordillo et al. 2021). More importantly, outcomes from functional approaches can contribute to conservation and management strategies (Miatta et al. 2021, Thrush et al. 2021). For example, the functional analysis carried out on the southern Australian coast highlighted habitats in need of management due to their low functional diversity and functional redundancy (e.g. the Coorong Lagoon system) (Chapter 4, Lam-Gordillo et al. 2021).

Soft sediment habitats with low functional redundancy, (i.e. habitats in the Coorong system), were further explored using functional perspectives. Outcomes showed changes in macrobenthic fauna and their functional traits across a salinity gradient (estuarine to hypersaline) (Chapter 5, Lam-Gordillo et al. 2022). Similar to the study along the South Australian coast (Chapter 4, Lam-Gordillo et al. 2021) and in other regions (e.g. Wong and Dowd 2015; Gladstone-Gallagher et al. 2017; Gammal et al. 2019), different relationships between macrobenthic fauna, functional traits and environmental conditions were recorded along the Coorong, influenced by the environmental characteristics of each site (Chapter 5, Lam-Gordillo et al. 2022, Hewitt et al. 2008; Douglas et al. 2019; Gammal et al. 2019; Henseler et al. 2019; Villnäs et al. 2019). Relationships between macrobenthic fauna and sediment biogeochemistry has been previously described in other systems (e.g. Braeckman et al. 2014; Villnäs et al. 2019; Bon et al. 2021). My PhD project revealed that the changes on macrobenthic fauna and functional traits correlated with changes in sediment biogeochemistry, which could be explained by the functional traits that these organisms expressed. For example, macrobenthic fauna promotes the oxygenation of sediment by bioturbating activities, trigging exchange of porewater nutrients, and nitrification and denitrification processes (Welsh 2003; Stief 2013; Norkko et al. 2019; Wyness et al. 2021). These outcomes further highlight the importance of macrobenthic communities as main drivers of ecosystem functioning, particularly promoting nutrient cycling and sediment mineralisation by bioturbating processes.

This new information for the southern temperate soft sediments in Australia advances the understanding of the macrofauna-ecosystem functioning relationship, and further highlights the importance of preserving healthy benthic communities to ensure the functioning of soft sediment ecosystems.

7.4 Response of macrobenthic fauna to environmental conditions in soft sediments of southern Australia

Macrobenthic organisms have striking influences on sediment biogeochemistry and nutrient fluxes of soft sediment habitats (Welsh 2003; Snelgrove et al. 2014; Belley and Snelgrove 2016). These organisms are also considered as powerful bio-indicators, as they are sensitive to changes in environmental conditions with rapid response to anthropogenic disturbances (Tweedley et al. 2012; Borja et al. 2015). In southern Australian soft sediments, there is little understanding on how changes in macrobenthic fauna and their functional traits influence the sediment biogeochemistry and nutrient fluxes. Outcomes from this PhD thesis showed that how changes in macrobenthic fauna and their functional traits were closely related to specific environmental characteristics of (Chapter 4, Lam-Gordillo et al. 2021), and to changes in sediment biogeochemistry (Chapter 5, Lam-Gordillo et al. 2022). Similar results have been reported in other southern temperate soft sediments (e.g. Lohrer et al. 2004; Gladstone-Gallagher 2017; Douglas et al. 2019; Hillman et al. 2020; O'Meara et al. 2020), documenting the relationship between macrobenthic fauna and sediment biogeochemistry, and in general, the influence of these organisms on ecosystem functioning (Thrush et al. 2006; Hewitt et al. 2008; Thrush et al. 2017; Gammal et al. 2019; Thomas et al. 2020; Schenone et al. 2020). Results from my chapter 5 (Lam-Gordillo et al. 2022) showed that in areas where bioturbating macrofauna were present, low concentrations of nutrients and organic matter were recorded, while in areas with surface-crawler macrofauna only, nutrients and organic matter accumulated. These outcomes showed how macrobenthic fauna influence sediment biogeochemistry, highlighting that the presence/absence of certain functional traits is more relevant for changes in sediment biogeochemistry and nutrient fluxes than the macrobenthic taxa *perse* (Norkko et al. 2013; Thomas et al. 2020; Thrush et al. 2021). In particular, the functional trait bioturbation emerged as one of the most important for ecosystem functions such as nutrient cycling and sediment mineralisation (Chapter 5, Lam-Gordillo et al. 2022), as previously exemplified in other ecosystems (e.g. Welsh 2003; Lohrer et al. 2004; Kirstensen et al. 2012; Breaeckman et al. 2010; Gladstone-Gallagher 2017; Wyness et al 2021).

The functional trait bioturbation was further explored in an *in situ* experiment, and its response to hostile (i.e. sulfide-rich) sediments was tested (Chapter 6). Results from this PhD thesis showed that the preservation and/or reintroduction of bioturbating macrofauna improves sediment conditions and promotes sediment oxygenation, that in turn enhances nutrient cycling and sediment mineralisation. Previous experimental and field studies describe the influence of bioturbation and oxygenation on soft sediments (Volkenborn et al. 2012; Banks et al. 2013; Bosh et al 2015; Kauppi et al. 2018; Norkko et al. 2019; Hillman et al. 2020), which support the findings from this PhD thesis. Furthermore, my results showed that bioturbation by macrobenthic fauna remediated the hostile conditions in sediments, i.e. concentrations of sulfide, ammonium, and total carbon content were reduced over time due to sediment oxygenation and porewater exchange facilitated by bioturbation processes. It was also revealed that macrobenthic bioturbation promoted the colonization of other macrobenthic organisms in sediments that were previously hostile (Chapter 6).

The information gathered from Chapter 4, 5, and 6 in this PhD thesis could be transferable to other marine ecosystems, highlighting the significance of preserving macrobenthic communities for enhancing resilience to adverse conditions, viable nature-based remediation benefits, and to ensure the functioning of ecosystems.

7.5 Implications of functional approaches for conservation and management

Historically, conservation and management efforts have been based on the assessment of individual taxa, taxonomic diversity (e.g. species richness, diversity, evenness), and particular habitat characteristics. Incorporating functional approaches to conservation and management efforts could result in accurate identification of areas to conserve and greater conservation gains, as functional approaches provide information on functional diversity and its relationship with the functioning of ecosystems (Brenmer et al. 2006; Brenmer 2008; Miatta et al. 2021; Thrush et al. 2021).

The outcomes from this PhD thesis demonstrate the relevance of including functional approaches to conservation and management of soft sediment ecosystems (Chapters 3-6). With the rapidly changing climate and other human-induced pressures, biodiversity is decreasing, modifying the functioning of ecosystems. Functional assessment can help us to understand how anthropogenic impacts on macrobenthic communities influence changes in the functioning of soft sediment ecosystems, highlighting areas to prioritise conservation efforts based upon functional outcomes (Chapter 4, Lam-Gordillo et al. 2021; Chapter 5, Lam-Gordillo et al. 2022). Previous studies have also highlighted the use of functional approaches to assess anthropogenic impacts, predict changes in ecosystem functioning (van der Linden et al. 2012; Verissimo et al. 2012; Villnäs et al. 2019; Thrush et al. 2021), and provide management and conservation strategies (Bremner 2008; Villnäs et al. 2019; Miatta et al. 2021).

For example, my PhD findings showed that functional diversity and functional redundancy were different across the south Australian coast, as a result of site-dependent environmental conditions and habitat characteristics. The functional approaches identified that macrobenthic communities in coastal embayment habitats were more resilient and likely to maintain their ecosystem functioning in an event of change (i.e., taxa loss), due to high functional diversity and redundancy (Chapter 4, Lam-Gordillo et al. 2021). In comparison, lagoon habitats (e.g. Coorong system) were identified as vulnerable to further loss of benthic taxa and structural changes (i.e., ecosystem functioning loss) caused by anthropogenic or natural environmental changes, due to low functional diversity and redundancy (Chapter 4, Lam-Gordillo et al. 2021). Similar results were described in studies carried out in the Northern Hemisphere (e.g. van der Linden et al. 2012; 2016), showing differences in functional diversity and functional redundancy across locations analysed, which allowed the identification of sites potentially threatened (i.e., taxa loss) by anthropogenic disturbances (e.g. van der Linden et al. 2012; 2016).

The functional approaches applied in this PhD thesis also showed that functional traits are relevant for healthy functioning of ecosystems and should be considered in conservation and management plans, as previously suggested in other studies (Bremner 2008; Miatta et al. 2021; Thrush et al. 2021). In the estuarine system assessed in this PhD project, it was identified that the functional traits such as bioturbation and burrower influenced the sediment biogeochemistry (Chapter 5, Lam-Gordillo et al. 2022; Chapter 6). Loss of such functional traits would potentially affect the functioning of this estuarine ecosystem more than the loss of a specific taxa as these functional traits are shared with other taxa inhabiting the same ecosystem (Chapter 5, Lam-Gordillo et al. 2022; Chapter 6).

Overall, the findings from this PhD thesis suggest that to understand the relationship between macrobenthic organisms and ecosystem functioning, and assist better conservation and management planning, complementary use of taxonomic and functional approaches should be applied in assessments of soft sediments habitats. My findings highlight that functional traits, functional diversity, and traditional biodiversity descriptors are needed to understand the macrobenthic – ecosystem functioning relationships, which aligned with previous suggestions (Thrush et al. 2017; Gammal et al. 2020; Thrush et al. 2021). For example, the *in situ* experiment revealed that macrobenthic organisms, and more specifically their bioturbation functional trait could help as an ecological option for remediating hostile (i.e. hypersaline, sulfide-rich) sediments in estuarine ecosystems. These outcomes can be adapted and used in management plans of large-scale conservation projects for improving estuarine ecosystem conditions. The application of both taxonomic and functional approaches allows to obtain a holistic understanding of the functioning in marine soft sediments (Thrush et al. 2017; Thrush et al. 2021), depicting relevant areas and functions that need to be conserved and managed for preserving the functioning of these ecosystems.

7.6 Outlook and Final Concluding Remarks

The aim of this PhD thesis was to to understand the functional ecology of macrobenthic communities and investigate the relationship between macrobenthic fauna and ecosystem functioning using functional perspectives along the South Australian coastline. The findings showed for the first time the macrobenthic functional diversity and its relationship with ecosystem functioning in southern Australian soft sediment ecosystems. Result from the global analysis identified a lack of functional assessments and functional trait classifications for southern Australia. Further investigations were performed to close this knowledge gap. A new openly available functional trait classification database was introduced (SAMT), and further functional assessment were carried out in southern Australian soft sediment habitats. The outcomes of my studies highlighted idiosyncratic spatial and temporal patterns on functional diversity and functional traits along the South Australian coastline, and site-dependent correlations with the environmental conditions. The potential role of macrobenthic fauna on ecosystem functioning was also identified. Macrobenthic fauna and their functional traits influenced changes in sediment biogeochemistry (e.g. nutrient and organic matter concentrations). More importantly, the functional trait bioturbation was identified as the most relevant for remediating sulfide-rich sediment over time, enhancing nutrient cycling, sediment mineralization, and recolonization of other macrobenthic fauna.

Further directions and studies on coastal soft sediment habitats can build on the outcomes presented in this PhD thesis. The research field of ecosystem functioning in marine and coastal ecosystems is still growing. This study advanced the understanding of functional perspectives and closed the knowledge gap in the southern Australia region. The patterns described in this thesis could be tested across larger spatial and temporal scales in a range of marine and coastal ecosystems in this region or elsewhere in the world. Results from the *in situ* experiment should be compared with experiments in artificial and field-based mesocosms, to gain a better understanding of how macrobenthic fauna influence the ecosystem functioning under different scenarios (e.g. climate change, drought, hypersalinity, eutrophication).

Furthermore, while recent investigations have made progress aiming to link Biodiversity to Ecosystem Services (BES), an integrative study addressing the linkage between macrobenthic diversity, functional traits, ecosystem processes, ecosystem functioning, and ecosystem services is still needed. Future research should be guide by the outcomes presented in this thesis to undertake holistic assessments and unravel how multiple ecological processes interact. This will provide a better understanding of the underlying mechanism occurring from biota to ecosystem services that underpin many human needs and values.

There are many avenues in which results from this thesis can be used to apply informed knowledge on the relationship of biodiversity and ecosystem functioning. The thesis gives examples to inform decision making on which biodiversity measures and ecosystem functions to consider for planning and conservation efforts. In general, it is essential to include the Biodiversity-Ecosystem Functioning relationship more broadly to address outstanding questions such as how the connectivity between communities and habitats influences the functioning of marine soft sediment ecosystems, and how the undergoing climate change influences this interlinked relationship between the macrobenthic fauna and ecosystem functioning.

Overall, the outcomes of this PhD thesis demonstrated that a combination of traditional taxonomy and functional approaches is essential for a holistic understanding of how marine soft sediments function and respond to the ongoing anthropogenic pressures. Such information is crucial for adequate conservation and management plans of these ecosystems.

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Appendices

Appendix A. Supplementary information for Chapter 2.

Table S1. List of research articles used for the analysis of ecosystem functioning of marine macrobenthic fauna communities.

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Table S2. Numerical measures used for quantifying ecosystem functioning. Multiple frequency is considered when multiple numerical methods were used in the same publication. Single frequency stands for numerical methods that were used alone in each publication.

Numerical method	Acronym	Multiple frequency	Single frequency
Taxonomic diversity	S	65	3
Abundance	A	59	2
Biological Trait analysis	BTA	56	3
Biomass	B	51	4
Fuzzy Correspondence Analysis	FCA	45	
Shannon-Wiener diversity Index	H'	44	2
Rao's quadratic entropy	*Q*	22	
Functional diversity	FD	20	
Pielou's index	J’	15	
Functional redundancy	FR	11	
Community-Weighted Mean	CWM	9	
Community Bioirrigation Potential	BIPc	8	3
Functional Evenness	FEve	7	
Taxonomic Distinctness	TDist	6	
Functional Richness	FRic	6	
Functional dispersion	FDis	5	
Functional divergence	FDiv	5	
Infaunal Trophic Index	ITI	3	
Trophic Group Analysis	TGA	3	
Bioturbation Potential	BP	3	
Margalef index	Mar	3	
Somatic Production	Ps	2	
Trophic Diversity	TrD	2	
Number of Predator Species	PSR	2	
Trophic Web Models	TWM	1	
Emergent group hypothesis	EGH	1	1
Thermodynamic-Oriented Indicators	TOI	1	
Trait richness	TR	1	
Expected number of deposit feeders	EDF	1	
Total secondary production	TSP	1	
Proportional contribution to production	PCP	1	
Stable Isotope	SI	1	
Fatty acid	FA	1	
Number of links	L	1	
Linkage density	LS	1	
Nestedness of interactions	NODF	1	
Irrigation Potential	IP	1	
Index or Relative Importance	IRI	1	
Respiration rate	Rr	1	

Figure S1. Author collaboration network. Nodes represent relations between the top 35 authors in terms of the numbers of authored publications in the dataset; line connections are co-authorships; nodes size is proportional to the number of publications; node colours represented strongest associations between networks.

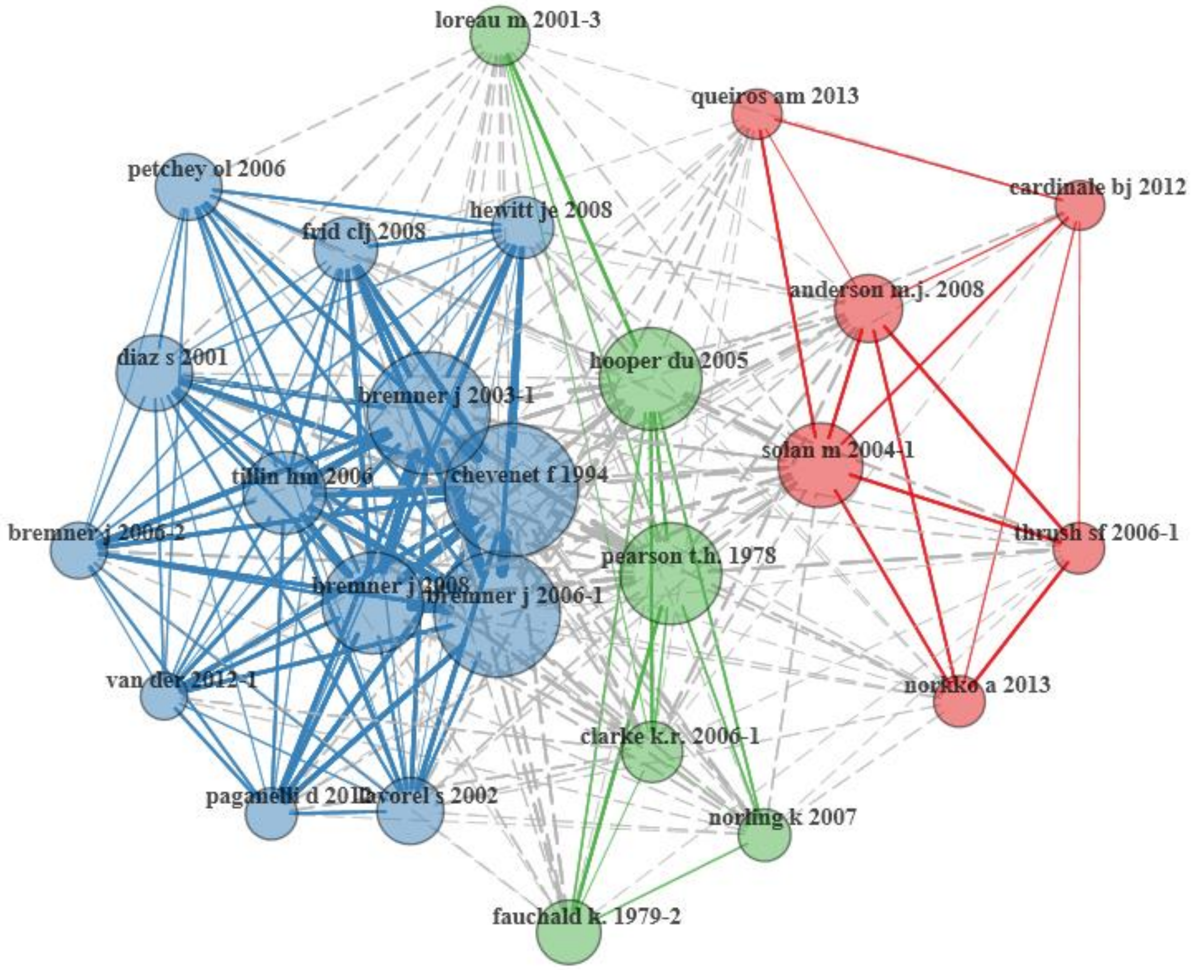


Figure S2. Co-citation network based on publication references. Nodes represent relations between cited publications using the top 20 most cited authors; node size is proportional to the number of times the article was cited; nodes colours represented strongest associations between networks.

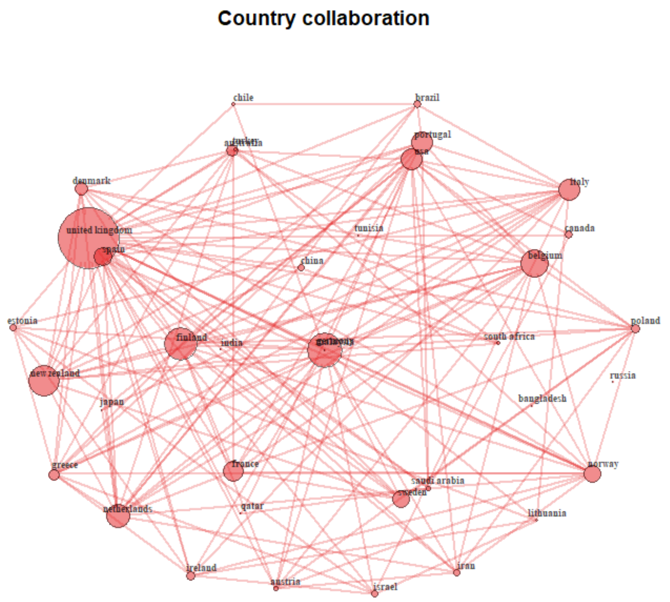


Figure S3. Country collaboration network analysis. Nodes size is proportional to the number of publications by country, line connections represent the association between countries.

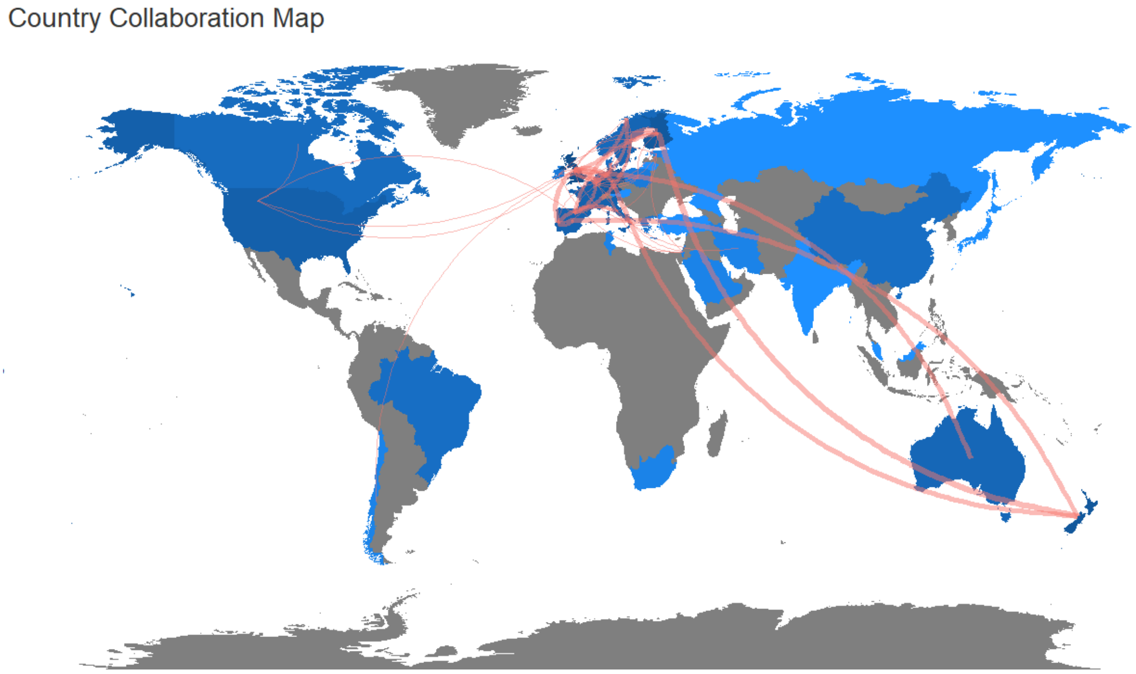
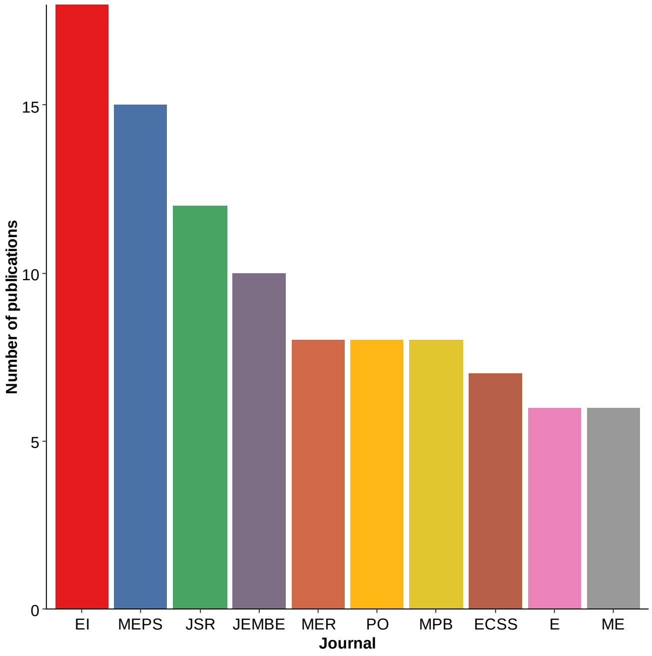


Figure S4. Country collaboration map. Lines size is proportional to the number of publications by country, line connections represent the association between countries.

A)



B)

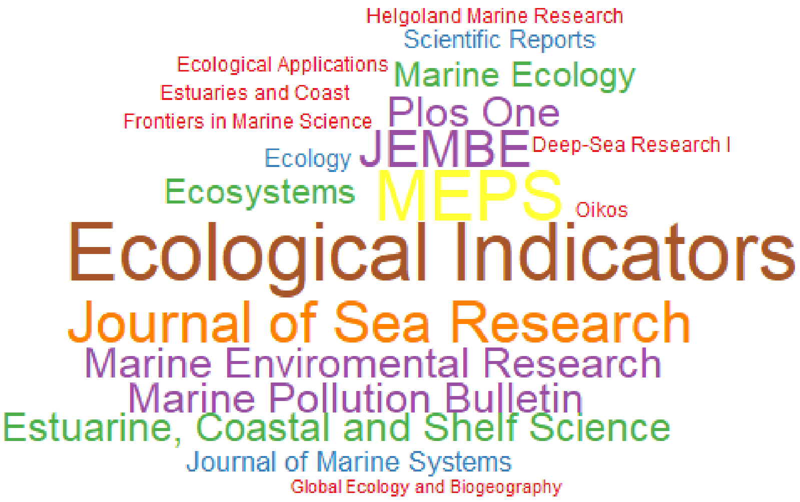


Figure S5. A) Number of publications per journal, only showing the top 10 journals. EI: Ecological indicators; MEPS: Marine Ecology Progress Series; JSR: Journal of Sea Research; JEMBE: Journal of Experimental Marine Biology and Ecology; MER: Marine Environmental Research; PO: Plos One; ECSS: Estuarine, Coastal and Shelf Science; ME: Marine Ecology; MPB: Marine Pollution Bulletin; E: Ecosystems. **B)** Wordcloud analysis of journals names included in the study, word size is proportional to the frequency of given journal in the dataset.

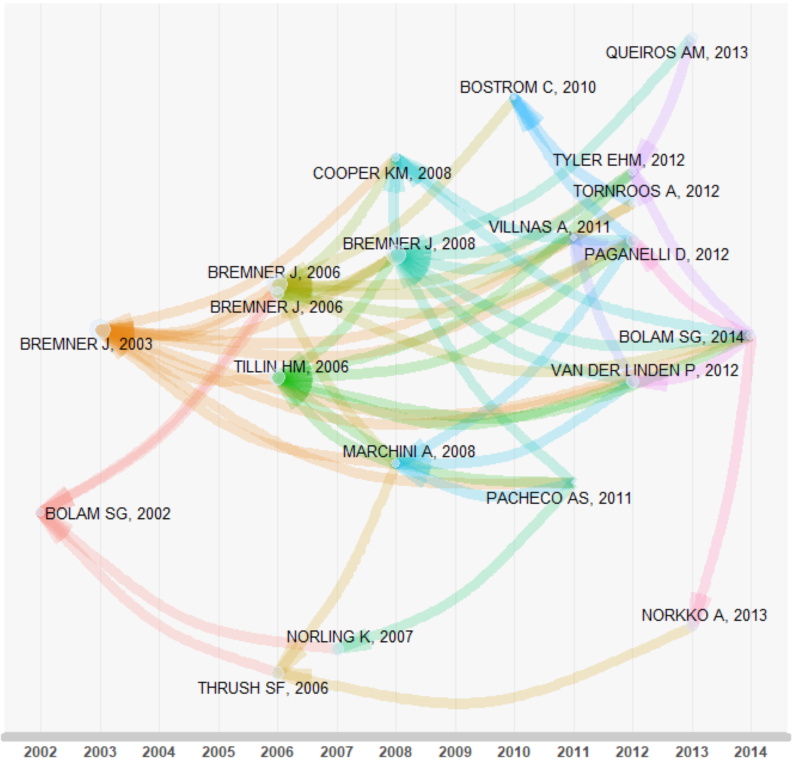


Figure S6. Historical publication network based on direct citation linkages of the included studies across the publication years.

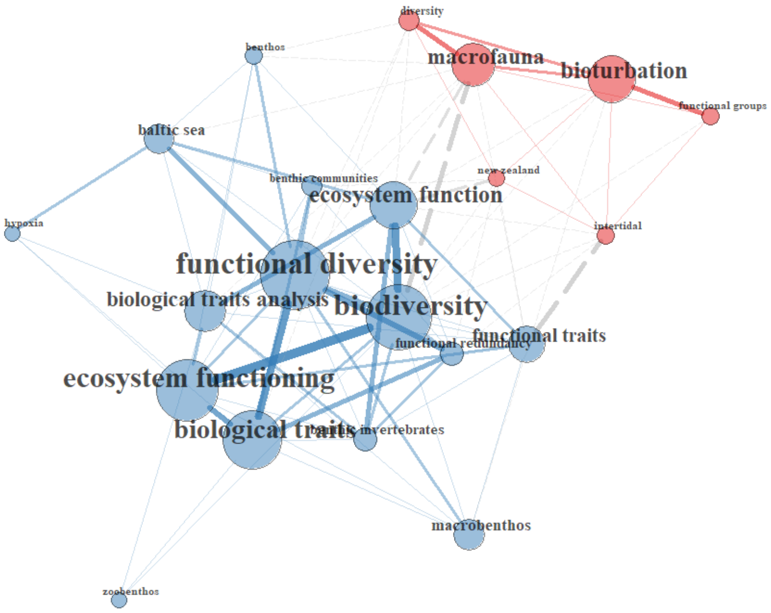


Figure S7. Topic network based on co-word analysis through authors keyword co-occurrences. The network displays two well defined interconnected groups based on the most frequent terms found through the authors keywords.

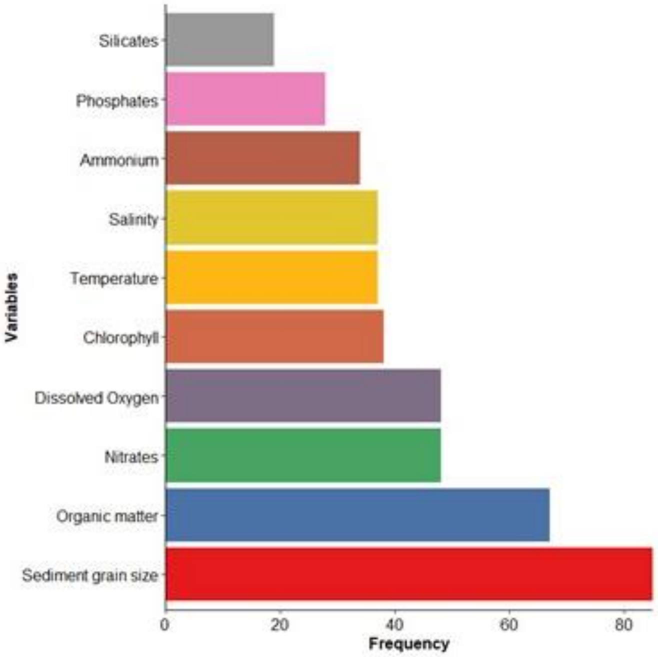


Figure S8. Frequency of the most common physicochemical variables related with ecosystem functioning.

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Review

Ecosystem functioning and functional approaches on marine macrobenthic fauna: A research synthesis towards a global consensus

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ABSTRACT

The global trend in losing biodiversity is affecting ecosystems due to changes in their functions and services. Biodiversity and Ecosystem Functioning has become increasingly topical over the last decades, and still a developing research field. Marine macrobenthic fauna are important providers of ecosystem functioning by regulating the fluxes of energy and matter. However, anthropogenic impacts have triggered changes in their structure and function at the community and ecosystem level. Despite advances in recent years, a wider application of biodiversity and ecosystem functioning relationship in benthic communities has been restrained by missing information on biological traits of species and inconsistencies in terminology, methodologies and approaches used. This review synthesizes the current status of knowledge on the functional approaches of marine macrobenthic fauna and their contribution to ecosystem functioning, using a new method named research weaving analysis. We thus provide a research synthesis combining bibliometric analysis and systematic mapping (spread of evidence). We described advancements in the current knowledge and synthesized the most common functional approaches, terminology and numerical methodologies used. A conceptual step-by-step guide is presented to assist future assessments of ecosystem functioning for marine macrobenthic fauna, and suggestions made for coherent use of terminology, trait selection and metrics to measure ecosystem functioning. The analyses presented will support the development of a framework to conduct globally comparable analyses of ecosystem functioning in marine benthic ecosystems.

1. Introduction

Biodiversity is declining worldwide causing changes in ecosystem functioning and services (Sala and Knowlton, 2006; Wright et al., 2006; Butchart et al., 2010; McCauley et al., 2015; IPBES, 2019). Over the last few decades, the rate of biodiversity loss and changes in ecosystems have motivated research towards understanding the relationship between Biodiversity and Ecosystem Functioning (BEF). Research directions have included investigations on ecological processes and how changes in biodiversity affect ecosystem functioning and services, elucidating the mechanisms that underpin the biodiversity and functional relationship (Naeem et al., 2002; Hooper et al., 2005; Reiss et al., 2009; Cadotte et al., 2011; van der Plas, 2019).

Ecosystem functioning is defined as the combined effects of all natural processes that sustain an ecosystem (Table 1). The concept of Biodiversity and Ecosystem Functioning emerged in the early 1990′s (Naeem et al., 1994; Tilman et al., 1996), and has evolved since then, but mainly in terrestrial (Díaz and Cabido, 2001; Tilman et al., 2014; van der Plas, 2019) and freshwater ecology (Lecerf and Richardson, 2010; Schmera et al., 2017). A large body of research shows that greater diversity leads to an increase in the number of expressed biological traits and greater effects on ecosystem functioning, compared to less diverse assemblages that have poor functional expression (Chapin et al., 2000; Hooper et al., 2005; Hillebrand and Matthiessen, 2009; Reiss et al., 2009; Snelgrove et al., 2014). The strength and direction of the BEF relationship can, however, be highly variable and subject to environmental context (Strong et al., 2015; Thrush et al. 2017; van der Plas 2019).

In order to assess the BEF relationship several approaches have been used. Functional diversity (FD) is the most relevant measure for understanding the relationship between biological diversity, the functioning of organisms, and the links to ecosystem functioning (Díaz and Cabido, 2001; Hooper et al., 2005; Wright et al. 2006; Lefcheck and Duffy, 2015; Legras et al., 2018). Functional diversity is defined as the value and range of functional traits (Table 1) and has been quantified by grouping species with shared taxonomic, physiological and

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Table 1
Terminology used in the context of Biodiversity-Ecosystem Functioning and suggested definitions for (a) general terms and (b) trait specific terms.

Key terms	Definition
(a) General terms	
Biodiversity	The extent of all genetic, taxonomic and ecological diversity over all spatial and temporal scales (Reiss et al., 2009; Snelgrove et al., 2014)
Ecosystem functioning	The combined effects of all natural processes that sustain an ecosystem (Reiss et al., 2009; Degen et al., 2018; Gladstone-Gallagher et al., 2019)
Ecosystem goods and services	The ecosystem services are the conditions and processes through which natural ecosystems sustain and fulfil human life. The ecosystems goods are products obtained from ecosystems. In general, both are products of ecosystem functioning that are of value to humans, or with benefits that humans obtain from ecosystems (Reiss et al., 2009; Snelgrove et al., 2014; Degen et al., 2018)
Ecosystem process	Changes in energy and matter over time and space through biological activity, within the ecosystem, due to abiotic (physical and chemical) and biotic (organism) factors and interactions (Reiss et al., 2009)
Ecosystem modelling	The development and analysis of mathematical and statistical models of ecological processes (Pittroff and Pedersen 2005)
Functional divergence	Degree to which the maximum abundance of functional traits deviate from the centre of the functional space within the same community (Mason et al., 2005; Mouchet et al., 2010; Schmera et al., 2017)
Functional diversity	The value and range of functional traits that influence ecosystem functioning (Tilman et al., 1996; Díaz and Cabido, 2001; Reiss et al., 2009; Schmera et al., 2017; Degen et al., 2018)
Functional evenness	Distribution of abundance among functional traits (Mason et al., 2005; Mouchet et al., 2010; Schmera et al., 2017)
Functional richness	Amount of functional trait space occupied by an assemblage of multiple species (Mason et al., 2005; Mouchet et al., 2010; Schmera et al., 2017)
(b) Trait terminology	
Trait	Any morphological, physiological or phenological feature measurable at species level.
Biological trait	A defined and measurable (presence/absence, or fuzzy coding) property of organisms, usually at the individual level and used comparatively across species (Reiss et al., 2009; Degen et al., 2018)
Functional trait	Component of an organisms' phenotype that determines its effect on ecosystem functioning; also referred to as functional characters (Petchey and Gaston, 2006; Reiss et al., 2009; Degen et al., 2018; Weiss and Ray, 2019)
Effect traits	Expression of a trait that shapes how organisms affect ecosystem functioning (Beauchard et al., 2017; Degen et al., 2018)
Response traits	Traits that determine how organisms respond to changes in the environment (Degen et al., 2018)
Trait modalities	Categories in which any trait can be subdivided

morphological characteristics (Wright et al., 2006). The number of ways to measure FD is continually evolving, but usually split into three main components; (1) functional richness, (2) functional evenness, and (3) functional divergence (Petchey and Gaston, 2006; Mouchet et al., 2010; Legras et al., 2018, see Table 1 for definitions). However, numerous other metrics to measure FD have been developed over time (e.g. community bio-irrigation potential, community weight means, functional complementary, functional redundancy, functional regularity and Rao's Quadratic Entropy) (Petchey and Gaston, 2006; Cadotte et al., 2011; Queiros et al., 2013; Song et al., 2014; Schmera et al., 2017).

Functional diversity generally involves knowledge of the components of biodiversity that influence ecological processes or ecosystem functioning (Petchey and Gaston, 2006; Schmera et al., 2017), whereby approaches that measure FD are usually based on functional traits (Díaz and Cabido, 2001; Petchey and Gaston, 2006; Hillebrand and Matthiessen, 2009). Functional traits are the components of an organisms' phenotype that determine its effect on ecosystem functioning (Petchey and Gaston 2006; Reiss et al., 2009; Degen et al., 2018; Weiss and Ray 2019). Functional traits can be selected by either (1) incorporating a wide range of information on biological traits regardless of the taxonomic group (Cadotte et al., 2011; Verissimo et al., 2012) or, (2) selection of an appropriate set of traits that depend on the specific objectives and processes to be measured in any particular study (Reiss et al., 2009).

Marine macrobenthic communities in soft sediments are important providers of ecosystem functioning. They regulate the fluxes of energy and matter and are bioindicators of ecosystem health due to their sensitivity to natural and anthropogenic disturbance (Borja et al., 2000; Reiss et al., 2009; Snelgrove et al., 2014; de Juan et al., 2015; Lefcheck and Duffy, 2015). Anthropogenic disturbances such as trawling, dredging or pollution, can affect growth, mortality, recruitment rate and dispersal ability of benthic species (Lohrer et al., 2010, Naeem et al., 2012; Villnäs et al., 2013; Dannheim et al., 2014; Shojaei et al., 2015), altering the structure and functioning of benthic communities (Worm et al., 2006; van der Linden et al., 2012; Thrush et al. 2017), and therefore ecosystems.

Efforts have been made to understand, describe and measure BEF relationships for macrobenthic fauna in marine ecosystems, using manipulative experiments (Stachowicz et al., 2007), analysing the seafloor biodiversity-ecosystem functioning (Snelgrove et al., 2014), creating frameworks for polar oceans (Degen et al., 2018), and describing the functioning of mudflats (Dissanayake et al., 2018). However, several gaps persist in the knowledge of ecosystem functioning in benthic communities, arising from missing information on the biological traits of specific species, and inconsistency in terminology, methodologies and approaches used (Tyler et al., 2012; Strong et al., 2015; Thrush et al., 2017; Paterson et al., 2019). A framework describing the links between macrobenthic fauna, biological traits, ecological processes and ecosystem functioning and services is thus still missing.

In order to advance a more coherent approach in BEF of marine macrobenthic fauna, we present a research weaving analysis, combining bibliometric analysis with systematic mapping (Nakagawa et al., 2019). This novel approach allowed an advanced and visualised synthesis of the research to date about the connection between biological traits, ecological processes, and ecosystem functions. Through the systematic review of BEF literature on marine macrobenthic fauna around the world, we provide an overview on the spread of evidence and bibliographic analysis. We further analysed the literature content under several categories to identify how ecosystem functioning and functional diversity are currently conceptualized and measured. To enhance comparability between studies, we encourage the use of a general and standardized approach that includes coherent terminology, quantitative methods for choosing biological traits, and consistent use of metrics to measure ecosystem functioning. We also provided a conceptual step-by-step guide to assess ecosystem functioning for marine macrobenthic fauna.

2. Methods

2.1. Literature and database mining

The databases SCOPUS (Elsevier; elsevier.com) and Web of Science (WoS, Thompson Reuters; webofknowledge.com) were used to compile all studies published before November 2019. The literature searches were performed using the tool 'combination of sets' (WoS) and 'combine queries' (SCOPUS), which allowed us to find the articles that contained any of all the possible combinations using the following terms: 'macrofauna', 'macroinvertebrate(s)', 'macrobenthic', 'ecosystem function(ing)', 'ecosystem multifunctionality', 'functional diversity',

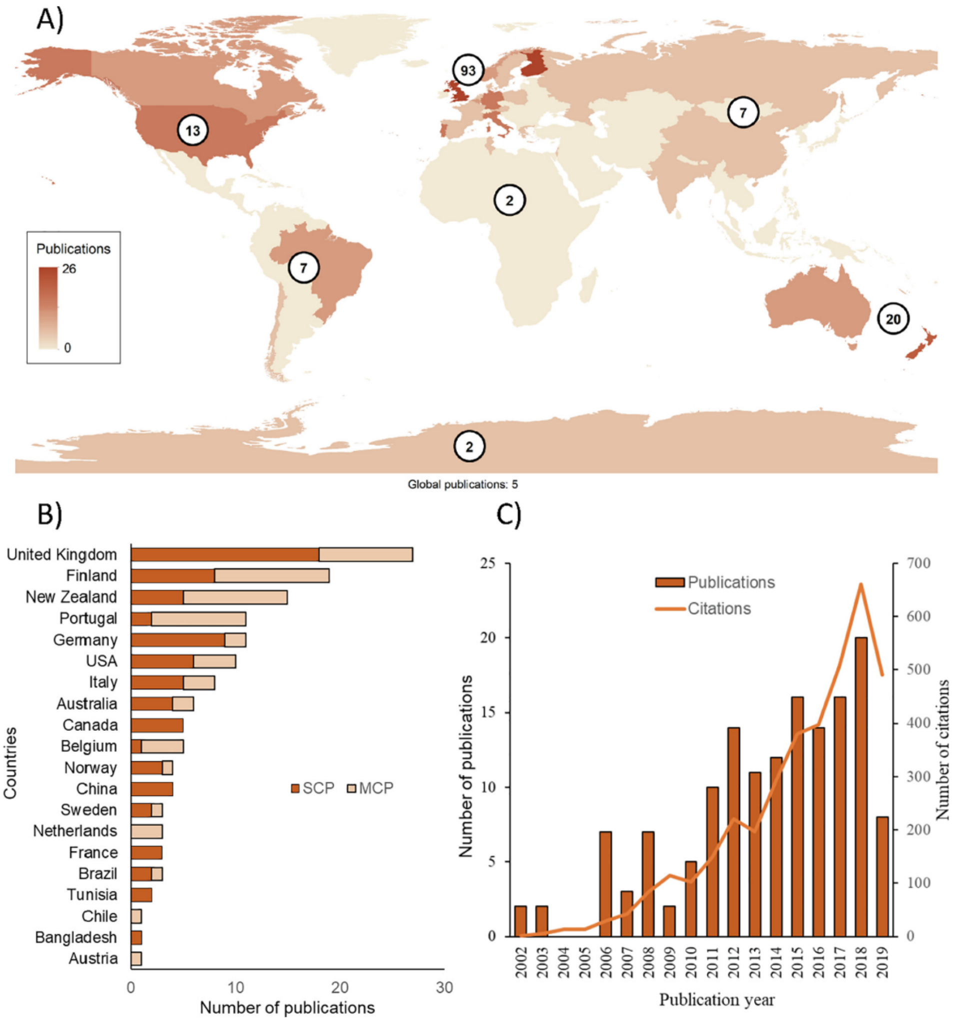

Fig. 1. Spread of evidence of studies on ecosystem functioning of marine macrobenthic fauna. A) Geographical distribution of the origin of the publication of the included studies. Numbers inside of circles represent the number of publications per continent. Colour intensity is proportional to the number of first authors affiliated to a given country. B) The top 20 most productive countries; SCP: single country publication; MCP: multiple country publication. C) The number of peer-reviewed publications and citations on ecosystem functioning of marine macrobenthic fauna across time.

'functional traits', 'biological traits'; in the fields of 'Article title, Abstract, Keywords' for SCOPUS and; in 'topics' (Article title, Abstract, Author, Keywords and Keywords plus) for WoS. This search resulted in 1813 published studies (1092 in SCOPUS, all of them were in WoS). Within these results, a primary examination of the titles and abstracts was done, retaining only the publications that met the following criteria of: (1) environment (marine habitat), (2) organisms (all macrobenthic fauna), (3) statistically tested, and (4) study type (e.g. only scientific peer-reviewed publications), yielding a total of 239 publications. A second and final examination of the publications was done where we carefully read through each article to verify its relevance to ecosystem functioning of marine macrobenthic fauna, resulting in 93 publications that did not meet the required criteria. In addition, a cross-referencing of the publications gathered additional publications outside of the initial review process (3 publications), resulting in a final total of 149 publications on the research field of ecosystem functioning and functional diversity of marine macrobenthic fauna that included soft and hard bottom marine habitats (Table S1 in supplementary material).

2.2. Review style and data analyses

To investigate the relationship of marine macrobenthic biodiversity and ecosystem functioning, we performed a new systematic approach named 'research weaving'. This type of research synthesis combines

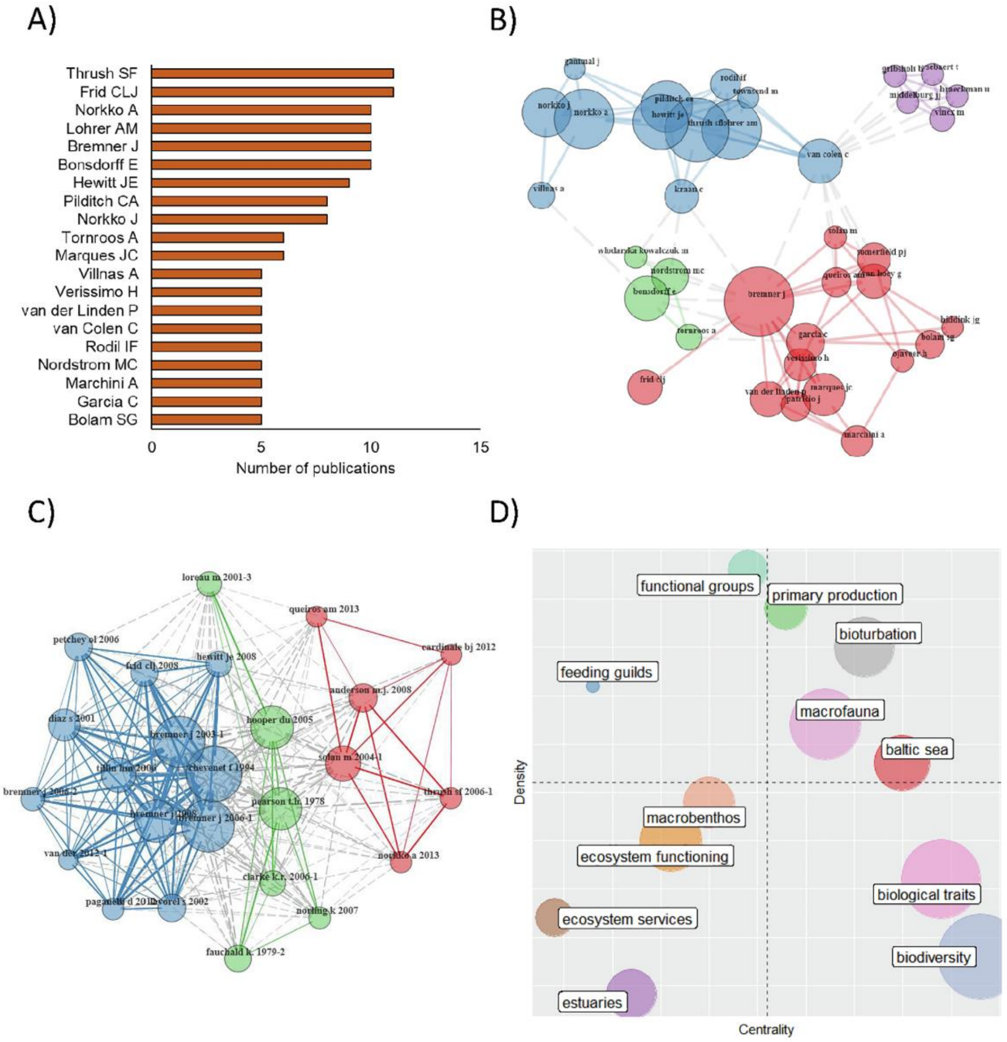

Fig. 2. Bibliographic analysis of publications on ecosystem functioning of marine macrobenthic fauna. A) Most productive authors. B) Author collaboration network. Nodes represent relations between the top 35 authors in terms of the numbers of authored publications in the dataset; line connections are co-authorships; nodes size is proportional to the number of publications; node colours represented strongest associations between networks. C) Co-citation network based on publication references. Nodes represent relations between cited publications using the top 20 most cited authors; node size is proportional to the number of times the article was cited; nodes colours represented strongest associations between networks. D) Thematic map of keywords based on co-word analysis through authors keyword co-occurrences.

bibliometrics and systematic mapping, summarizing and visualizing the information content, history and networks across and within publications of a specific topic (Nakagawa et al., 2019).

Bibliographic analyses were performed using the bibliometrix-R package (Aria and Cuccurullo, 2017) in R v3.5.0 (R development Core Team, 2018). An author collaboration network was created using a 'fruchterman' method base on the top 35 authors with more collaborations. For the co-citation network, we used the 25 most co-cited publications and a 'fruchterman' method. The thematic map of keywords was performed using a co-word analysis based on the authors key words.

2.3. Review categories and general statistics

The database used for this review was analysed in three ways: (1) Using Clarivate Analytics (Web of Science), the general statistics of citations, web of science categories, source titles (i.e. journal titles), and research areas were obtained; (2) the Bibliometix-R package (Aria and

Table 2
Number of publications on ecosystem functioning of marine benthic fauna for the top 10 web of science categories and journals.

Web of Science category	No.	Journal	No.
Marine Freshwater Biology	88	Ecological Indicators	18
Ecology	52	Marine Ecology Progress Series	16
Oceanography	49	Journal of Sea Research	13
Environmental Sciences	43	Journal of Experimental Marine Biology and Ecology	10
Biodiversity Conservation	21	Marine Environmental Research	8
Multidisciplinary Sciences	12	Plos One	8
Toxicology	8	Marine Pollution Bulletin	8
Geosciences Multidisciplinary	7	Estuarine, Coastal and Shelf Science	7
Evolutionary Biology	3	Marine Ecology and Evolutionary Perspective	6
Fisheries	3	Ecosystems	6

Cuccurullo, 2017) was also used for collecting additional information: number of publications per year, annual percentage growth rate, number of publications per country (single and multiple), and number of publications per author and; (3) information from different categories was extracted by reading each of the peer-reviewed publications included in our dataset. Although, this strategy is time consuming, it was preferred to the option provided in Clarivate Analytics, obtaining information unavailable from automated search. For example, these categories were based on the location where the studies were undertaken, in contrast with automatic sorting that uses the authors' affiliation. Publication were categorised by type of study separating; experimental manipulation, field surveys, distribution modelling, ecological modelling, meta analysis, methods, reviews and tool evaluations. Publications were also grouped by the ecosystem type where the study took place; beach, coastal, offshore (including deep sea), estuary, laboratory, mangrove, and seagrass. In another category, publications were classified according to their study organisms; macrobenthic communities as combinations of groups of multiple taxa or groups of particular taxa such as Annelida, Decapoda, Echinodermata and Mollusca. When analysing the publications, we identified that ecosystem functioning was addressed in different ways, so a classification was created to allocate each publication. As the terminology used for biological traits varies throughout the literature, a classification of traits and their modalities was performed. The variety of numerical methods for assessing ecosystem functioning was further analysed based on the publications reviewed, and sorted by their most common use (see Supplementary data Table S2). Finally, an approach category was identified; methodological approach (i.e. taxonomic diversity vs functional diversity), spatial approach (i.e. differences between sites), temporal approach (i.e. differences across time), and experimental approaches.

3. Bibliometric influence and evidence of BEF for macrobenthic fauna

3.1. Geographical and temporal spread of evidence

Investigations of marine macrobenthic fauna and their contributions to ecosystem functioning have increased due to growing interest in the

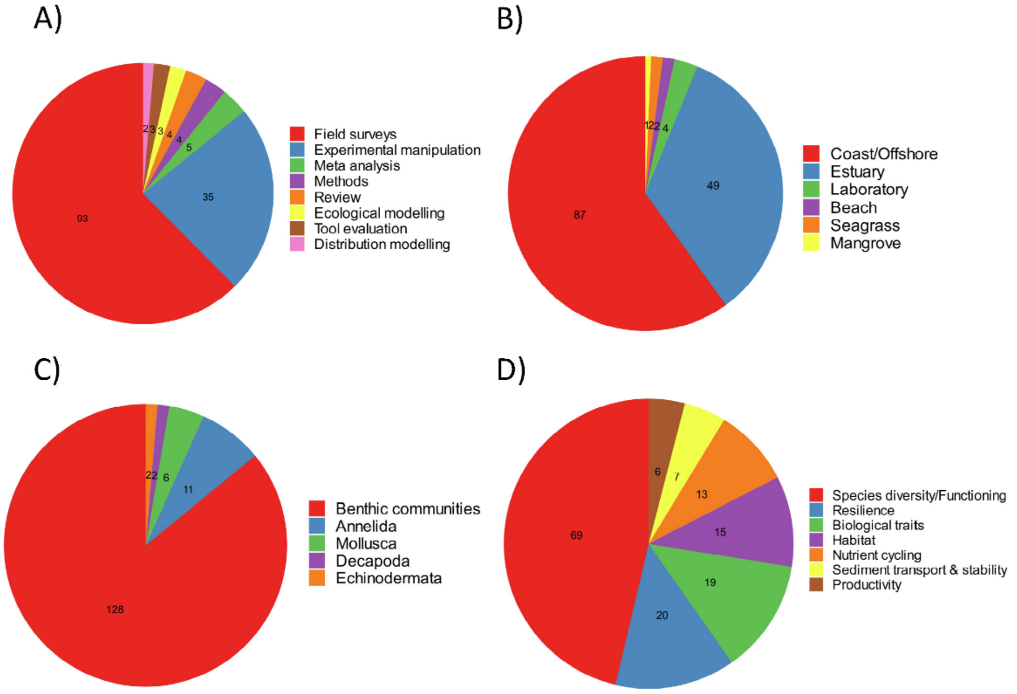

Fig. 3. Pie charts summarising the attributes found in the publications on ecosystem functioning of marine macrobenthic fauna communities. A) Number of publications per type of study. B) Number of publications per ecosystem type where the studies where performed (n = 145). C) Number of publications per taxa. D) Broad categories of ecosystem functioning that were studied. The numbers in each sector of the pie charts indicates the number of publications, with 149 papers reviewed for the analysis. For B), the ecosystem type studied could only be assigned to 145 publications.

Table 3
Approaches in assessing ecosystem functioning of marine macrobenthic fauna. Methodological: Taxonomic diversity vs functional diversity; Spatial: differences between sites; Temporal: differences across time; Experimental: manipulation of the environment and organisms.

	Methodological approach	Spatial approach	Temporal approach	Experimental approach
Number of publications (n)	30	78	26	36
Significant differences	15	70	24	36
No significant differences	15	8	4	0

field, and the value of functional perspectives for environmental decision making (e.g. Van der Linden et al., 2016). The majority of studies were performed in the Northern Hemisphere (115 publications), compared to 29 publications from the Southern Hemisphere. Only five publications had a global perspective as they included information (e.g. organisms) from multiple continents (Fig. 1A).

When publications were classified based on the continent where the studies were conducted, 62% of all publications were from Europe (93 articles), based on strong collaborations of authors from universities across Europe (e.g. Bremner et al., 2003; van der Linden et al., 2012; Norkko et al., 2013; Villnäs et al., 2018), creating networks for the advancement of ecosystem functioning of marine macrobenthic fauna. In comparison, Oceania was represented by 13.6% of the publications, followed by North America with 8.7%, while BEF was less frequently studied in South America (4.7%), Asia (4.7%), Africa (1.3%), and Antarctica (1.3%) (Fig. 1A).

A total of 29 countries had performed investigations into ecosystem functioning of marine macrobenthic fauna. Most publications on BEF, combining both single and multiple country collaborations, were from the United Kingdom (26 publications), Finland (18 publications) and New Zealand (15 publications) (Fig. 1B). Due to the high number of publications, the United Kingdom was also identified as the country that collaborates most with other countries.

Ecosystem functioning of marine macrobenthic fauna was first raised in the 1990 s, identifying traits and functions of specific macrobenthic species (e.g. Posey, 1990). However, it was not until 2002 that studies about ecosystem functioning of macrobenthic fauna included broader concepts, applicability and multiple traits per macrobenthic species (e.g. Bolam et al., 2002; Bremner et al., 2006, Bremner, 2008). In 2004–2005 no publications on this theme were recorded, but since 2005 there has been a general increase (Fig. 1C) with an average annual growth rate in publications of 9.7%. The number of citations in this research field has also grown, with a total of 3705 citations across the 17 years period (Fig. 1C).

3.2. Bibliographic analysis

Ecosystem functioning of marine macrobenthic fauna have been addressed worldwide (Fig. 1), and even though the bibliographic influence is strongly interconnected, the field is dominated by six principal authors with 10–11 publications each contributing to 41% of the publications collectively (Fig. 2A). The author collaboration network displayed four groups of interlinked collaborations (Fig. 2B). These groups reflected the strong collaboration within Europe. The co-citation network analysis based on the publications' references showed three well defined author groups based on seven central publications (Fig. 2C). These publications were often cited because they pioneered theoretical foundations about ecosystem functioning (Solan et al., 2004, Hooper et al., 2005), or stated fundamental information about macrobenthic response, including biological factors, to organic enrichment (Pearson and Rosenberg, 1978), and created or developed the methodologies for using biological traits in marine macrobenthic fauna (Chevenet et al., 1994; Bremner et al., 2003, Bremner et al., 2006, Bremner, 2008).

Publications on ecosystem functioning have been classified into different categories (Table 2). Around 31% of the publications on ecosystem functioning of marine macrobenthic fauna were primarily classified as Marine Freshwater Biology. Ecosystem functioning publications have also been categorised as ecology (18%), oceanography (17%), as well as environmental sciences (15%). Publications of marine macrobenthic fauna and ecosystem functioning were found in 46 journals. The majority of the articles were published in two research journals: Ecological Indicators (Elsevier) with 18 publications and Marine Ecology Progress Series (Inter-Research Science Publisher) with 16 publications. However, another eight journals contained a considerable number (e.g. 6–13 each) of publications in this field (Table 2).

The most frequently used terms for studying ecosystem functioning of marine macrobenthic fauna emerging through a co-word analysis from keywords are presented in a thematic map (Fig. 2D). According to Cobo et al. (2011) themes in the upper-left quadrat are highly developed and very specialized themes (e.g. functional groups, feeding guilds); in the upper-right quadrat are the motor-themes, themes well developed and important for structuring the research field (e.g. macrofauna and bioturbation); themes in the bottom-left quadrat represent emerging themes, themes that need development due to the research field is growing towards them (e.g. ecosystem functioning, ecosystem services); and themes in the bottom-right quadrat are basic themes (e.g. biological traits, biodiversity).

4. Current status of research into ecosystem functioning and functional diversity of marine macrobenthic fauna

The reviewed publications were analysed using several categories to summarise the current state of the research field. Analysing by the category 'type of study' revealed that most of the publications on ecosystem functioning of marine macrobenthic fauna were based on field surveys (62% of publications) and experimental manipulation (24% of publications) (Fig. 3A). Using the category 'ecosystem type' revealed that most of the studies were conducted on the coast/offshore, which included tidal flats and deep sea environments (56% of publications), and in estuaries with 33% of publications (Fig. 3B). Also, a large proportion of publications (68%) performed their research in subtidal environments, and only 31% of them were performed in intertidal environments (n = 136 publications). In addition, the majority of the publications were performed on soft sediments (97% of publications), and only 3% on hard bottom habitats (n = 143).

The category 'study organisms' showed that the majority of publications analysed multiple taxa (e.g. 98% of all publications), yet, a number of publications used particular groups of taxa (Fig. 3C).

Grouping the publications by the 'ecosystem function' they investigated that the majority focused on species diversity and its influence on ecosystem functioning (46% of all publications), and comparatively less publications investigated other aspects, such as those related with resilience and biological traits (13% each) (Fig. 3D).

For the category 'approach', four main directions for addressing ecosystem functioning were identified: (1) methodological approach, including publications which compared differences between taxonomic diversity and functional diversity; (2) spatial approach, referring to publications which examined differences in functional diversity between sites; (3) temporal approach, which identified publications where differences in functional diversity were assessed across time (e.g. seasons, years) and; (4) experimental approach, which included

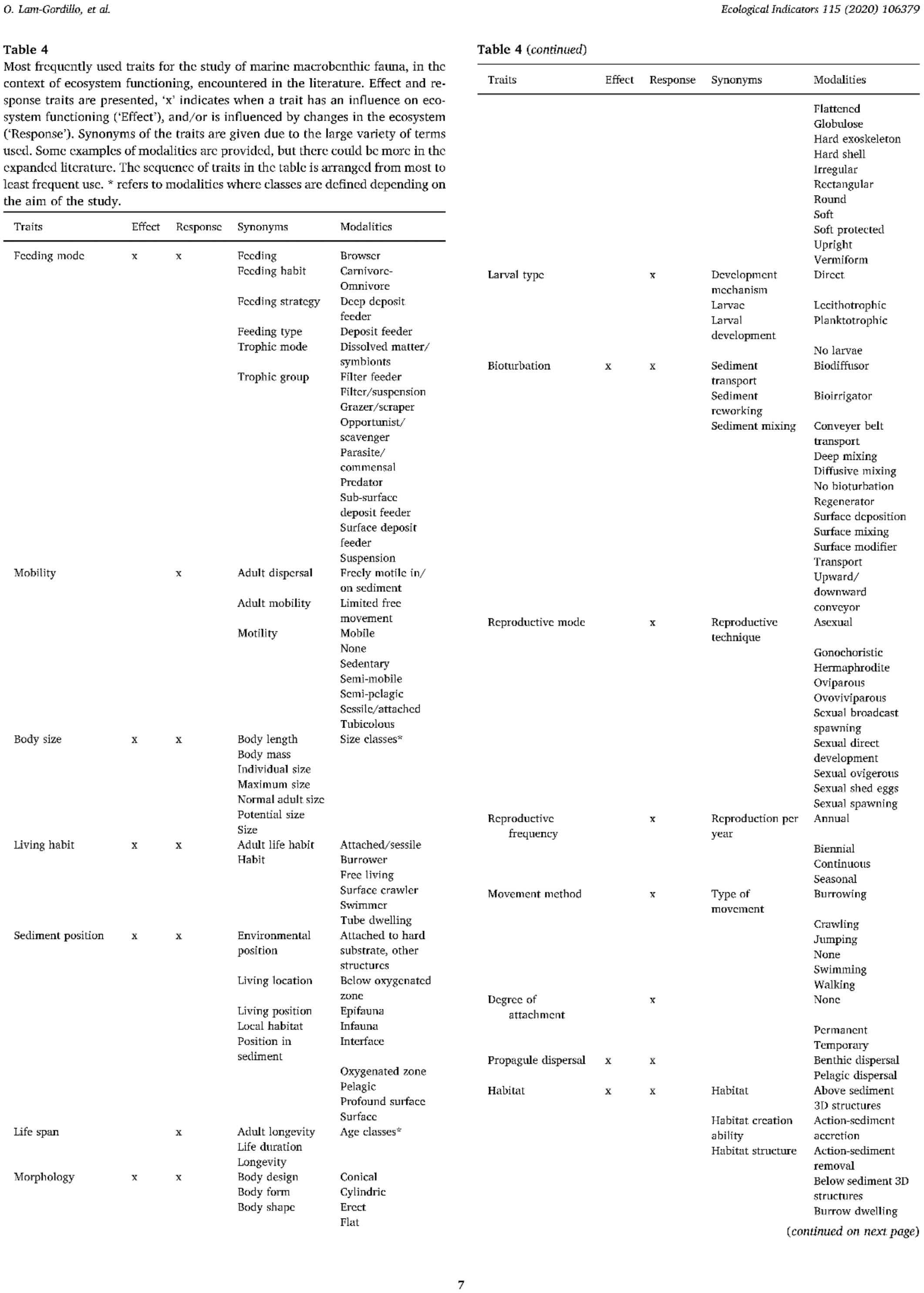

Table 4
Most frequently used traits for the study of marine macrobenthic fauna, in the context of ecosystem functioning, encountered in the literature. Effect and response traits are presented, 'x' indicates when a trait has an influence on ecosystem functioning ('Effect'), and/or is influenced by changes in the ecosystem ('Response'). Synonyms of the traits are given due to the large variety of terms used. Some examples of modalities are provided, but there could be more in the expanded literature. The sequence of traits in the table is arranged from most to least frequent use. * refers to modalities where classes are defined depending on the aim of the study.

Traits	Effect	Response	Synonyms	Modalities
Feeding mode	x	x	Feeding Feeding habit Feeding strategy Feeding type Trophic mode Trophic group	Browser Carnivore-Omnivore Deep deposit feeder Deposit feeder Dissolved matter/symbionts Filter feeder Filter/suspension Grazer/scraper Opportunist/scavenger Parasite/commensal Predator Sub-surface deposit feeder Surface deposit feeder Suspension
Mobility		x	Adult dispersal Adult mobility Motility	Freely motile in/on sediment Limited free movement Mobile None Sedentary Semi-mobile Semi-pelagic Sessile/attached Tubicolous
Body size	x	x	Body length Body mass Individual size Maximum size Normal adult size Potential size Size	Size classes*
Living habit	x	x	Adult life habit Habit	Attached/sessile Burrower Free living Surface crawler Swimmer Tube dwelling
Sediment position	x	x	Environmental position Living location Living position Local habitat Position in sediment	Attached to hard substrate, other structures Below oxygenated zone Epifauna Infauna Interface Oxygenated zone Pelagic Profound surface Surface
Life span		x	Adult longevity Life duration Longevity	Age classes*
Morphology	x	x	Body design Body form Body shape	Conical Cylindric Erect Flat Flattened Globulose Hard exoskeleton Hard shell Irregular Rectangular Round Soft Soft protected Upright Vermiform
Larval type		x	Development mechanism Larvae Larval development	Direct Lecithotrophic Planktotrophic No larvae
Bioturbation	x	x	Sediment transport Sediment reworking Sediment mixing	Biodiffusor Bioirrigator Conveyer belt transport Deep mixing Diffusive mixing No bioturbation Regenerator Surface deposition Surface mixing Surface modifier Transport Upward/downward conveyor
Reproductive mode		x	Reproductive technique	Asexual Gonochoristic Hermaphrodite Oviparous Ovoviviparous Sexual broadcast spawning Sexual direct development Sexual ovigerous Sexual shed eggs Sexual spawning
Reproductive frequency		x	Reproduction per year	Annual Biennial Continuous Seasonal
Movement method		x	Type of movement	Burrowing Crawling Jumping None Swimming Walking
Degree of attachment		x		None Permanent Temporary
Propagule dispersal	x	x		Benthic dispersal Pelagic dispersal
Habitat	x	x	Habitat Habitat creation ability Habitat structure	Above sediment 3D structures Action-sediment accretion Action-sediment removal Below sediment 3D structures Burrow dwelling

(*continued on next page*)

Table 4 (*continued*)

Traits	Effect	Response	Synonyms	Modalities
				Creating troughs, trampling on sediment Forming biogenic epibenthic structures Form-settlement/ attached site Form-shelter Hole/pit Mound Non-permanent burrow None Permanent burrow Surface dwelling Tube dwelling
Body flexibility		x		Degrees classes*
Sexual differentiation		x		Gonochoristic Hermaphrodite
Indicator role		x	AMBI-Bentix	First-order opportunistic Indifferent Second-order opportunistic Sensitive Tolerant
Salinity preference		x		Oligohaline (0–5) Mesohaline (5–18) Polyhaline (18–30) Euhaline (30–40) Hyperhaline (> 40)
Sociability	x	x		Colonial Gregarious Solitary
Migration	x	x	Dispersal habit	Life stage migration Non-migratory Seasonal migration
Substratum affinity		x		Grain sediment classes*
Productivity				Low Medium High
Hypoxia sensitivity		x		Low Medium High

publications where manipulations of the environment and organisms were applied (Table 3).

A methodological approach was used in 20% of the publications. Most of these publications found a positive relationship between taxonomic and functional diversity (e.g. Bolam, 2014; Wong and Dowd, 2015), but differences between taxonomic and functional diversity emerged as well (e.g. Belley and Snelgrove, 2016; Kokarev et al., 2017). This aligns with Cadotte et al. (2011) who demonstrated that the relationship between taxonomic and functional diversity is not positive in every case. A spatial approach was applied in 52% of the publications, and most of the publications described significant differences in functional diversity between sites (Table 3; e.g. Liu et al., 2019). Only a low proportion of publications (19%) applied a temporal approach, and most of those publications found significant temporal differences (Table 3; e.g. Taupp and Wetzel 2019). Lastly, 24% of publications applied experimental approaches to their research, and all found significant relationships between macrobenthic species and sediment condition with the most common trend showing changes in nutrient cycling depending on the number and type of species involved in the experiments (e.g. Norkko et al. 2013; Thrush et al. 2017).

5. Towards unifying research on ecosystem functioning of marine macrobenthic fauna

5.1. Terminology and definitions

The research field of ecosystem functioning uses particular terminology, however, the terms used and their underlying concepts lack uniformity and robustness and in most of the cases definitions are not provided at all (Bremner 2008; Degen, 2018; Weiss and Ray 2019), leading to confusion in understanding and wrong assumptions (e.g. Macleod et al., 2008; Bolam 2014; Rezek et al., 2017). We suggest that it is imperative to specify and define the terminology used in publications, as a coherent terminology can simplify the future progression of this research field at a global scale. As a consensus for terminology, we propose definitions for key terms on ecosystem functioning of marine macrobenthic fauna, presenting Table 1 to guide further studies, based on terms most frequently used and important for assessing ecosystem functioning (e.g. Table 1; Beauchard et al., 2017; Degen et al., 2018).

5.2. Biological traits

With growing interest in BEF for marine macrobenthic fauna the complexity of trait categories used has increased (Bremner, 2008, Beauchard et al., 2017). The majority of publications analysed relied on biological traits to assess macrobenthic fauna (78% of publications, or 115 publications). We identified that 129 publications used biological trait categories, and 10 of 26 were the most frequently used. Out of the biological traits most often used in publications, feeding mode was the most frequent trait (87% of publications), followed by mobility, body size and living habit (60.5%, 58% and 56% of publications respectively).

Considering that the selection of biological traits will always depend on the specific objectives of any particular study (Reiss et al., 2009), multiple biological traits have been identified through our dataset (Table 4). In some cases, different traits have been proposed, but with the same theoretical meaning as already established traits (e.g. Tornroos et al., 2013; Darr et al., 2014, synonyms in Table 4), resulting in a lack of consistency across publications. For a better comparability and coherent understanding of biological traits, it is necessary to use a standardized framework of biological trait categories. Some examples are the framework proposed by Bremner et al. (2003; 2006); Beauchard et al. (2017) which is not specific to macrobenthic fauna; Degen et al. (2018) which is specific to polar oceans; or the one we propose in Table 4, where traits are specified along with their synonyms (different theoretical meaning found through the literature), and the categories or modalities, providing a robust baseline for the standardization of the research field.

Another issue emerging from our literature review is the procedure for the selection of biological traits, as most of the publications used only those traits where information was available for species studied. Quantitative methods for choosing traits and weighting traits have been developed (Petchey and Gaston 2006), however refinement of traits is still needed. For many species of marine macrobenthic fauna, knowledge gaps on their biological and ecological information complicate biological trait allocation. In addition, due to the lack of identification keys for many benthic macroinvertebrates, studies with varying levels of taxonomic resolution and the inclusion of morphospecies make selection of biological traits even more difficult (Bremner, 2008, Beauchard et al., 2017; Degen et al., 2018). Recently, Weiss and Ray (2019) proposed a standardized method when selecting biological traits, providing a guide to support functional ecological comparisons across taxa. However, further research using such an approach still needs to be done to verify its validity.

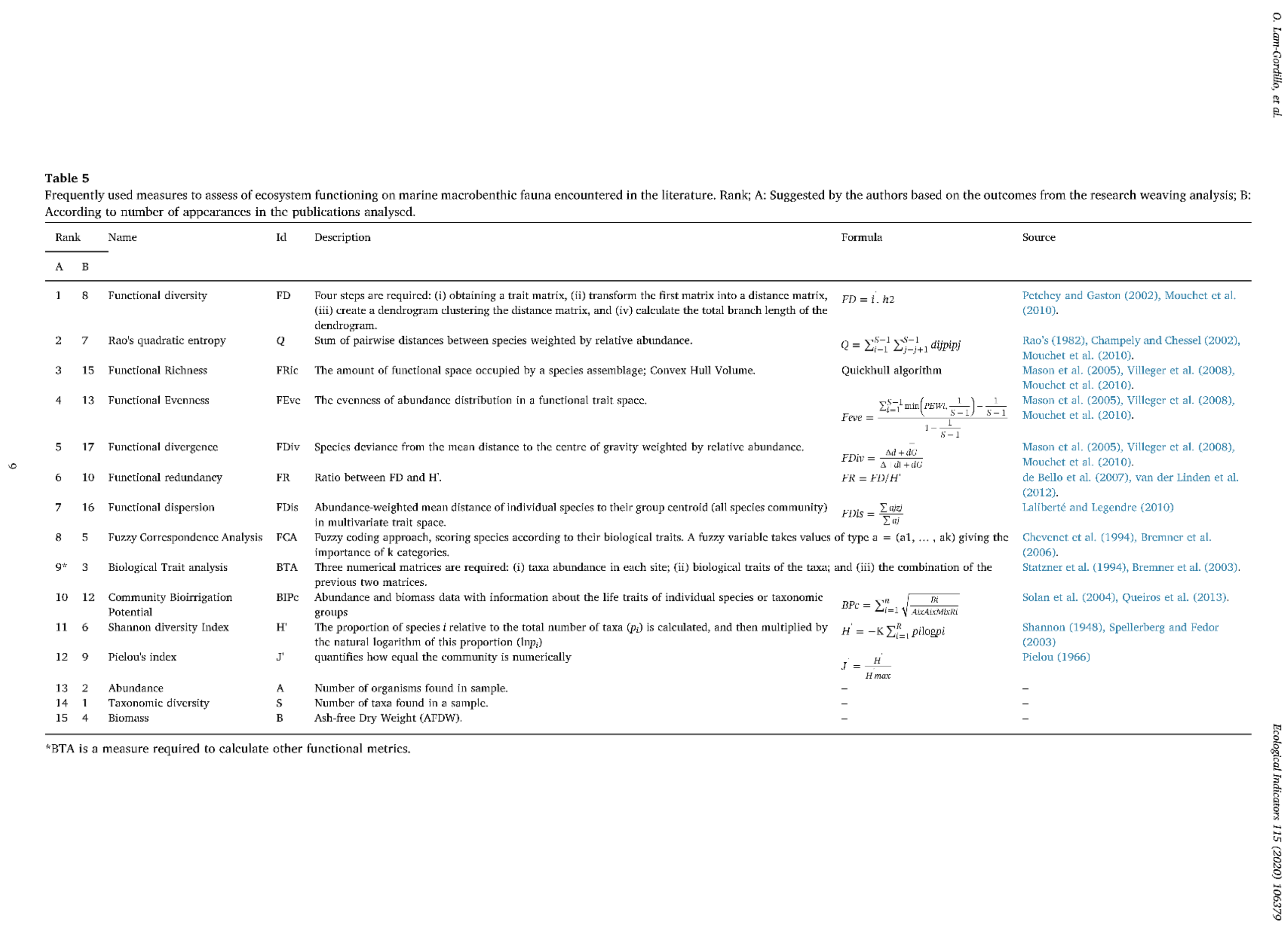

Table 5
Frequently used measures to assess of ecosystem functioning on marine macrobenthic fauna encountered in the literature. Rank; A: Suggested by the authors based on the outcomes from the research weaving analysis; B: According to number of appearances in the publications analysed.

Rank		Name	Id	Description	Formula	Source
A	B					
1	8	Functional diversity	FD	Four steps are required: (i) obtaining a trait matrix, (ii) transform the first matrix into a distance matrix, (iii) create a dendrogram clustering the distance matrix, and (iv) calculate the total branch length of the dendrogram.	$FD = \dot{i}\,.\,h2$	Petchey and Gaston (2002), Mouchet et al. (2010).
2	7	Rao's quadratic entropy	Q	Sum of pairwise distances between species weighted by relative abundance.	$Q = \sum_{i-1}^{S-1} \sum_{j-j+1}^{S-1} dijpipj$	Rao's (1982), Champely and Chessel (2002), Mouchet et al. (2010).
3	15	Functional Richness	FRic	The amount of functional space occupied by a species assemblage; Convex Hull Volume.	Quickhull algorithm	Mason et al. (2005), Villeger et al. (2008), Mouchet et al. (2010).
4	13	Functional Evenness	FEve	The evenness of abundance distribution in a functional trait space.	$Feve = \frac{\sum_{i=1}^{S-1} \min\left(PEWi, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$	Mason et al. (2005), Villeger et al. (2008), Mouchet et al. (2010).
5	17	Functional divergence	FDiv	Species deviance from the mean distance to the centre of gravity weighted by relative abundance.	$FDiv = \frac{\Delta d + \bar{d}G}{\Delta \mid d\mid + dG}$	Mason et al. (2005), Villeger et al. (2008), Mouchet et al. (2010).
6	10	Functional redundancy	FR	Ratio between FD and H'.	$FR = FD/H'$	de Bello et al. (2007), van der Linden et al. (2012).
7	16	Functional dispersion	FDis	Abundance-weighted mean distance of individual species to their group centroid (all species community) in multivariate trait space.	$FDis = \frac{\sum ajzj}{\sum aj}$	Laliberté and Legendre (2010)
8	5	Fuzzy Correspondence Analysis	FCA	Fuzzy coding approach, scoring species according to their biological traits. A fuzzy variable takes values of type a = (a1, … , ak) giving the importance of k categories.		Chevenet et al. (1994), Bremner et al. (2006).
9*	3	Biological Trait analysis	BTA	Three numerical matrices are required: (i) taxa abundance in each site; (ii) biological traits of the taxa; and (iii) the combination of the previous two matrices.		Statzner et al. (1994), Bremner et al. (2003).
10	12	Community Bioirrigation Potential	BIPc	Abundance and biomass data with information about the life traits of individual species or taxonomic groups	$BPc = \sum_{i=1}^{n} \sqrt{\frac{Bi}{AixAixMixRi}}$	Solan et al. (2004), Queiros et al. (2013).
11	6	Shannon diversity Index	H'	The proportion of species *i* relative to the total number of taxa (p_i) is calculated, and then multiplied by the natural logarithm of this proportion ($\ln p_i$)	$H^{'} = -\mathrm{K} \sum_{i=1}^{R} pilogpi$	Shannon (1948), Spellerberg and Fedor (2003)
12	9	Pielou's index	J'	quantifies how equal the community is numerically	$J^{'} = \frac{H^{'}}{H\,max}$	Pielou (1966)
13	2	Abundance	A	Number of organisms found in sample.	–	–
14	1	Taxonomic diversity	S	Number of taxa found in a sample.	–	–
15	4	Biomass	B	Ash-free Dry Weight (AFDW).	–	–

*BTA is a measure required to calculate other functional metrics.

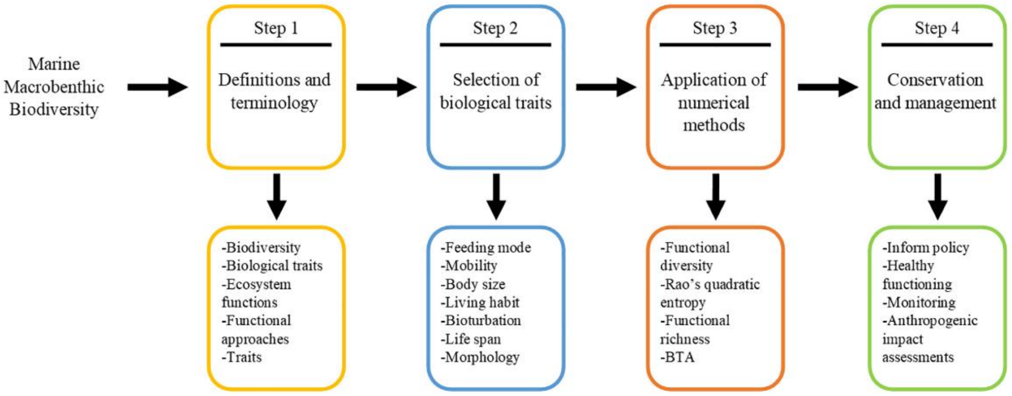

Fig. 4. Conceptual step-by-step guide for assessing ecosystem functioning of marine macrobenthic fauna.

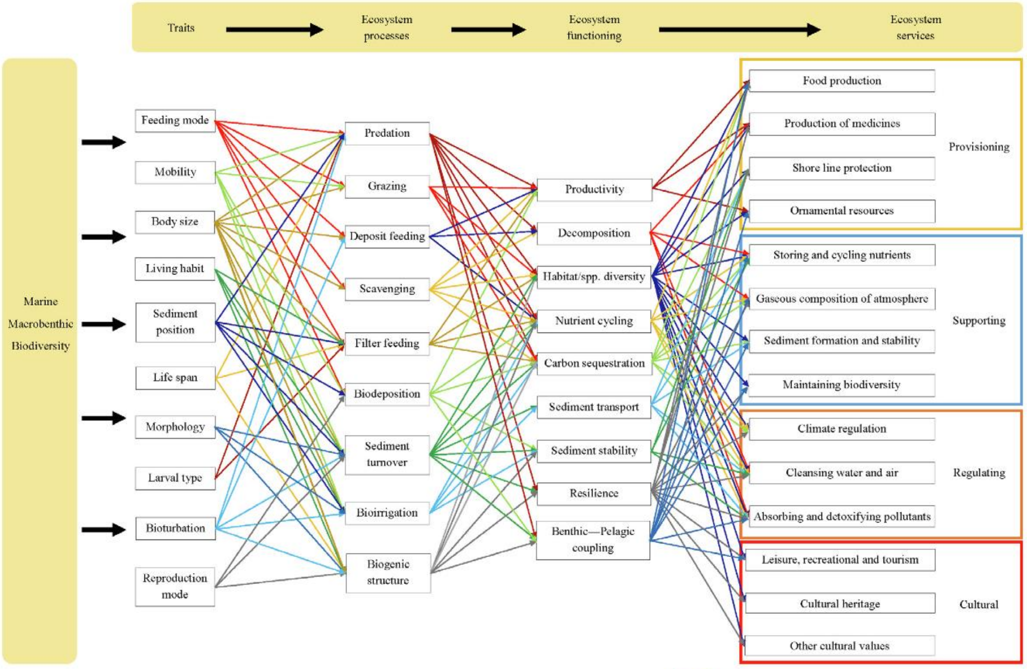

Fig. 5. Interlinkages among biodiversity of marine macrobenthic fauna, traits (the ten most frequently used, see Table 2), ecosystem processes, ecosystem functioning and ecosystem services. Note that this multi-ecosystem linkage is not restricted and can include other traits, processes, functioning and services in the expanded literature. Information was collated from: Norling et al., 2007; Bremner, 2008; Townsend et al., 2011; Norkko et al., 2013; Queiros et al., 2013; Snelgrove et al., 2014; Song et al., 2014; Clare et al., 2015; Frid et al., 2016; Weigel et al., 2016; Beauchard et al., 2017; Thrush et al., 2017; van der Linden et al., 2017; Dissanayake et al., 2018; Liu et al., 2019.

5.3. Consistency in numerical methods

A large variety of methodologies and approaches for addressing ecosystem functioning of marine macrobenthic fauna has been identified (e.g. van der Linden et al., 2012; Belley and Snelgrove, 2016; Gusmao et al., 2016; Baldrighi et al., 2017). Out of all publications, 86% used at least one numerical method to assess ecosystem functioning out of 39 different numerical metrics which were applied in the reviewed publications. However, only 17 numerical metrics were found in more than five publications (see Supplementary Data Table S2 for a full list). The numerical methods more recurrently used as a proxy for ecosystem functioning were taxonomic diversity (65 publications), abundance (59 publications) and biological traits (56 publications), taking into consideration that in the majority of the publications a combination of multiple numerical methods was used.

The variety in numerical methods found across studies was due to differences between authors, geographic areas, taxonomic groups and study type. Applying several metrics to measure how an ecosystem functions is not always practical. The wide variety of methods used, and the lack of accurate definitions that we identified across the publications, revealed the need for consistency to measure ecosystem functioning. For example, some publications used taxonomic diversity and abundance as a measure for ecosystem functioning (e.g. Lohrer et al., 2010; Pratt et al., 2015), whereas functional diversity was found less often, although functional diversity is the key component of biodiversity for reliably studying ecosystem functioning (Hooper et al., 2005; Wright et al., 2006; Legras et al., 2018).

To avoid misinterpretations in the fast-growing field of BEF research on marine macrobenthic fauna, it is imperative to standardize the metrics and methods used. Therefore, we suggest following the most important and previously established methodological frameworks when assessing ecosystem functioning (Table 5). Otherwise, results from different studies and geographical areas cannot be reliably compared, which may mask significant information or lead to wrong conclusions (Petchey and Gaston, 2006; Bremner, 2008; Snelgrove et al., 2014).

6. Outlook

With ecosystem functioning of marine macrobenthic fauna growing as a research field, our analysis revealed the complexities of multiple methodologies and usage of terminology, creating discrepancies across publications. Such inconsistencies limit the potential of comparing and exploring study outcomes between different geographical areas.

Here, we provide a conceptual step-by-step guide on approaching ecosystem functioning for marine macrobenthic fauna (Fig. 4). The following steps are imperative for advancing the research field: (1) Defining the terminology used in each publication to avoid misinterpretations and wrong conclusions. Although most of the terms are widely used, a global consensus on their definitions for ecosystem functioning in marine macrobenthic fauna is lacking. To facilitate more consistent use of terminology, we propose to use the definitions presented in Table 1.

(2) Selection of biological traits that are most suitable to address the study aims, based on species information available and previously standardized frameworks. The overview presented in Table 4 can be used as a standardised resource base for information about traits, synonyms, traits-modalities, and whether traits can indicate an effect or a response at ecosystem level (see also Beauchard et al., 2017; Degen et al., 2018; Weiss and Ray, 2019).

(3) We recommend that numerical methodologies should follow an ordered system, prioritizing the use, at least, of one of the top six measures to assess ecosystem functioning (see ranks A in Table 5). Of those measures, functional diversity is the most relevant for understanding the links between ecosystem functioning and marine macrobenthic fauna.

(4) Outcomes from ecosystem functioning assessment can be used as valuable tools for informing conservation policy and management of natural ecosystems.

We also suggest, for a full understanding of how an ecosystem is functioning, to develop more specific approaches, where the complex interlinkages across traits, ecosystem processes, ecosystem functions and services are considered. Single or multiple traits can influence several ecosystem functions, or one ecosystem function could be affected by several traits. For example, body size as a biological trait category influences several ecological processes such as predation, scavenging and bioturbation, which can then affect single or multiple functions in the ecosystem (e.g. productivity, nutrient cycling and sediment transport) and, depending on the ecosystem functions involved, one or more ecosystem services (Fig. 5).

7. Concluding remarks

In this review, we presented the first ecological synthesis that uses the approach of research weaving for analysing the ecosystem functioning and functional diversity of marine macrobenthic fauna. Thus, we provide a detailed description of the influence and evidence of the current knowledge of ecosystem functioning in marine macrobenthic fauna.

The analysis revealed that advances in this research field are challenged by multiple knowledge gaps, several different theoretical ideas, terminology and methods used. The patchiness in research globally further indicated that BEF for benthic communities is understudied in many geographical areas. The heterogeneity in terminology, lack of consistency in selection of biological traits, and inconsistencies in numerical methodologies, making it difficulties to extrapolate and compare findings on ecosystem functioning of marine benthic ecosystems, potentially leading to wrong conclusions. Therefore, we have proposed a conceptual guide suggesting the use of standardized terminology, selection of biological traits and numerical methodologies. We also emphasize the need to address the complex interlinkages between biological traits, ecological processes, ecosystem functions and services, to improve our understanding and management of these ecosystems.

With the advancement of technology, and with the willingness to expand established worldwide collaborations and research networks, the availability of information and resources (e.g. trait databases, methodologies) in this research field will only increase. However, consensus on standardised approaches is mandatory for reducing the knowledge-gap in ecosystem functioning of marine macrobenthic fauna on a global scale.

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Author's contributions

OLG conceived the ideas and developed the outline for the manuscript. All authors designed the methodology and collected the data. OLG analysed the data, prepared the figures and tables. All authors contributed critically to the manuscript draft and gave final approval for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106379.

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Appendix B. Supplementary information for Chapter 3.

Table S1. Summary information of the taxa datasets used for The South Australian Macrobenthic Traits database. n: number of samples.

Localities	Zone		Habitat		n
	Intertidal	Subtidal	Mudflat	Mussel beds	
Port Douglas					
Eely Point					
Mount Dutton Bay					
Long Beach	x		x		15
Crinoline Point	x			x	6
Kellidie Bay	x		x		15
Blanche Harbor	x			x	6
Curlew Point	x			x	6
Port Germein	x		x		15
Fisherman Bay	x		x		15
Coobowie	x			x	12
Tiddy Widdy	x		x		13
Port Arthur	x				15
Port Parham	x		x		15
Thompson's Beach	x		x		20
Middle Beach	x		x		35
Port Gawler	x		x	x	36
Section Bank	x		x	x	54
Glenelg		x	x		200
Port Stanvac		x	x		200
Port Noarlunga		x	x		200
Onkaparinga	x		x		30
Normanville	x		x		12
Hindmarsh River	x		x		18
Inman River	x		x		10
Monument Rd	x		x		30
Tarni warra	x		x		10
Hunters Creek	x		x		30
Mundoo Channel	x		x		30
Ewe Island	x		x		30
Pelican Point	x		x		45
Mulbin Yerrok	x		x		30
Noonameena	x		x		45
Parnka Point	x		x		30
Villa de Yumpa	x		x		30
Jack Point	x		x		30
Loop Rd	x		x		30

Table S2. Bibliographic references where trait information by taxa was retrieved.

Taxa	References
Acanthochitona sp.	Glynn 1970; Edgar 2008; Gowlett-Holmes 2008.
Acanthochitona sueurii	Glynn 1970; Edgar 2008; Gowlett-Holmes 2008.
Acrosterigma cygnorum	Lamprell & Whitehead 1992; Gowlett-Holmes 2008; BIOTIC (online resource).
Aglaophamus australiensis	Fauchald 1965; Rainer 1977; Beesley et al. 2000;
Amaryllididae	Lowry & Stoddart 2002; Crustacea.net (online resource).
Amblypneustes ovum	Williamson & Steinber 2002; Gowlett-Holmes 2008; O'Hara & Byrne 2017.
Amblypneustes pallidus	Williamson & Steinber 2002; Gowlett-Holmes 2008; O'Hara & Byrne 2017.
Ampeliscidae	Lowry & Poore 1985, King 2009, Durkina et a. 2017; Crustacea.net (online resource).
Ampharetidae	Beesley et al. 2000
Amphibalanus amphitrite	Satheesh & Wesley 2009; Burden et al. 2014.
Amphinomidae	Beesley et al. 2000
Amphipholis squamata	Unno 2000; Boissin et al. 2010; BIOTIC (online resource).
Amphipoda	Hale 1927; Gowlett-Holmes 2008; Crustacea.net (online resource).
Amphoroidella elliptica	Hale 1927; Bruce 2003; Crustacea.net (online resource).
Ampithoidae	Poore & Lowry 1997; Peart 2007a; Peart 2007b; Hughes & Peart 2013; Crustacea.net (online resource).
Anapella cycladea	Lamprell & Whitehead 1992; Edgar 2008; Herrmann et al. 2009.
Antarcturidae	Hale 1927; Poore 2001; Poore 2015; Crustacea.net (online resource).
Antheluridae	Hale 1927; Poore & Lewton 1998; Crustaceana.net (online resource).
Anthopleura hermaphroditica	Edgar 2008; Spano et al. 2013; Spano & Haussermann 2017.
Anthozoa	Edgar 2008.
Anthuridae	Hale 1927; Cadien & Brusca 1993; Crustacea.net (online resource).
Aoridae	Hale 1927; Drake & Arias 1995; Myers 2005; Hughes 2017; Crustacea.net (online resource).
Aphroditidae	Beesley et al. 2000.
Aplidium sp.	Edgar 2008; Gowlett-Holmes 2008.
Aplysia sp.	Angeloni et al. 2002; Gowlett-Holmes 2008; Lee et al. 2014; Nimbs et al. 2017.
Apseudidae	Hale 1927; Blazwicz-Paszkowycz & Bamber 2007a; Blazwicz-Paszkowycz & Bamber 2007b; Rumbold et al. 2012; Ferreira et al. 2015; Rumbold et al. 2015; Crustacea.net (online resources).
Arenicolidae	Beesley et al. 2000.
Aristiidae	Hale 1927; Stoddart & Lowry 2010; Crustaceana.net (online resource).
Arthritica semen	Wells & Threlfall 1982; Jaspersen & Lutzen 2009.
Ascidia sp.	Edgar 2008; Gowlett-Holmes 2008.
Ascidiacea	Edgar 2008; Gowlett-Holmes 2008.

Atactodea cuneata	Hooker & Creese 1995a; Hooker & Creese 1995b; Lamprell & Whitehead 1992; https://researchspace.auckland.ac.nz/handle/2292/5758; https://www.biodiversitylibrary.org/item/28580#page/10/mode/1up.
Australonereis ehlersi	Dorsey 1981; Beesley et al. 2000; De Roach 2006.
Australostichopus mollis	Slater 2009; Zamora & Jeffs 2013
Austrocochlea constricta	Underwood & Creese 1976; Rintala 2014 https://www.gbri.org.au/SpeciesList/AustrocochleaConstricta%7CAidanRintala.aspx?PageContentID=5174.
Austrominius adelaidae	Jones 2012.
Balanus sp.	Edgar 2008; Gowlett-Holmes 2008; Thiyagarajan et al. 2005
Bassina sp.	Lamprell & Whitehead 1992.
Bedeva paivae	Black 1976; Gowlett-Holmes 2008.
Bedeva vinosa	Black 1976; Gowlett-Holmes 2008.
Bellidilia laevis	Hale 1927; Poore 2004; Gowlett-Holmes 2008.
Bellidilia undecimspinosa	Hale 1927; Poore 2004; Gowlett-Holmes 2008.
Bembicium nanum	Underwood 1975; Edgar 2008; Gowlett-Holmes 2008; https://seashellsofnsw.org.au/Littorinidae/Pages/Bembicium_nanum.htm.
Bembicium vittatum	Edgar 2008; Gowlett-Holmes 2008; online resource.
Biffarius arenosus	Hale 1927; Poore 2004; Stapleton et al. 2001; Butler et al. 2009.
Biffarius limosus	Hale 1927; Poore 2004.
Boccardiella limnicola	Beesley et al. 2000.
Brachidontes rostratus	Lamprell & Whitehead 1992; Gowlett-Holmes 2008; El-Deeb et al. 2018; El-Sayed et al. 2018.
Brachidontes sp.	Lamprell & Whitehead 1992; Gowlett-Holmes 2008; El-Deeb et al. 2018; El-Sayed et al. 2018.
Brachynotus spinosus	Hale 1927; Griffin 1969; Griffin1971; Poore 2004.
Bulla quoyii	Lamprell & Whitehead 1992; Gowlett-Holmes 2008; Malaquias et al. 2008.
Byblis sp.	Lowry & Poore 1985, King 2009, Durkina et a. 2017; Crustacea.net (online resource).
Cacozeliana granarium	Murray 1969; Gowlett-Holmes 2008.
Cadulus vincentianus	Lamprell & Healy 1998.
Callianassidae	Hale 1927; Poore 2004.
Callista kingii	Lamprell & Whitehead 1992; Beaver et al. 2016.
Capitellidae	Petraitis 1985; Beesley et al. 2000. https://naturalhistory2.si.edu/smsfp/irlspec/Capitella_capitata.htm
Caprella danilevskii	Hale 1927; Takeuchi & Hirano 1991; Crustacea.net (online resource).
Caprellidae	Hale 1927; Bynum 1978; Gowlett-Holmes 2008; Takeuchi & Hirano 1991; De Paula et al. 2016; Crustacea.net (online resource).
Cardiidae	Lamprell & Whitehead 1992; Edgar 2008; ter Poorten et al. 2017.
Cardita crassicosta	Lamprell & Whitehead 1992.
Caridea	Hale 1927; Poore 2004; Gowlett-Holmes 2008.
Carpoapseudes austroafricanus	Hale 1927; Blazwicz-Paszkowycz & Bamber 2007a; Blazwicz-Paszkowycz & Bamber 2007b; Rumbold et al. 2012; Ferreira et al. 2015; Rumbold et al. 2015; Crustacea.net (online resources).

Cassidinopsis lacertosa	Hale 1927; Bruce 2003; Crustacea.net (online resource).
Cellana tramoserica	Fletcher 1984: Bulleri et al. 2004.
Centrocardita rosulenta	Lamprell & Whitehead 1992.
Ceratocumatidae	Hale 1927.
Ceratopogonidae	Mullen & Hribar 1988; Dourado et al. 2017; https://www.mdfrc.org.au/bugguide/index.htm.
Cerceis tridentata	Hale 1927; Bruce 2003; Crustacea.net (online resource).
Cerithiidae	Murray 1969; Gowlett-Holmes 2008.
Chama sp.	Lamprell & Whitehead 1992; Gowlett-Holmes 2008.
Chamaesipho tasmanica	Jeffery 1997; Jeffery & Underwood 2001; Edgar 2008; Gowlett-Holmes 2008.
Chironomidae larvae	Coffman & Ferrington 1996 in Merritt & Cummins 1996; Foote 1987 in Stehr 1987; https://www.mdfrc.org.au/bugguide/index.htm; https://animaldiversity.org/accounts/Chironomidae/
Chitonopsis spatulifrons	Hale 1927; Bruce 2003; Crustacea.net (online resource).
Chondrochelia ignota	Hale 1927; Blazwicz-Paszkowycz & Bamber 2007a; Blazwicz-Paszkowycz & Bamber 2007b; Rumbold et al. 2012; Ferreira et al. 2015; Rumbold et al. 2015; Crustacea.net (online resources).
Cirolana cranchii	Hale 1927; Wong & Moore 1996.
Cirratulidae	Beesley et al. 2000.
Cirriformia sp.	Beesley et al. 2000.
Clanculus dunkeri	Jansen 1993; Gowlett-Holmes 2008.
Clanculus limbatus	Jansen 1993; Gowlett-Holmes 2008.
Clanculus philippi	Jansen 1993; Gowlett-Holmes 2008.
Clanculus plebejus	Jansen 1993; Gowlett-Holmes 2008.
Cominella lineolata	Edgar 2008; Gowlett-Holmes 2008; https://collections.museumvictoria.com.au/species/8722
Condylocardiinae	Lamprell & Whitehead 1992; Middelfart 2002.
Conuber conicum	Kingsley-Smith et al. 2005; Richardson et al. 2005; Kulikova et al. 2007; Gowlett-Holmes 2008; Huelsken et al. 2008; https://seashellsofnsw.org.au/Naticidae/Pages/Conuber_conicum.htm; https://molluscsoftasmania.org.au/project/conuber-conicum/
Corophiidae	Hale 1927; Prato & Biandolino 2006; Myers 2009; Crustacea.net (online resource).
Crabyzos longicaudatus	Hale 1927; Poore & Ton 1993; Edgar 2008; Gowlett-Holmes 2008.
Cryptocnemus vincentianus	Hale 1927; Lam-Gordillo et al. 2019.
Cumacea	Hale 1927; Gerken 2001; Akiyama & Yamamoto 2004; Gerken 2013; Gerken 2014.
Cyclaspis spilotes	Hale 1927; Gerken 2001; Gerken 2013.
Cyclaspis tribulis	Hale 1927; Gerken 2001; Gerken 2013.
Cyproideidae	Hale 1927; Barnard & Karman 1991; Lowry & Azman 2008; Azman 2009; Crustacea.net (online resource).
Dexaminidae	Hale 1927; Barnard & Karman 1991; Crustacea.net (online resource).
Diastylidae	Hale 1927; Gerken 2014.
Dolichopodidae larvae	LaSalle & Bishop 1990; Cicero et al. 2017; https://www.mdfrc.org.au/bugguide/index.htm.
Dorvilleidae	Beesley et al. 2000.

Dosinia sp.	Lamprell & Whitehead 1992; Nie et al. 2016.
Duplicaria kieneri	Miller 1975; https://seashellsofnsw.org.au/Terebridae/Pages/Terebridae_intro.htm; http://www.gastropods.com/5/Shell_4905.shtml
Ebalia intermedia	Hale 1927; Poore 2004; Gowlett-Holmes 2008.
Electroma papilionacea	Gowlett-Holmes 2008; https://molluscsoftasmania.org.au/project/electroma-papilionacea/
Eoacmaea calamus	Edgar 2008; Gowlett-Holmes 2008; online resource.
Epitonium tenerum	Kilburn 1985; Huang & Lee 2016.
Equichlamys bifrons	Lamprell & Whitehead 1992; Wolf & White 1995; Gowlett-Holmes 2008.
Euchone variabilis	Hutchings and Murray 1984; Beesley et al. 2000.
Euidotea bakeri	Hale 1927; Edgar 2008; Gowlett-Holmes 2008; https://collections.museumvictoria.com.au/species/13606; https://www.sealifebase.se/summary/Euidotea-bakeri.html
Eunicidae	Beesley et al. 2000.
Euphrosinidae	Beesley et al. 2000.
Eusiridae	Hale 1927; Smith & Williams 1983; Barnard & Karman 1991; Crustacea.net (online resources).
Exosphaeroma alii	Hale 1927; Wall et al. 2015; Crustacea.net (online resources).
Exosphaeroma bicolor	Hale 1927; Wall et al. 2015; Crustacea.net (online resources).
Ficopomatus enigmaticus	Dew 1959; Beesley et al. 2000; Styan et al. 2017.
Fissurellidae	Creese 1981; Aktipis et al. 2010; Gowlett-Holmes 2008; Leon-Cisneros et al. 2017.
Flabelligeridae	Beesley et al. 2000.
Galathea australiens	Hale 1927; Poore 2004; Gowlett-Holmes 2008.
Gammaridae	Hale 1927; Barnard & Karman 1991; Subida et al. 2005; Crustacea.net (online resource).
Gazameda iredalei	Marwick & Hutt 1956; Gowlett-Holmes 2008; Allmon 2011.
Glyceridae	Beesley et al. 2000.
Glycymeris radians	Iredale 1929; Gowlett-Holmes 2008; Peharda et al. 2013.
Gnathia mulieraria	Hale 1927; Cohen & Poore 1994; Tanaka 2007; Crustacea.net (online resource).
Golfingia sp.	Murina 1984; Beesley et al. 2000; Endmonds 2000; Edgar 2008; Gowlett-Holmes 2008; Adrianov & Maiorova 2010; Rice & Pilger ND.
Gomeza bicornis	Hale 1927; Poore 2004.
Goniadidae	Beesley et al. 2000.
Granata sp.	Gowlett-Holmes 2008; Herbet 2012.
Gynodiastylis truncatifrons	Hale 1927; Gerken 2001.
Halicarcinus ovatus	Hale 1927; Griffin & Yaldwyn 1971; Lucas 1972; Poore 2004; Gowlett-Holmes 2008.
Haloniscus searlei	Hale 1927; Bayly & Ellis 1969; Ellis & Williams 1969; Williams 1983; Blin et al. 1989.
Haustorius sp.	Hale 1927; Dennell 1932; Croker 1967; Kamihira 1981; Highsmith & Coyle 1991.
Helograpsus haswellianus	Poore 2004; Breitfuss et al. 2004; Gowlett-Holmes 2008; Katrak et al. 2008; Katrak & Dittmann 2011.

Heteroserolis australiensis	Hale 1927; Harrison & Poore 1984.
Hiatella australis	Edgar 2008; Gowlett-Holmes 2008; van der Molen et al. 2007.
Hiatula alba	Lamprell & Whitehead 1992; Matthews & Fairweather 2003; Matthews & Fairweather 2004; Gowlett-Holmes 2008.
Holopneustes purpurascens	Williamson & Steinberg 2002; Swanson et al. 2006.
Holothuria (Panningothuria) austrinabassa	Tuwo & Conand 1992; O'loughlin et al. 2007; Gowlett-Holmes 2008; Benitez-Villalobos et al. 2013.
Holothuroidea	Tuwo & Conand 1992; O'loughlin et al. 2007; Gowlett-Holmes 2008; Benitez-Villalobos et al. 2013.
Hyalidae	Lowry 1980; Tsoi 1999; Tsoi & Chu 2005; Crustacea.net (online resource).
Hydrobiidae	Ponder et al. 1991; Kabat and Hershler 1993; Ponder et al. 1999.
Isaeidae	Myers 1995; Weslawski & Legezynska 2002.
Ischnochiton sp.	Edgar 2008; Gowlett-Holmes 2008; Grayson & Chapman 2004; Liversage & Benkendorff 2017.
Ischnochiton variegatus	Smith & Robertson 1970; Edgar 2008; Gowlett-Holmes 2008; online resource.
Janiridae	Hale 1927; Hessler & Stromberg 1989; Wilson & Wagele 1994; Linse et al. 2014; Crustacea.net (online resource).
Katelysia peronii	Nielsen 1963; Roberts 1984; Lamprell & Whitehead 1992; Bellchambers 1998; Cantin 2010; Dent et al. 2016.
Katelysia rhytiphora	Nielsen 1963; Roberts 1984; Lamprell & Whitehead 1992; Bellchambers 1998; Edgar 2008; Dent et al. 2016.
Katelysia scalarina	Nielsen 1963; Roberts 1984; Lamprell & Whitehead 1992; Bellchambers 1998; Edgar 2008; Cantin 2010; Dent et al. 2016.
Laternula sp.	Lamprell & Whitehead 1992; Ahn 1993; Philipp et al. 2008; Kang et al. 2009.
Leptocheliidae	Hale 1927; Blazwicz-Paszkowycz & Bamber 2012; Rumbold et al. 2012; Ferreira et al. 2015; Rumbold et al. 2015; Crustacea.net (online resource).
Leucosoleniidae	Edgar 2008; Gowlett-Holmes 2008; Borojevic et al. 2000.
Liloa brevis	Burn 2006; Saunders 2009; Too et al. 2014; Nimbs & Smith 2016.
Limaria orientalis	Lamprell & Whitehead 1992; Gowlett-Holmes 2008; online resource.
Limatula strangei	Flemming 1977; Lamprell & Whitehead 1992; Gowlett-Holmes 2008.
Litocheira bispinosa	Hale 1927; Griffin & Yaldwyn 1971; Poore 2004; Gowlett-Holmes 2008.
Litogynodiastylis turgida	Hale 1927; Gerken 2001.
Lophopagurus (Lophopagurus) nanus	Hale 1927; Poore 2004; Wada et al. 2000; Mantelatto et al. 2007; Gowlett-Holmes 2008; Korn et al. 2018; Kornienko et al. 2019.
Lottiidae	Nakano & Ozawa 2005; Edgar 2008; Gowlett-Holmes 2008.
Lucinidae	Lamprell & Whitehead 1992; Glover & Taylos 2001; Gowlett-Holmes 2008; Taylor et al. 2011.
Lumbrineridae	Beesley et al. 2000.
Lutraria rhynchaena	Lamprell & Whitehead 1992; Gowlett-Holmes 2008; Gan et al. 2016.
Lysianassidae	Hale 1927; Sainte-Marie 1986; Lowry & Stoddart 1995; Kilgallen & Lowry 2013.

Macomona deltoidalis	Ponder 1975; Lamprell & Whitehead 1992; https://molluscsoftasmania.org.au/project/macomona-deltoidalis/
Mactridae	Healy & Lamprell 1992; Lamprell & Whitehead 1992; Gowlett-Holmes 2008.
Mactrotoma antecedens	Healy & Lamprell 1992; Lamprell & Whitehead 1992.
Magellania flavescens	Edgar 2008; Gowlett-Holmes 2008; Baird et al. 2013.
Magelonidae	Beesley et al. 2000.
Maldanidae	Beesley et al. 2000.
Mesanthura maculata	Hale 1927; Poore & Ton 1986; Cadien & Brusca 1993; Crustacea.net (online resource).
Metapenaeopsis novaeguineae	Hale 1927; Poore 2004; Gowlett-Holmes 2008.
Mimachlamys sp.	Iredale 1929; Lamprell & Whitehead 1992; Zacharin 1995; Gowlett-Holmes 2008; Dijkstra & Beu 2018.
Mitrella australis	https://seashellsofnsw.org.au/Columbellidae/Pages/Columbellidae_intro.htm
Mitrella lincolnensis	https://seashellsofnsw.org.au/Columbellidae/Pages/Columbellidae_intro.htm
Mopaliidae	Edgar 2008; Gowlett-Holmes 2008; Vendrasco et al. 2008; Lord 2011; Sigwart et al. 2013.
Musculus nana	Gowlett-Holmes 2008; Ab Rahim et al. 2016.
Myadora albida	Healy et al. 2015.
Mysella sp.	Passos et al. 2004.
Mysidae	Fenton 1986; Panampunnayil 1986; Jocque & Blom 2009; Lill et al. 2010.
Nassariidae	McKillup & Butler 1979; Chan & Morton 2005; Edgar 2008; Gowlett-Holmes 2008.
Nassarius pauperatus	McKillup & Butler 1979; Chan & Morton 2005; Edgar 2008; Gowlett-Holmes 2008.
Nassarius pyrrhus	Chan & Morton 2005; Edgar 2008; Gowlett-Holmes 2008.
Natatolana vieta	Hale 1927; Bruce 1986; Keable 2006; Crustacea.net (online resource).
Natica sp.	Kingsley-Smith et al. 2005; Richardson et al. 2005; Kulikova et al. 2007; Edgar 2008; Gowlett-Holmes 2008; Huelsken et al. 2008.
Neanthes vaalii	Beesley et al. 2000; Baken 2002.
Neastacilla deducta	Hale 1927; King 2003; Crustacea.net (online resource).
Nebaliidae	Hale 1927; Vetter 1996; Walker-Smith & Poore 2001.
Nemertea	Egan & Anderson 1979; Edgar 2008; Gowlett-Holmes 2008.
Nemocardium sp.	Lamprell & Whitehead 1992; ter Poorten 2013.
Neocallichirus angelikae	Sakai 2000; Poore 2004.
Neotrigonia sp.	Tevesz 1975; Morton 1987; Lamprell & Whitehead 1992; Glavinic 2010.
Nephtyidae	Fauchald 1963; Rainer & Hutchings 1977; Beesley et al. 2000.
Nereididae	Beesley et al. 2000.
Nerita atramentosa	Underwood 1975; Gowlett-Holmes 2008; Edgar 2008; Przeslawski 2011.
Notoacmea flammea	Ponder & Creese 1980; Gowlett-Holmes 2008; Edgar 2008; https://www.sealifebase.ca/summary/Notoacmea-flammea.html
Notospermus sp.	Egan & Anderson 1979; Gowlett-Holmes 2008; Edgar 2008.

Nototeredo edax	McKoy 1980; Rayner 1983; Mann & Gallager 1985; MacIntosh et al. 2014.
Oenonidae	Beesley et al. 2000.
Oligochaeta	Parish 1981; Bonomi & Erseus 1984; Giere 2006; Edgar 2008; Pinder 2010; Lobo & de Gama 2011.
Onuphidae	Beesley et al. 2000.
Opheliidae	Beesley et al. 2000.
Ophiactis tricolor	McGovern 2002a; McGovern 2002b; Edgar 2008.
Ophiomyxa australis	Edgar 2008; Franklin & O'Hara 2008; Gowlett-Holmes 2008.
Ophionereis sp.	Selvakumaraswamy & Byrne 1995; Edgar 2008; Gowlett-Holmes 2008; Yokoyama & Amaral 2011.
Ophiothrix caespitosa	Selvakumaraswamy & Byrne 2000; Edgar 2008; Gowlett-Holmes 2008.
Ophiuroidea	Selvakumaraswamy & Byrne 1995; Selvakumaraswamy & Byrne 2000; Edgar 2008; Franklin & O'Hara 2008; Gowlett-Holmes 2008; Yokoyama & Amaral 2011.
Orbiniidae	Beesley et al. 2000.
Oweniidae	Beesley et al. 2000.
Paguridae	Hale 1927; Poore 2004; Wada et al. 2000; Mantelatto et al. 2007; Gowlett-Holmes 2008; Korn et al. 2018; Kornienko et al. 2019.
Palaemon intermedius	Hale 1927; Walker & Poore 2003; Poore 2004; Bilgin & Samsun 2006; Gowlett-Holmes 2008; Mortari et al. 2010.
Paradentalium intercalatum	Lamprell & Healy 1998.
Paragrapsus gaimardii	Hale 1927; Poore 2004; Gowlett-Holmes 2008.
Paraonidae	Beesley et al. 2000.
Paraproto spinosa	Hale 1927; Takeuchi & Hirano 1991; Guerra-Garcia & Takeuchi 2004.
Parapseudidae	Hale 1927; Blazwicz-Paszkowycz & Bamber 2007a; Blazwicz-Paszkowycz & Bamber 2007b; Ferreira et al. 2015; Rumbold et al. 2015; Crustacea.net (online resource).
Parastacilla bakeri	Hale 1927; King 2000; Crustacea.net (online resource).
Pardaliscidae	Hale, 1927; Barnard & Karaman 1991; Crustacea.net (online resource).
Parvulastra exigua	Edgar 2008; Gowlett-Holmes 2008; Roediger & Bolton 2008; Barbosa et al. 2012; Nguyen & Byrne 2014.
Patellidae	Woods 1876; Ridgway et al. 1998; Edgar 2008; Zegaoula et al. 2016; online resource.
Pectinariidae	Beesley et al. 2000; Hutchings et al. 2002.
Peculator porphyria	Bouchet & Kantor 2000; Bouchet & Kantor 2004; Harasewych & Kantor 2005; https://seashellsofnsw.org.au/Volutomitridae/Pages/volutomitridae_intro.htm; https://molluscsoftasmania.org.au/project/peculator-porphyria/
Penaeus latisulcatus	Hale 1927; Gordon 1979; Penn 1980; Poore 2004; Hackett 2017.
Perthiidae	Hale 1927; Gowlett-Holmes 2008; Crustacea.net (online resource).
Phasianotrochus eximius	Edgar 2008; Gowlett-Holmes 2008; Bell et al. 2014; https://molluscsoftasmania.org.au/project/phasianotrochus-eximius/
Philine angasi	Rudman 1972; Edgar 2008; Gowlett-Holmes 2008; Price et al. 2011; Nimbs & Smith 2016.

Phoratopodidae	Hale 1927; Bruce 1981.
Phoxocephalidae	Barnard & Drummond 1978; Slattery 1985; Barnard & Karaman 1991.
Phyllodoce novaehollandiae	Beesley et al. 2000.
Phyllodocidae	Beesley et al. 2000.
Pilumnopeus serratifrons	Hale 1927; Greenwood & Fielder 1984; Davie 2002b; Poore 2004; Gowlett-Holmes 2008.
Pinna bicolor	Butler 1987; Lamprell & Whitehead 1992; Gowlett-Holmes 2008; Idris et al. 2012.
Placamen flindersi	Lamprell & Whitehead 1992.
Plakarthriidae	Hale 1927; Wilson et al. 1976; Poore & Brandt 2001.
Platynympha longicaudata	Hale 1927; Bruce 2003; Crustacea.net (online resource).
Polynoidae	Beesley et al. 2000.
Polyplacophora	Edgar 2008; Gowlett-Holmes 2008; Sigwart et al. 2013.
Portunus pelagicus	Hale 1927; Poore 2004; Gowlett-Holmes 2008; Johnson et al. 2010.
Propefusus australis	Edgar 2008; Gowlett-Holmes 2008; https://www.sealifebase.ca/summary/Fusinus-australis.html
Pteriidae	Southgate & Lucas 2008; Milione & Southgate 2012.
Pterochelus triformis	Vokes 1993; Edgar 2008; Gowlett-Holmes 2008.
Rathbunaria orientalis	Davie 2002a; Poore 2004; NG 2010.
Rhyssoplax sp.	Edgar 2008; Gowlett-Holmes 2008; Sigwart et al. 2013.
Rissoina crassa	Ponder 1984; Gowlett-Holmes 2008.
Rissoina fasciata	Ponder 1984; Gowlett-Holmes 2008.
Sabellariidae	Beesley et al. 2000; Hutchings et al. 2012.
Sabellidae	Beesley et al. 2000.
Sabia australis	Morton & Jones 2000; https://seashellsofnsw.org.au/Hipponicidae/Pages/Hipponix_australis.htm
Saccella crassa	Hutchings & Haedrich 1984; Morton 2012.
Salinator fragilis	Golding et al. 2007; Golding et al. 2008; https://seashellsofnsw.org.au/Amphibolidae/Pages/Amphibolidae_intro.htm.
Scissurella cyprina	Geiger & Jansen 2004; https://seashellsofnsw.org.au/Scissurellidae/Pages/scissurellidae_intro.htm
Serpulidae	Dew 1959; Beesley et al. 2000.
Sigalionidae	Beesley et al. 2000.
Simplisetia aequisetis	Beesley et al. 2000.
Sipuncula	Beesley et al. 2000; Edgar 2008; Gowlett-Holmes 2008.
Solemya australis	Reid & Brand 1987; Pennec & Beninger 2000.
Sphaerosyllis sp.	Beesley et al. 2000.
Spionidae	Beesley et al. 2000.
Spisula trigonella	Murawski & Serchuk 1982; Cerrato & Keith 1992; Gaspar et al. 1995.
Stenochiton cymodocealis	Ashby 1923; Gowlett-Holmes 2008.
Stenochiton pilsbryanus	Ashby 1923; Gowlett-Holmes 2008.
Stenochiton sp.	Ashby 1923; Gowlett-Holmes 2008.

Stimdromia lateralis	Jamieson et al. 1993; Poore 2004; Gowlett-Holmes 2008.
Syllidae	Beesley et al. 2000.
Synischia levidensis	Hale 1927; Poore & Ton 1993.
Tanaidacea	Hale 1927; Blazwicz-Paszkowycz & Bamber 2007a; Blazwicz-Paszkowycz & Bamber 2007b; Ferreira et al. 2015; Rumbold et al. 2015; Crustacea.net (online resource).
Tanea sagittata	Kingsley-Smith et al. 2005; Richardson et al. 2005; Kulikova et al. 2007; Edgar 2008; Gowlett-Holmes 2008; Huelsken et al. 2008.
Tasmanoplax latifrons	Nye 1974; Simons & Jones 1981; Pasupathi & Kannupandi 1988a; Pasupathi & Kannupandi 1988b; Poore 2004.
Tawera lagopus	Nielsen 1963; Roberts 1984; Lamprell & Whitehead 1992; Bellchambers 1998; Edgar 2008; Dent et al. 2016; https://molluscsoftasmania.org.au/project/tawera-lagopus/
Tellinides margaritinus	Lamprell & Whitehead 1992; http://portphillipmarinelife.net.au/species/5648; http://www.marlin.ac.uk/biotic/browse.php?sp=4354
Tellina sp.	Lamprell & Whitehead 1992; http://portphillipmarinelife.net.au/species/5648; http://www.marlin.ac.uk/biotic/browse.php?sp=4354
Temnopleurus michaelseni	Williamson & Steinberg 2002; Gowlett-Holmes 2008; https://molluscsoftasmania.org.au/project/tellinides-margaritinus/
Terebellidae	Beesley et al. 2000.
Trapezidae	Lamprell & Whitehead 1992; Tan & Low 2013.
Trichobranchidae	Beesley et al. 2000; Hutchings & Peart 2000.
Tucetona sp.	Iredale 1929; Lamprell & Whitehead 1992; Crncevic et al. 2013.
Turritellidae	Marwick & Hutt 1956; Garrad 1982; Allmon 2011.
Uniophora granifera	Edgar 2008; Gowlett-Holmes 2008; O'Hara & Byrne 2017.
Veneridae	Nielsen 1963; Roberts 1984; Lamprell & Whitehead 1992; Bellchambers 1998; Edgar 2008; Dent et al. 2016; online resource.
Venerupis anomala	Lamprell & Whitehead 1992; Mohammad et al. 2014.
Vitrinellidae	Bartsch 1952; Pilsbry & Olsson 1952; Bieler & Mikkelsen 1988; Marshall 1988; Rolan & Sellanes 2004.
Xenostrobus inconstans	Gowlett-Holmes 2008; Colgan & da Costa 2013.
Zeacumantus diemenensis	Adachi & Wada 1999; Gowlett-Holmes 2008.
Zeacumantus plumbeus	Adachi & Wada 1999; Gowlett-Holmes 2008.

Online resources

Crustacea.net	http://www.crustacea.net/crustace/amphipoda/index.htm
BIOTIC	http://www.marlin.ac.uk/biotic/
WoRMS	http://www.marinespecies.org
ATLAS of Living Australia	http://www.ala.org.au
Sealife Base	https://www.sealifebase.ca/
Bug guide	https://www.mdfrc.org.au/bugguide/index.htm

Table S3. Full reference list.

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Table S4. List of the taxa included in The South Australian Macrobenthic Traits database.

Phylum	Class	Order	Family	Species	AphiaID
Annelida	Oligochaeta				2036
Annelida	Polychaeta	Amphinomida	Amphinomidae		960
Annelida	Polychaeta	Amphinomida	Euphrosinidae		961
Annelida	Polychaeta	Eunicida	Dorvilleidae		971
Annelida	Polychaeta	Eunicida	Eunicidae		966
Annelida	Polychaeta	Eunicida	Lumbrineridae		967
Annelida	Polychaeta	Eunicida	Onuphidae		965
Annelida	Polychaeta	Phyllodocida	Aphroditidae		938
Annelida	Polychaeta	Phyllodocida	Glyceridae		952
Annelida	Polychaeta	Phyllodocida	Goniadidae		953
Annelida	Polychaeta	Phyllodocida	Nephtyidae		956
Annelida	Polychaeta	Phyllodocida	Nephtyidae	*Aglaophamus australiensis*	547399
Annelida	Polychaeta	Phyllodocida	Nereididae		22496
Annelida	Polychaeta	Phyllodocida	Nereididae	*Australonereis ehlersi*	333062
Annelida	Polychaeta	Phyllodocida	Nereididae	*Neanthes vaalii*	334112
Annelida	Polychaeta	Phyllodocida	Nereididae	*Simplisetia aequisetis*	334804
Annelida	Polychaeta	Phyllodocida	Phyllodocidae		931
Annelida	Polychaeta	Phyllodocida	Phyllodocidae	*Phyllodoce novaehollandiae*	330618
Annelida	Polychaeta	Phyllodocida	Polynoidae		939
Annelida	Polychaeta	Phyllodocida	Sigalionidae		943
Annelida	Polychaeta	Phyllodocida	Syllidae		948
Annelida	Polychaeta	Phyllodocida	Syllidae	*Sphaerosyllis sp.*	129677
Annelida	Polychaeta	Sabellida	Oweniidae		975
Annelida	Polychaeta	Sabellida	Sabellidae	*Euchone variabilis*	327558
Annelida	Polychaeta	Sabellida	Sabellidae		985
Annelida	Polychaeta	Sabellida	Serpulidae		988
Annelida	Polychaeta	Sabellida	Serpulidae	*Ficopomatus enigmaticus*	130988
Annelida	Polychaeta	Spionida	Spionidae	*Boccardiella limnicola*	872564
Annelida	Polychaeta	Spionida	Spionidae		913
Annelida	Polychaeta	Terebellida	Ampharetidae		981
Annelida	Polychaeta	Terebellida	Cirratulidae		919
Annelida	Polychaeta	Terebellida	Cirratulidae	*Cirriformia sp.*	129245
Annelida	Polychaeta	Terebellida	Flabelligeridae		976
Annelida	Polychaeta	Terebellida	Pectinariidae		980
Annelida	Polychaeta	Terebellida	Terebellidae		982
Annelida	Polychaeta	Terebellida	Trichobranchidae		983
Annelida	Polychaeta		Arenicolidae		922
Annelida	Polychaeta		Capitellidae		921
Annelida	Polychaeta		Magelonidae		914
Annelida	Polychaeta		Maldanidae		923
Annelida	Polychaeta		Oenonidae		22610

Annelida	Polychaeta		Opheliidae		924
Annelida	Polychaeta		Orbiniidae		902
Annelida	Polychaeta		Paraonidae		903
Annelida	Polychaeta		Sabellariidae		979
Arthropoda	Hexanauplia	Sessilia	Austrobalanidae	*Austrominius adelaidae*	535009
Arthropoda	Hexanauplia	Sessilia	Balanidae	*Amphibalanus amphitrite*	421137
Arthropoda	Hexanauplia	Sessilia	Balanidae	*Balanus sp.*	106122
Arthropoda	Hexanauplia	Sessilia	Chthamalidae	*Chamaesipho tasmanica*	733183
Arthropoda	Insecta	Diptera	Ceratopogonidae		150940
Arthropoda	Insecta	Diptera	Chironomidae		118100
Arthropoda	Insecta	Diptera	Dolichopodidae		150930
Arthropoda	Malacostraca	Amphipoda			1135
Arthropoda	Malacostraca	Amphipoda	Amaryllididae		236743
Arthropoda	Malacostraca	Amphipoda	Ampeliscidae		101364
Arthropoda	Malacostraca	Amphipoda	Ampeliscidae	*Byblis sp.*	101446
Arthropoda	Malacostraca	Amphipoda	Ampithoidae		101366
Arthropoda	Malacostraca	Amphipoda	Aoridae		101368
Arthropoda	Malacostraca	Amphipoda	Aristiidae		236740
Arthropoda	Malacostraca	Amphipoda	Caprellidae		101361
Arthropoda	Malacostraca	Amphipoda	Caprellidae	*Caprella danilevskii*	101827
Arthropoda	Malacostraca	Amphipoda	Caprellidae	*Paraproto spinosa*	431139
Arthropoda	Malacostraca	Amphipoda	Corophiidae		101376
Arthropoda	Malacostraca	Amphipoda	Cyproideidae		236744
Arthropoda	Malacostraca	Amphipoda	Dexaminidae		101378
Arthropoda	Malacostraca	Amphipoda	Eusiridae		101380
Arthropoda	Malacostraca	Amphipoda	Gammaridae		101383
Arthropoda	Malacostraca	Amphipoda	Haustoriidae	*Haustorius sp.*	101546
Arthropoda	Malacostraca	Amphipoda	Hyalidae		101385
Arthropoda	Malacostraca	Amphipoda	Isaeidae		101388
Arthropoda	Malacostraca	Amphipoda	Lysianassidae		101395
Arthropoda	Malacostraca	Amphipoda	Pardaliscidae	Pardaliscidae	101401
Arthropoda	Malacostraca	Amphipoda	Perthiidae		548463
Arthropoda	Malacostraca	Amphipoda	Phoxocephalidae		101403
Arthropoda	Malacostraca	Cumacea			1137
Arthropoda	Malacostraca	Cumacea	Bodotriidae	*Cyclaspis spilotes*	181750
Arthropoda	Malacostraca	Cumacea	Bodotriidae	*Cyclaspis tribulis*	181762
Arthropoda	Malacostraca	Cumacea	Ceratocumatidae		110379
Arthropoda	Malacostraca	Cumacea	Diastylidae		110380
Arthropoda	Malacostraca	Cumacea	Gynodiastylidae	*Gynodiastylis truncatifrons*	182189
Arthropoda	Malacostraca	Cumacea	Gynodiastylidae	*Litogynodiastylis turgida*	489289
Arthropoda	Malacostraca	Decapoda	Callianassidae	*Biffarius arenosus*	477612
Arthropoda	Malacostraca	Decapoda	Callianassidae	*Biffarius limosus*	NA
Arthropoda	Malacostraca	Decapoda	Callianassidae	*Neocallichirus angelikae*	477724
Arthropoda	Malacostraca	Decapoda	Callianassidae		106800

Arthropoda	Malacostraca	Decapoda	Caridea		106674
Arthropoda	Malacostraca	Decapoda	Corystidae	*Gomeza bicornis*	209576
Arthropoda	Malacostraca	Decapoda	Dromiidae	*Stimdromia lateralis*	440108
Arthropoda	Malacostraca	Decapoda	Galatheidae	*Galathea australiens*	210092
Arthropoda	Malacostraca	Decapoda	Hymenosomatidae	*Halicarcinus ovatus*	441784
Arthropoda	Malacostraca	Decapoda	Leucosiidae	*Bellidilia laevis*	441104
Arthropoda	Malacostraca	Decapoda	Leucosiidae	*Bellidilia undecimspinosa*	441105
Arthropoda	Malacostraca	Decapoda	Leucosiidae	*Cryptocnemus vincentianus*	441066
Arthropoda	Malacostraca	Decapoda	Leucosiidae	*Ebalia intermedia*	441125
Arthropoda	Malacostraca	Decapoda	Litocheiridae	*Litocheira bispinosa*	441005
Arthropoda	Malacostraca	Decapoda	Macrophthalmidae	*Tasmanoplax latifrons*	558102
Arthropoda	Malacostraca	Decapoda	Paguridae	*Lophopagurus (Lophopagurus) nanus*	366494
Arthropoda	Malacostraca	Decapoda	Paguridae		106738
Arthropoda	Malacostraca	Decapoda	Palaemonidae	*Palaemon intermedius*	514452
Arthropoda	Malacostraca	Decapoda	Penaeidae	*Metapenaeopsis novaeguineae*	377510
Arthropoda	Malacostraca	Decapoda	Penaeidae	*Penaeus latisulcatus*	210372
Arthropoda	Malacostraca	Decapoda	Piluminidae	*Pilumnopeus serratifrons*	395025
Arthropoda	Malacostraca	Decapoda	Planopilumnidae	*Rathbunaria orientalis*	558010
Arthropoda	Malacostraca	Decapoda	Portunidae	*Portunus pelagicus*	1061754
Arthropoda	Malacostraca	Decapoda	Varunidae	*Brachynotus spinosus*	444761
Arthropoda	Malacostraca	Decapoda	Varunidae	*Helograpsus haswellianus*	444729
Arthropoda	Malacostraca	Decapoda	Varunidae	*Paragrapsus gaimardii*	444743
Arthropoda	Malacostraca	Isopoda	Antarcturidae		174627
Arthropoda	Malacostraca	Isopoda	Antheluridae		118243
Arthropoda	Malacostraca	Isopoda	Anthuridae		118244
Arthropoda	Malacostraca	Isopoda	Anthuridae	*Mesanthura maculata*	211375
Arthropoda	Malacostraca	Isopoda	Arcturidae	*Neastacilla deducta*	261418
Arthropoda	Malacostraca	Isopoda	Arcturidae	*Parastacilla bakeri*	261924
Arthropoda	Malacostraca	Isopoda	Cirolanidae	*Cirolana cranchii*	118839
Arthropoda	Malacostraca	Isopoda	Cirolanidae	*Natatolana vieta*	256708
Arthropoda	Malacostraca	Isopoda	Gnathiidae	*Gnathia mulieraria*	257195
Arthropoda	Malacostraca	Isopoda	Idoteidae	*Crabyzos longicaudatus*	259908
Arthropoda	Malacostraca	Isopoda	Idoteidae	*Euidotea bakeri*	260323
Arthropoda	Malacostraca	Isopoda	Idoteidae	*Synischia levidensis*	263447
Arthropoda	Malacostraca	Isopoda	Janiridae		118258
Arthropoda	Malacostraca	Isopoda	Philisciidae	*Haloniscus searlei*	260492
Arthropoda	Malacostraca	Isopoda	Phoratopodidae		248305
Arthropoda	Malacostraca	Isopoda	Plakarthriidae		248307
Arthropoda	Malacostraca	Isopoda	Serolidae	*Heteroserolis australiensis*	260632
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Amphoroidella elliptica*	258839
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Cassidinopsis lacertosa*	258141

Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Cerceis tridentata*	259708
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Chitonopsis spatulifrons*	259775
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Exosphaeroma alii*	257012
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Exosphaeroma bicolor*	257018
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Platynympha longicaudata*	262176
Arthropoda	Malacostraca	Leptostraca	Nebaliidae		147029
Arthropoda	Malacostraca	Mysida	Mysidae		119822
Arthropoda	Malacostraca	Tanaidacea			1133
Arthropoda	Malacostraca	Tanaidacea	Apseudidae		136153
Arthropoda	Malacostraca	Tanaidacea	Apseudidae	*Carpoapseudes austroafricanus*	247122
Arthropoda	Malacostraca	Tanaidacea	Leptocheliidae		136160
Arthropoda	Malacostraca	Tanaidacea	Parapseudidae		136156
Arthropoda	Malacostraca	Tanaidacea	Paratanaidae	*Chondrochelia ignota*	880869
Brachiopoda	Rhynchonellata	Terebratulida	Terebratellidae	*Magellania flavescens*	235686
Chordata	Ascidiacea				1839
Chordata	Ascidiacea	Aplousobranchia	Polyclinidae	*Aplidium sp.*	103474
Chordata	Ascidiacea	Phlebobranchia	Ascidiidae	*Ascidia sp.*	103483
Cnidaria	Anthozoa				1292
Cnidaria	Anthozoa	Actiniaria	Actiniidae	*Anthopleura hermaphroditica*	283353
Echinodermata	Asteroidea	Forcipulatida	Asteriidae	*Uniophora granifera*	292860
Echinodermata	Asteroidea	Valvatida	Asterinidae	*Parvulastra exigua*	459556
Echinodermata	Echinoidea	Camarodonta	Temnopleuridae	*Amblypneustes ovum*	513100
Echinodermata	Echinoidea	Camarodonta	Temnopleuridae	*Amblypneustes pallidus*	513102
Echinodermata	Echinoidea	Camarodonta	Temnopleuridae	*Holopneustes purpurascens*	569179
Echinodermata	Echinoidea	Camarodonta	Temnopleuridae	*Temnopleurus michaelseni*	513594
Echinodermata	Holothuroidea				123083
Echinodermata	Holothuroidea	Holothuriida	Holothuriidae	*Holothuria (Panningothuria) austrinabassa*	529055
Echinodermata	Holothuroidea	Synallactida	Stichopodidae	*Australostichopus mollis*	529443
Echinodermata	Ophiuroidea				123084
Echinodermata	Ophiuroidea	Amphilepidida	Amphiuridae	*Amphipholis squamata*	125064
Echinodermata	Ophiuroidea	Amphilepidida	Ophiactidae	*Ophiactis tricolor*	243472
Echinodermata	Ophiuroidea	Amphilepidida	Ophionereididae	*Ophionereis sp.*	123553
Echinodermata	Ophiuroidea	Amphilepidida	Ophiotrichidae	*Ophiothrix caespitosa*	244975
Echinodermata	Ophiuroidea	Ophiacanthida	Ophiomyxidae	*Ophiomyxa australis*	212437
Mollusca	Bivalvia	Adapedonta	Hiatellidae	*Hiatella australis*	545939
Mollusca	Bivalvia	Arcida	Glycymerididae	*Glycymeris radians*	213522
Mollusca	Bivalvia	Arcida	Glycymerididae	*Tucetona sp.*	204544
Mollusca	Bivalvia	Cardiida	Cardiidae		229
Mollusca	Bivalvia	Cardiida	Cardiidae	*Acrosterigma cygnorum*	381166
Mollusca	Bivalvia	Cardiida	Cardiidae	*Nemocardium sp.*	152920

Mollusca	Bivalvia	Cardiida	Carditidae	*Cardita crassicosta*	207679
Mollusca	Bivalvia	Cardiida	Carditidae		391090
Mollusca	Bivalvia	Cardiida	Psammobiidae	*Hiatula alba*	747137
Mollusca	Bivalvia	Cardiida	Tellinidae	*Macomona deltoidalis*	711134
Mollusca	Bivalvia	Cardiida	Tellinidae	*Tellinides margaritinus*	710898
Mollusca	Bivalvia	Cardiida	Tellinidae	*Tellina sp.*	138533
Mollusca	Bivalvia	Carditida	Carditidae	*Centrocardita rosulenta*	504887
Mollusca	Bivalvia	Galeommatida	Lasaeidae	*Arthritica semen*	754846
Mollusca	Bivalvia	Galeommatida	Lasaeidae	*Mysella sp.*	138186
Mollusca	Bivalvia	Limida	Limidae	*Limaria orientalis*	397092
Mollusca	Bivalvia	Limida	Limidae	*Limatula strangei*	505534
Mollusca	Bivalvia	Lucinida	Lucinidae		218
Mollusca	Bivalvia	Myida	Teredinidae	*Nototeredo edax*	397155
Mollusca	Bivalvia	Mytilida	Mytilidae	*Brachidontes rostratus*	505983
Mollusca	Bivalvia	Mytilida	Mytilidae	*Brachidontes sp.*	138215
Mollusca	Bivalvia	Mytilida	Mytilidae	*Musculus nana*	1030633
Mollusca	Bivalvia	Mytilida	Mytilidae	*Xenostrobus inconstans*	744581
Mollusca	Bivalvia	Nuculanida	Nuculanidae	*Saccella crassa*	866923
Mollusca	Bivalvia	Ostreida	Pinnidae	*Pinna bicolor*	207896
Mollusca	Bivalvia	Ostreida	Pteriidae		1775
Mollusca	Bivalvia	Ostreida	Vulsellidae	*Electroma papilionacea*	507101
Mollusca	Bivalvia	Pectinida	Pectinidae	*Equichlamys bifrons*	391844
Mollusca	Bivalvia	Pectinida	Pectinidae	*Mimachlamys sp.*	236718
Mollusca	Bivalvia	Solemyida	Solemyidae	*Solemya australis*	214549
Mollusca	Bivalvia	Trigoniida	Trigoniidae	*Neotrigonia sp.*	492172
Mollusca	Bivalvia	Venerida	Chamidae	*Chama sp.*	137775
Mollusca	Bivalvia	Venerida	Mactridae		230
Mollusca	Bivalvia	Venerida	Mactridae	*Lutraria rhynchaena*	216442
Mollusca	Bivalvia	Venerida	Mactridae	*Mactrotoma antecedens*	505726
Mollusca	Bivalvia	Venerida	Mactridae	*Spisula trigonella*	505773
Mollusca	Bivalvia	Venerida	Mesodesmatidae	*Anapella cycladea*	505791
Mollusca	Bivalvia	Venerida	Mesodesmatidae	*Atactodea cuneata*	505794
Mollusca	Bivalvia	Venerida	Trapezidae		23130
Mollusca	Bivalvia	Venerida	Veneridae		243
Mollusca	Bivalvia	Venerida	Veneridae	*Bassina sp.*	492471
Mollusca	Bivalvia	Venerida	Veneridae	*Callista kingii*	507403
Mollusca	Bivalvia	Venerida	Veneridae	*Dosinia sp.*	138636
Mollusca	Bivalvia	Venerida	Veneridae	*Katelysia peronii*	507722
Mollusca	Bivalvia	Venerida	Veneridae	*Katelysia rhytiphora*	826363
Mollusca	Bivalvia	Venerida	Veneridae	*Katelysia scalarina*	507723
Mollusca	Bivalvia	Venerida	Veneridae	*Placamen flindersi*	507875
Mollusca	Bivalvia	Venerida	Veneridae	*Tawera lagopus*	507919
Mollusca	Bivalvia	Venerida	Veneridae	*Venerupis anomala*	507981
Mollusca	Bivalvia		Laternulidae	*Laternula sp.*	138106

Mollusca	Bivalvia		Myochamidae	*Myadora albida*	506808
Mollusca	Gastropoda	Aplysiida	Aplysiidae	*Aplysia sp.*	137654
Mollusca	Gastropoda	Caenogastropoda	Batillariidae	*Zeacumantus diemenensis*	446441
Mollusca	Gastropoda	Caenogastropoda	Batillariidae	*Zeacumantus plumbeus*	853041
Mollusca	Gastropoda	Caenogastropoda	Cerithiidae		128
Mollusca	Gastropoda	Caenogastropoda	Cerithiidae	*Cacozeliana granarium*	473085
Mollusca	Gastropoda	Caenogastropoda	Epitoniidae	*Epitonium tenerum*	523995
Mollusca	Gastropoda	Caenogastropoda	Turritellidae	*Gazameda iredalei*	446529
Mollusca	Gastropoda	Caenogastropoda	Turritellidae		127
Mollusca	Gastropoda	Cephalaspidea	Bullidae	*Bulla quoyii*	510438
Mollusca	Gastropoda	Cephalaspidea	Haminoeidae	*Liloa brevis*	531577
Mollusca	Gastropoda	Cephalaspidea	Philinidae	*Philine angasi*	531549
Mollusca	Gastropoda	Cycloneritida	Neritidae	*Nerita atramentosa*	713884
Mollusca	Gastropoda	Lepetellida	Fissurellidae		111
Mollusca	Gastropoda	Lepetellida	Scissurellidae	*Scissurella cyprina*	493050
Mollusca	Gastropoda	Littorinimorpha	Hipponicidae	*Sabia australis*	598647
Mollusca	Gastropoda	Littorinimorpha	Hydrobiidae		120
Mollusca	Gastropoda	Littorinimorpha	Littotinidae	*Bembicium nanum*	445492
Mollusca	Gastropoda	Littorinimorpha	Littotinidae	*Bembicium vittatum*	445480
Mollusca	Gastropoda	Littorinimorpha	Naticidae	Conuber conicum	585289
Mollusca	Gastropoda	Littorinimorpha	Naticidae	*Natica sp.*	138240
Mollusca	Gastropoda	Littorinimorpha	Naticidae	*Tanea sagittata*	570158
Mollusca	Gastropoda	Littorinimorpha	Rissoinidae	*Rissoina crassa*	598001
Mollusca	Gastropoda	Littorinimorpha	Rissoinidae	*Rissoina fasciata*	765955
Mollusca	Gastropoda	Littorinimorpha	Vitrinellidae		153704
Mollusca	Gastropoda	Lottioidea	Eoacmaeidae	*Eoacmaea calamus*	458652
Mollusca	Gastropoda	Neogastropoda	Buccinoidea	*Cominella lineolata*	490925
Mollusca	Gastropoda	Neogastropoda	Columbellidae	*Mitrella australis*	511477
Mollusca	Gastropoda	Neogastropoda	Columbellidae	*Mitrella lincolnensis*	511520
Mollusca	Gastropoda	Neogastropoda	Fasciolariidae	*Propefusus australis*	1319812
Mollusca	Gastropoda	Neogastropoda	Murcidae	*Bedeva paivae*	181032
Mollusca	Gastropoda	Neogastropoda	Murcidae	*Bedeva vinosa*	869741
Mollusca	Gastropoda	Neogastropoda	Muricidae	*Pterochelus triformis*	406234
Mollusca	Gastropoda	Neogastropoda	Nassariidae		151
Mollusca	Gastropoda	Neogastropoda	Nassariidae	*Nassarius pauperatus*	572153
Mollusca	Gastropoda	Neogastropoda	Nassariidae	*Nassarius pyrrhus*	572154
Mollusca	Gastropoda	Neogastropoda	Terebridae	*Duplicaria kieneri*	438575
Mollusca	Gastropoda	Neogastropoda	Volutomitridae	*Peculator porphyria*	450663
Mollusca	Gastropoda	Pylopulmonata	Amphibolidae	*Salinator fragilis*	549356
Mollusca	Gastropoda	Seguenziida	Chilodontidae	*Granata sp.*	512104
Mollusca	Gastropoda	Trochida	Trochidae	*Austrocochlea constricta*	546938
Mollusca	Gastropoda	Trochida	Trochidae	*Clanculus dunkeri*	594193
Mollusca	Gastropoda	Trochida	Trochidae	*Clanculus limbatus*	594200
Mollusca	Gastropoda	Trochida	Trochidae	*Clanculus philippi*	594206

Mollusca	Gastropoda	Trochida	Trochidae	*Clanculus plebejus*	594207
Mollusca	Gastropoda	Trochida	Trochidae	*Phasianotrochus eximius*	573223
Mollusca	Gastropoda		Lottiidae		7173
Mollusca	Gastropoda		Lottiidae	*Notoacmea flammea*	456623
Mollusca	Gastropoda		Nacellidae	*Cellana tramoserica*	325467
Mollusca	Gastropoda		Patellidae		113
Mollusca	Polyplacophora				55
Mollusca	Polyplacophora	Chitonida	Acanthochitonidae	*Acanthochitona sp.*	137613
Mollusca	Polyplacophora	Chitonida	Acanthochitonidae	*Acanthochitona sueurii*	386519
Mollusca	Polyplacophora	Chitonida	Chitonidae	*Rhyssoplax sp.*	385600
Mollusca	Polyplacophora	Chitonida	Ischnochitonidae	*Ischnochiton sp.*	138088
Mollusca	Polyplacophora	Chitonida	Ischnochitonidae	*Ischnochiton variegatus*	848106
Mollusca	Polyplacophora	Chitonida	Ischnochitonidae	*Stenochiton cymodocealis*	386066
Mollusca	Polyplacophora	Chitonida	Ischnochitonidae	*Stenochiton pilsbryanus*	386069
Mollusca	Polyplacophora	Chitonida	Ischnochitonidae	*Stenochiton sp.*	385550
Mollusca	Polyplacophora	Chitonida	Mopaliidae		23074
Mollusca	Scaphopoda	Dentallida	Dentaliidae	*Paradentalium intercalatum*	344529
Mollusca	Scaphopoda	Gadilia	Gadilidae	*Cadulus vincentianus*	344307
Nemertea					152391
Nemertea	Pilidophora	Heteronemertea	Lineidae	*Notospermus sp.*	122375
Porifera	Calcarea	Leucosolenida	Leucosoleniidae		131616
Sipuncula					1268
Sipuncula	Sipunculidea	Golfingiida	Golfingiidae	*Golfingia* sp.	136021

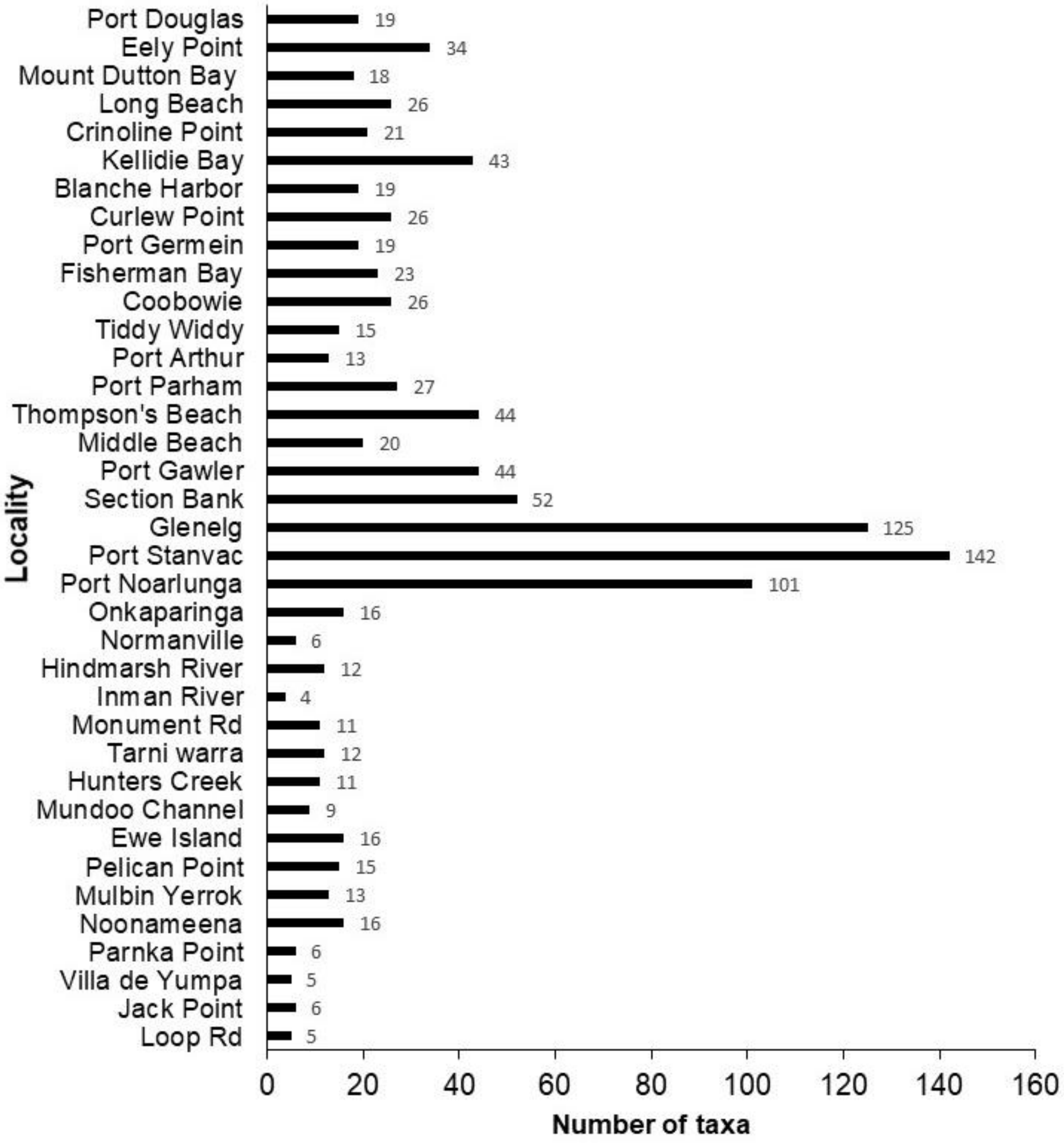


Figure S1. Number of taxa recorded across the 37 localities of South Australia from 2008 to 2020.

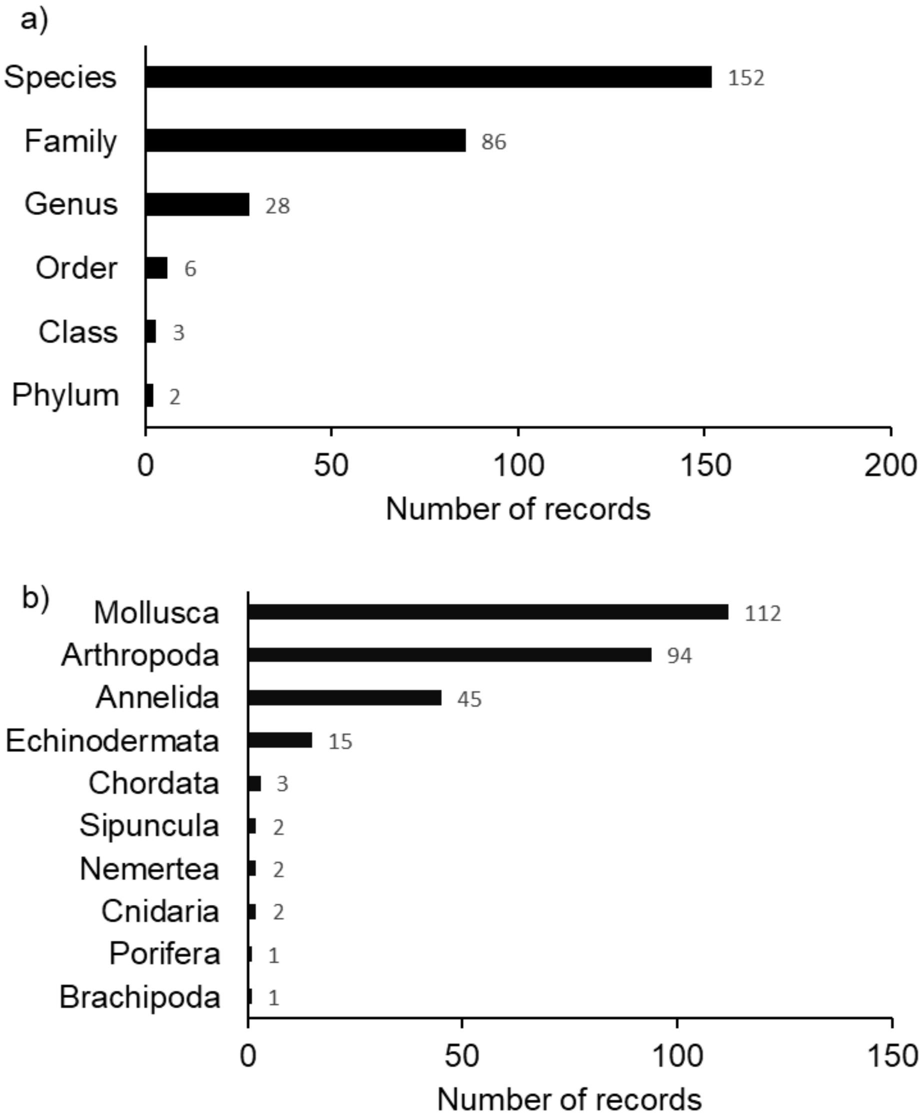
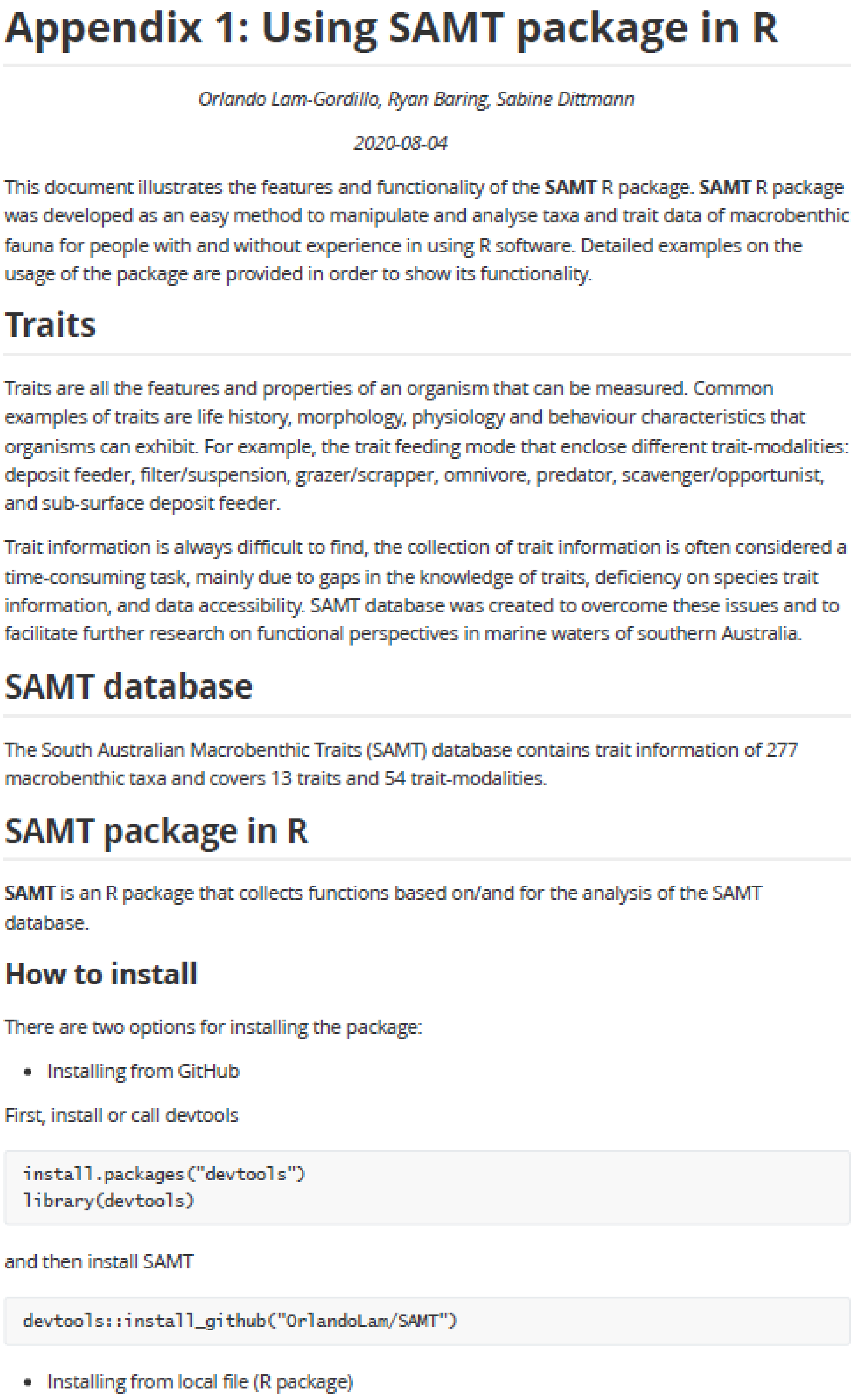


Figure S2. a) Number of taxa assessed at different levels of identification from all locations and sites from 2008 to 2020. b) Number of taxa recorded by Phylum across all locations and sites from 2008 to 2020.



Appendix 1: Using SAMT package in R

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This document illustrates the features and functionality of the **SAMT** R package. **SAMT** R package was developed as an easy method to manipulate and analyse taxa and trait data of macrobenthic fauna for people with and without experience in using R software. Detailed examples on the usage of the package are provided in order to show its functionality.

Traits

Traits are all the features and properties of an organism that can be measured. Common examples of traits are life history, morphology, physiology and behaviour characteristics that organisms can exhibit. For example, the trait feeding mode that enclose different trait-modalities: deposit feeder, filter/suspension, grazer/scrapper, omnivore, predator, scavenger/opportunist, and sub-surface deposit feeder.

Trait information is always difficult to find, the collection of trait information is often considered a time-consuming task, mainly due to gaps in the knowledge of traits, deficiency on species trait information, and data accessibility. SAMT database was created to overcome these issues and to facilitate further research on functional perspectives in marine waters of southern Australia.

SAMT database

The South Australian Macrobenthic Traits (SAMT) database contains trait information of 277 macrobenthic taxa and covers 13 traits and 54 trait-modalities.

SAMT package in R

SAMT is an R package that collects functions based on/and for the analysis of the SAMT database.

How to install

There are two options for installing the package:

- Installing from GitHub

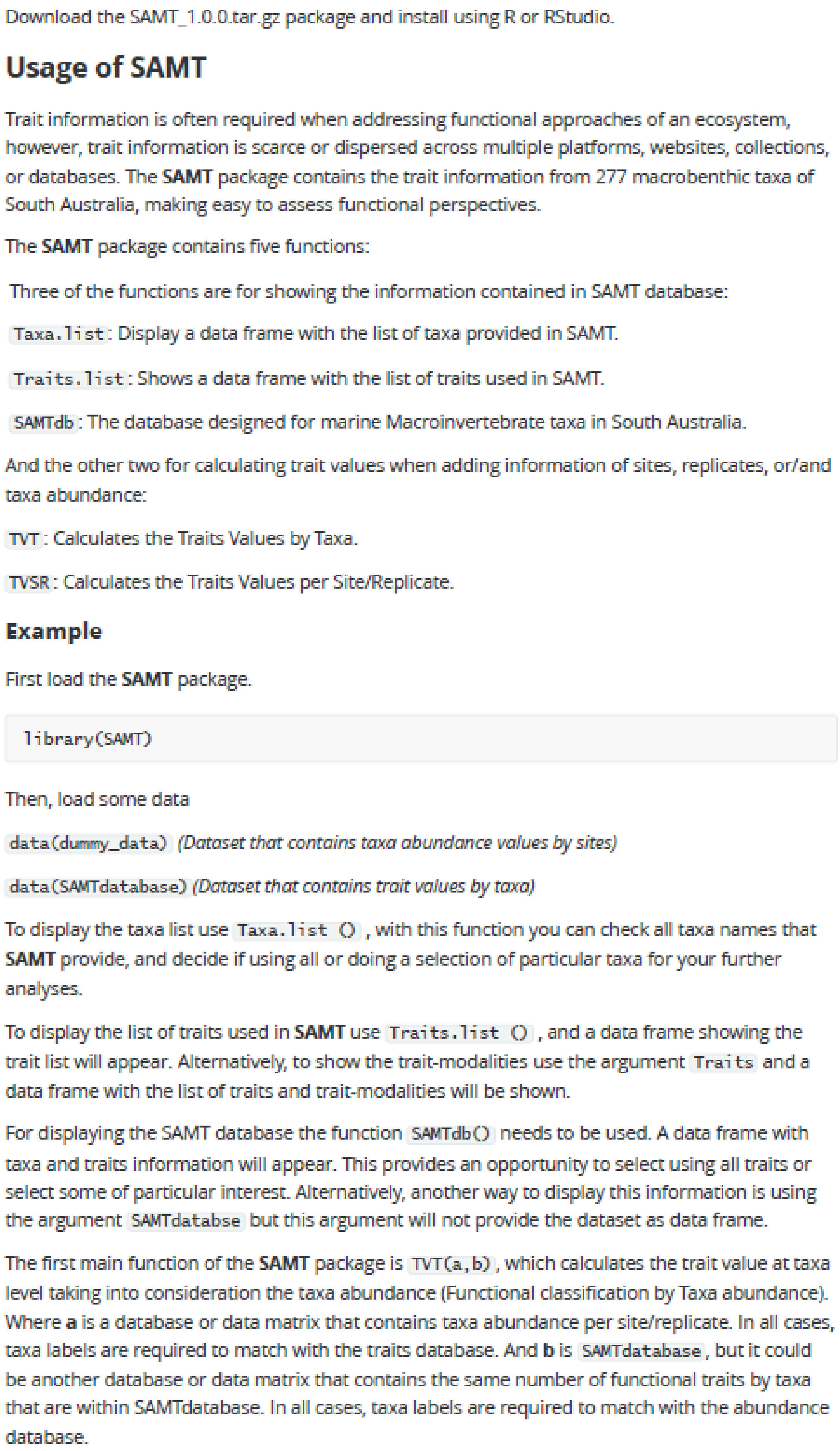
First, install or call devtools

```
install.packages("devtools")
library(devtools)
```

and then install SAMT

```
devtools::install_github("OrlandoLam/SAMT")
```

- Installing from local file (R package)



Download the SAMT_1.0.0.tar.gz package and install using R or RStudio.

Usage of SAMT

Trait information is often required when addressing functional approaches of an ecosystem, however, trait information is scarce or dispersed across multiple platforms, websites, collections, or databases. The **SAMT** package contains the trait information from 277 macrobenthic taxa of South Australia, making easy to assess functional perspectives.

The **SAMT** package contains five functions:

Three of the functions are for showing the information contained in SAMT database:

`Taxa.list`: Display a data frame with the list of taxa provided in SAMT.

`Traits.list`: Shows a data frame with the list of traits used in SAMT.

`SAMTdb`: The database designed for marine Macroinvertebrate taxa in South Australia.

And the other two for calculating trait values when adding information of sites, replicates, or/and taxa abundance:

`TVT`: Calculates the Traits Values by Taxa.

`TVSR`: Calculates the Traits Values per Site/Replicate.

Example

First load the **SAMT** package.

```
library(SAMT)
```

Then, load some data

`data(dummy_data)` *(Dataset that contains taxa abundance values by sites)*

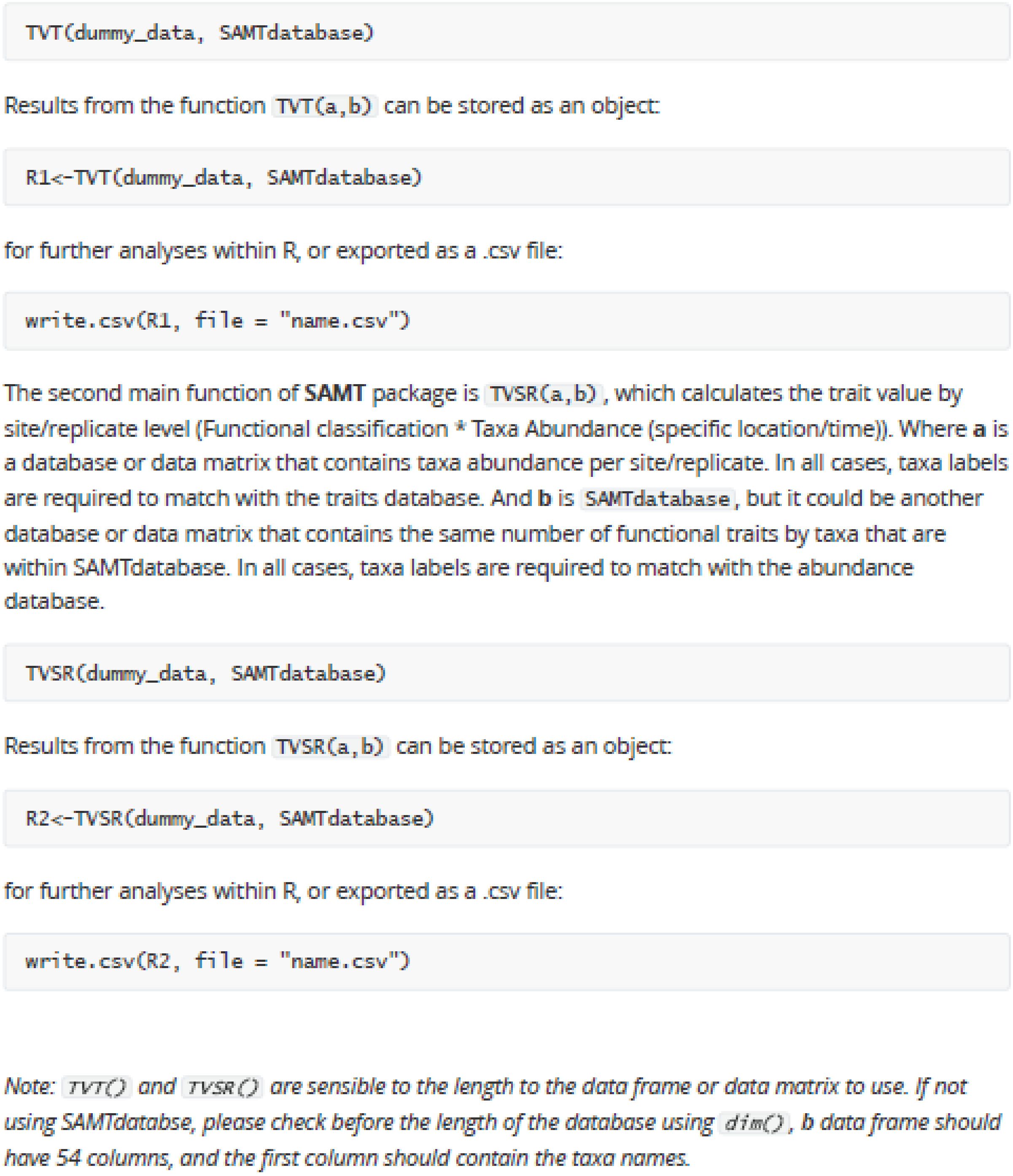
`data(SAMTdatabase)` *(Dataset that contains trait values by taxa)*

To display the taxa list use `Taxa.list ()` , with this function you can check all taxa names that **SAMT** provide, and decide if using all or doing a selection of particular taxa for your further analyses.

To display the list of traits used in **SAMT** use `Traits.list ()` , and a data frame showing the trait list will appear. Alternatively, to show the trait-modalities use the argument `Traits` and a data frame with the list of traits and trait-modalities will be shown.

For displaying the SAMT database the function `SAMTdb()` needs to be used. A data frame with taxa and traits information will appear. This provides an opportunity to select using all traits or select some of particular interest. Alternatively, another way to display this information is using the argument `SAMTdatabse` but this argument will not provide the dataset as data frame.

The first main function of the **SAMT** package is `TVT(a,b)`, which calculates the trait value at taxa level taking into consideration the taxa abundance (Functional classification by Taxa abundance). Where **a** is a database or data matrix that contains taxa abundance per site/replicate. In all cases, taxa labels are required to match with the traits database. And **b** is `SAMTdatabase`, but it could be another database or data matrix that contains the same number of functional traits by taxa that are within SAMTdatabase. In all cases, taxa labels are required to match with the abundance database.



```
TVT(dummy_data, SAMTdatabase)
```

Results from the function `TVT(a,b)` can be stored as an object:

```
R1<-TVT(dummy_data, SAMTdatabase)
```

for further analyses within R, or exported as a .csv file:

```
write.csv(R1, file = "name.csv")
```

The second main function of **SAMT** package is `TVSR(a,b)`, which calculates the trait value by site/replicate level (Functional classification * Taxa Abundance (specific location/time)). Where **a** is a database or data matrix that contains taxa abundance per site/replicate. In all cases, taxa labels are required to match with the traits database. And **b** is `SAMTdatabase`, but it could be another database or data matrix that contains the same number of functional traits by taxa that are within SAMTdatabase. In all cases, taxa labels are required to match with the abundance database.

```
TVSR(dummy_data, SAMTdatabase)
```

Results from the function `TVSR(a,b)` can be stored as an object:

```
R2<-TVSR(dummy_data, SAMTdatabase)
```

for further analyses within R, or exported as a .csv file:

```
write.csv(R2, file = "name.csv")
```

Note: `TVT()` and `TVSR()` are sensible to the length to the data frame or data matrix to use. If not using SAMTdatabse, please check before the length of the database using `dim()`, b data frame should have 54 columns, and the first column should contain the taxa names.

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ORIGINAL RESEARCH
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Establishing the South Australian Macrobenthic Traits (SAMT) database: A trait classification for functional assessments

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Abstract

Trait-based approaches are increasingly used as a proxy for understanding the relationship between biodiversity and ecosystem functioning. Macrobenthic fauna are considered one of the major providers of ecosystem functions in marine soft sediments; however, several gaps persist in the knowledge of their trait classification, limiting the potential use of functional assessments. While trait databases are available for the well-studied North Atlantic benthic fauna, no such trait classification system exists for Australia. Here, we present the South Australian Macrobenthic Traits (SAMT) database, the first comprehensive assessment of macrobenthic fauna traits in temperate Australian waters. The SAMT database includes 13 traits and 54 trait-modalities (e.g., life history, morphology, physiology, and behavior), and is based on records of macrobenthic fauna from South Australia. We provide trait information for more than 250 macrobenthic taxa, including outcomes from a fuzzy coding procedure, as well as an R package for using and analyzing the SAMT database. The establishment of the SAMT constitutes the foundation for a comprehensive macrobenthic trait database for the wider southern Australian region that could facilitate future research on functional perspectives, such as assessments of functional diversity and changes to ecosystem functioning.

KEYWORDS
Australia, benthos, Biological traits, ecosystem functioning, functional group, macrofauna

1 | INTRODUCTION

Trait-based approaches have become topical in ecological research for understanding the relationship between species (biodiversity) and ecosystem functioning, ecosystem processes, ecosystem services, or responses to anthropogenic disturbances (Bolam et al., 2016; Bremner et al., 2003, 2006; Cano-Barbcil et al., 2019; Weiss & Ray, 2019). Trait-based approaches are also used to measure several functional indices (e.g., functional diversity: functional divergence, functional redundancy, and functional richness) and can be used to perform analyses across species pools from distinct geographical areas (Degen & Faulwetter, 2019; Lam-Gordillo et al., 2020; Mason et al., 2005; Mouchet et al., 2010). Functional approaches are based on different subsets of traits (i.e., species characteristics) as a proxy of ecosystem functioning (Bremner, 2008; Bremner et al., 2006).

Traits can be defined as properties of organisms that can be measured, usually at the organism level and used comparatively across species. Examples of traits are the life history, morphology,

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physiology, and behavior characteristics that species can exhibit (Bremner et al., 2006; Degen et al., 2018; Lam-Gordillo et al., 2020; Petchey & Gaston, 2006; Reiss et al., 2009). Selection of traits is flexible and should include an appropriate range of traits relevant to the specific research question, that is, capture the characteristics of organism for the ecosystem processes under investigation (Beauchard et al., 2017; Costello et al., 2015; Lam-Gordillo et al., 2020; Petchey & Gaston, 2006).

The use of traits has gained momentum in marine ecology with an growth in published research in recent years, which has improved the understanding of the functioning of marine ecosystems (Cano-Barbcil et al., 2019; Castro et al., 2019; Costello et al., 2015; Lam-Gordillo et al., 2020). The increased interest in traits has been particularly evident in the assessment of macrobenthic communities (Beauchard et al., 2017; Degen et al., 2018; Dissanayake et al., 2018; Lam-Gordillo et al., 2020). Macrobenthic invertebrates have long been recognized as important providers of ecological processes and ecosystem functions in soft sediments due to their capability to enhance recycling of nutrients, modifying sediment properties (e.g., bioturbation, exchange processes). They are also useful bioindicators of pollution and other environmental stressors (Dissanayake et al., 2019; Liu et al., 2019; Reiss et al., 2009; Dittmann et al. 2015; Shojaei et al., 2015).

Throughout the literature, several traits have been proposed to assess the relationship between macrobenthic fauna and ecosystem functioning; however, there are no standardized definitions for traits. In addition, the deficiency on species trait information, data accessibility, and different levels of taxonomic resolution make the selection and use of traits even harder (Lam-Gordillo et al., 2020). In order to address these issues, some frameworks for assessing biological traits in marine fauna have been suggested, as well as standardized guidelines for the analysis and interpretation of this information (Beauchard et al., 2017; Degen et al., 2018; Lam-Gordillo et al., 2020).

The southern Australian coast is the longest east–west temperate coastline in the southern hemisphere with a diversity of sedimentary habitats (Short, 2020). However, information about traits of macrobenthic fauna from this region is scarce or nonexistent (Lam-Gordillo et al., 2020). The limited information about traits, combined with gaps in the taxonomic knowledge of southern Australian benthic species, has limited the use of functional assessments for management and conservation purposes, as well as understanding benthic ecosystem functioning in this part of the world.

Here, we present the South Australian Macrobenthic Traits database (SAMT), to advance trait-based approaches for southern temperate coastlines. The trait information provided is based on previous studies for comparability and presented in an easily accessible database for downloading and sharing among researchers (Beauchard et al., 2017; Costello et al., 2015; Degen et al., 2018; Lam-Gordillo et al., 2020). In addition, we present a flow chart detailing the step-by-step process of assessing ecosystem functioning and highlighting the utility of the SAMT database for accomplishing this task. This is the first comprehensive assessment of traits of the South Australian macrobenthic fauna, with the aim to facilitate further research across southern Australian temperate marine waters on functional perspectives, elucidating patterns on functional diversity and detect changes in ecosystem functioning.

2 | METHODS

2.1 | Data acquired

A dataset was compiled from previous projects led by the senior author on macrobenthic fauna in soft sediments of South Australia (Table S1), from 37 different localities within this region (Figure 1). The dataset encompasses records from inter- and shallow subtidal soft sediments in coastal embayments, lagoons, and inverse estuaries, representative of coastal sedimentary habitats along the arid and warm temperate coastline of southern Australia.

2.2 | Selection of traits

Selection of traits was based on the most commonly used traits for assessing macrobenthic fauna (Lam-Gordillo et al., 2020), ensuring that the selected biological traits could be compared across studies (Degen et al., 2018), geographical areas (Bremner et al., 2006), and are applicable to most benthic taxa (Costello et al., 2015). The selected traits capture the four subject areas "Biology," "Habitat," "Life-history," and "Larval" introduced by Costello et al. (2015) to structure trait categories. In total, based on Lam-Gordillo et al. (2020), 13 traits and 54 trait-modalities were assessed (Table 1).

2.3 | Trait allocation

Trait data were gathered from various published online sources, depending on the availability of information for each taxon. When trait information on a particular taxon was missing, its trait values were inferred from the nearest phylogenetic neighbor. For example, if no trait information was available at the species level, trait information was used from another species within the same genus; if information was unavailable at genus level, we considered information at family level. Additional considerations such as taxa distribution, resemblance, and expert judgment were also applied (see Tables S2 and S3).

2.4 | Fuzzy coding of traits

Each of the taxa analyzed was scored depending on the affinity that a taxon displayed with a trait-modality using a fuzzy coding procedure (Bremner, 2008; Bremner et al., 2006; Chevenet et al., 1994). A scoring range from 0 to 1 was used, with 0 being no affinity and 1 being high affinity to a trait. For example, coding the trait "Feeding

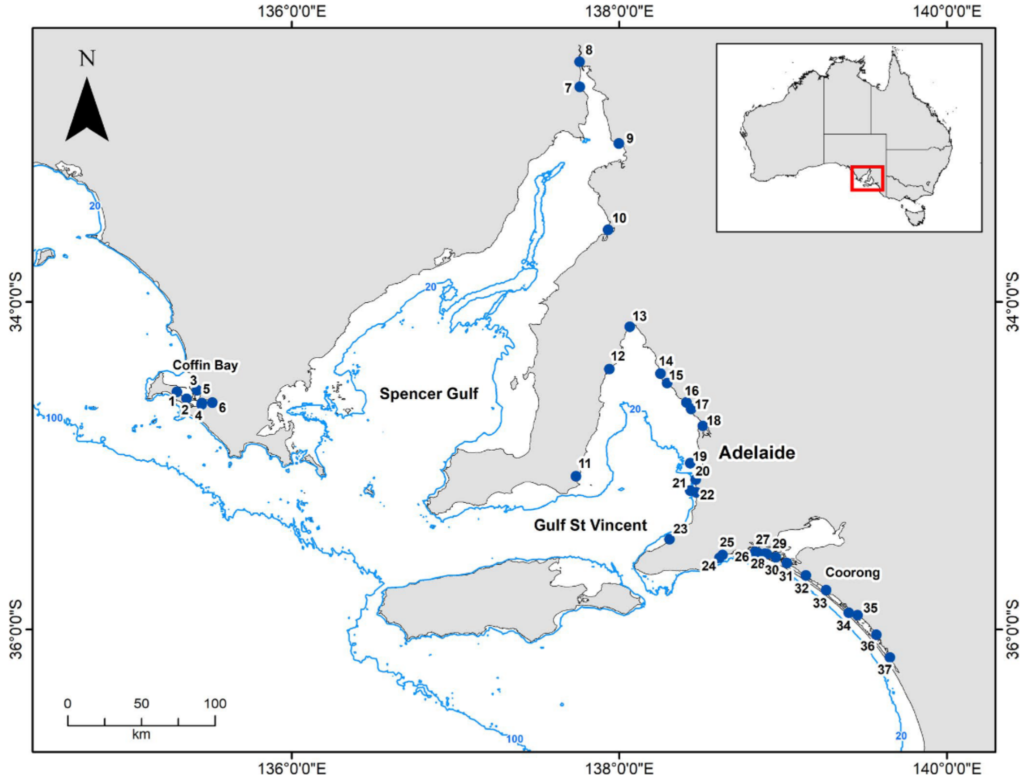


FIGURE 1 Localities of South Australia from where information about taxa traits were used in this study. (1) Port Douglas; (2) Eely Point; (3) Mount Dutton Bay; (4) Long Beach; (5) Crinoline Point; (6) Kellidie Bay; (7) Blanche Harbor; (8) Curlew Point; (9) Port Germain; (10) Fisherman Bay; (11) Coobowie; (12) Tiddy Widdy; (13) Port Arthur; (14) Port Parham; (15) Thompson's Beach; (16) Middle Beach; (17) Port Gawler; (18) Section Bank; (19) Glenelg; (20) Port Stanvac; (21) Port Noarlunga; (22) Onkaparinga; (23) Normanville; (24) Hindmarsh River; (25) Inman River; (26) Monument Rd; (27) Tarni Warra; (28) Hunters Creek; (29) Mundoo Channel; (30) Ewe Island; (31) Pelican Point; (32) Mulbin Yerrok; (33) Noonameena; (34) Parnka Point; (35) Villa de Yumpa; (36) Jack Point; (37) Loop Rd

mode” for *Aglaophamus australiensis* (Polychaeta), considered that *A. australiensis* is mostly a predatory species, however, it also exhibits some degree of subsurface deposit feeding, giving a fuzzy coding of 0.75 as predator, and 0.25 as subsurface deposit feeder, completing the full allocation of 1 for the feeding mode trait.

2.5 | Case study: assessment of the SAMT database

To elucidate the utility of the SAMT database on the assessment of ecosystem functioning, a functional assessment encompassing four main regions across South Australia was performed. The regions selected were Coffin Bay (locality 1, 3, 4, and 6), Spencer Gulf (locality 9–10), Gulf St. Vincent (locality 14–17), and the Coorong (locality 28, 31–33) (Figure 1). For this case study, we only selected information on macrobenthic fauna from intertidal mudflats. Trait selection was made in the context of ecosystem functioning; thus, we analyzed only traits that influence the functioning of ecosystems (i.e., effect traits) that included, bioturbator, body size, feeding mode, morphology, living habit, and sediment position (Lam-Gordillo et al., 2020).

Macrobenthic fauna were analyzed using both traditional biodiversity metric and functional approaches. The traditional biodiversity approaches included the analysis of taxonomic richness (S) and Simpson diversity index (1−λ) on macroinvertebrate abundances. For the functional approach, trait richness, Simpson index, and functional diversity (as Rao's quadratic entropy: RaoQ) were calculated on macroinvertebrate trait data. Diversity analyses and graphics were performed using R (R Core Team, 2017) and the packages “vegan” (Oksanen et al., 2019), “FD” (Laliberté et al., 2014), and “ggplot2” (Wickham, 2016). A univariate one-factor PERMutational ANalysis Of VAriance (PERMANOVA) using Euclidean distance for the single variable (either effect traits, taxa- or trait-based diversity index), permutation of residuals under a reduced model and 9,999 permutations was used to test for significant differences across

TABLE 1 Details of 13 traits and 54 trait-modalities included in the South Australian Macrobenthic Traits (SAMT) database

Subject area	Traits	Modalities	Definition	Function and processes	Reference
Biology	Bioturbator	Biodiffusor Bioirrigator No bioturbation Surface modifier	Transport processes & modification of sediments by organisms that directly/indirectly affect sediment composition	Nutrient cycling, sediment reworking, organic matter re-generation, influence on biogeochemistry	Kristensen et al. (2012); Queiros et al. (2013); Beauchard et al. (2017); Degen and Faulwetter (2019); Liu et al. (2019)
	Body size	Large (>20 mm) Medium (5–20 mm) Small (0.5–5 mm)	Maximum body size as adult	Influence on productivity, habitat facilitation, sediment reworking, oxygen consumption	Costello et al. (2015); Beauchard et al. (2017); Degen and Faulwetter (2019); Liu et al. (2019)
	Degree of attachment	None Permanent	Organism ability to attach to a substratum	Influence on metabolic production, trophic support, habitat facilitation	Bremner (2008); Liu et al. (2019)
	Feeding mode	Deposit feeder Filter/suspension Grazer/scraper Omnivore Predator Scavenger/opportunist Subsurface deposit feeder	The mode of food acquisition	Nutrient cycling, resource utilization & facilitation, species demographic control, trophic support	Costello et al. (2015); Beauchard et al. (2017); van der Linden et al. (2017); Degen and Faulwetter (2019); Liu et al. (2019)
	Mobility	Mobile Sessile/attached	Degree of movement	Nutrient cycling, sediment reworking, trophic support, food source	Costello et al. (2015); Degen and Faulwetter (2019); Liu et al. (2019)
	Morphology	Hard Hard exoskeleton Hard shell Irregular Round Soft/ Fragile Vermiform	External features & structural robustness of an adult organism	Sensitivity, food source, habitat facilitation, survival to disturbances, sediment reworking	Beauchard et al. (2017); Degen and Faulwetter (2019); Liu et al. (2019)
	Movement method	Burrower Crawler None Swimmer	Organism type of movement as an adult	Nutrient cycling, sediment transport, dispersal, recolonization, migration, ability to escape predation	Beauchard et al. (2017); Degen and Faulwetter (2019); Liu et al. (2019)
	Living habit	Burrower Free living/ Surface crawler Tube dwelling	Organism mode living as an adult	Nutrient cycling, sediment transport, dispersal, habitat creation & facilitation	van der Linden et al. (2017); Degen and Faulwetter (2019); Liu et al. (2019)

(Continues)

TABLE 1 (Continued)

Subject area	Traits	Modalities	Definition	Function and processes	Reference
Habitat	Sediment position	Attached Bentho-pelagic Deeper than 3 cm Surface shallow <3 cm	Organism relative position on the sediment	Nutrient cycling, sediment transport, habitat creation & facilitation	Costello et al. (2015); Beauchard et al. (2017); van der Linden et al. (2017); Degen and Faulwetter (2019); Liu et al. (2019)
Larval	Larval type	Pelagic -planktotrophic Pelagic lecthrotophic Benthic Brooder/ Direct developer No larvae	Larval type & feeding mode	Food source, ability of species dispersal, influence in nutrient cycling	van der Linden et al. (2017); Degen and Faulwetter (2019); Liu et al. (2019)
Life history	Life span	<1 year 1–3 years 3–10 years	Organism maximum life span as an adult	Community dynamics, resilience of organisms, reproduction, productivity	Beauchard et al. (2017); van der Linden et al. (2017); Degen and Faulwetter (2019); Liu et al. (2019)
	Reproductive frequency	Annual Continuous Seasonal	Times that the organism reproduces over time	Demographic resilience, population stock	Beauchard et al. (2017); Degen and Faulwetter (2019)
	Reproductive technique	Sexual, pelagic shed eggs Sexual, benthic shed eggs Sexual, encapsulation (gelatinous mass) Sexual, ovigerous, broad eggs Sexual direct development Asexual	The mode organism reproduces, mechanism of fertilization & propagules released	Species dispersal, carbon transport, demographic resilience	Costello et al. (2015); Beauchard et al. (2017); Degen and Faulwetter (2019)

regions (Anderson et al., 2008). All PERMANOVA tests were carried out using PRIMER v7 with PERMANOVA + add on.

3 | RESULTS

3.1 | Taxa included

In total, we generated trait information for 277 taxa (see Table S4 for a full list of taxa). The number of taxa varied (i.e., range from 4 to 142 per site, mean of 28) across the 37 localities of South Australia, with the greatest numbers from subtidal sediments in Gulf St Vincent (Figure S1). Different levels of taxonomic identification were assessed, 152 at the species level, followed by 28 at genus level, 86 at family level, and the remaining 11 taxa at higher levels (order, class, or phyla; Figure S2a). The phylum with most records was Mollusca (112 records, 40% of all taxa), followed by Arthropoda (94 records, 34% of all taxa) and Annelida (45 records, 16% of all taxa), with the remaining 10% belonging to other taxa (Echinodermata 15 taxa, one to three taxa each for Chordata, Sipunculida, Nemertea, Cnidaria, Porifera, and Brachiopoda; Figure S2b). Although Mollusca was the phylum with the highest number of records overall, Annelida was the phylum with the most records across localities (i.e., 43% of all sites) (Figure 2).

3.2 | Data sources

The information on traits was retrieved from diverse peer reviewed and expert sources, and a database was generated for easy interpretation and useability (Figure 3; Trait source table in "https://doi.org/10.6084/m9.figshare.12763154"). Including all the traits assessed, 90% of the information was provided from primary literature that included 48% from South Australian literature, 29% from

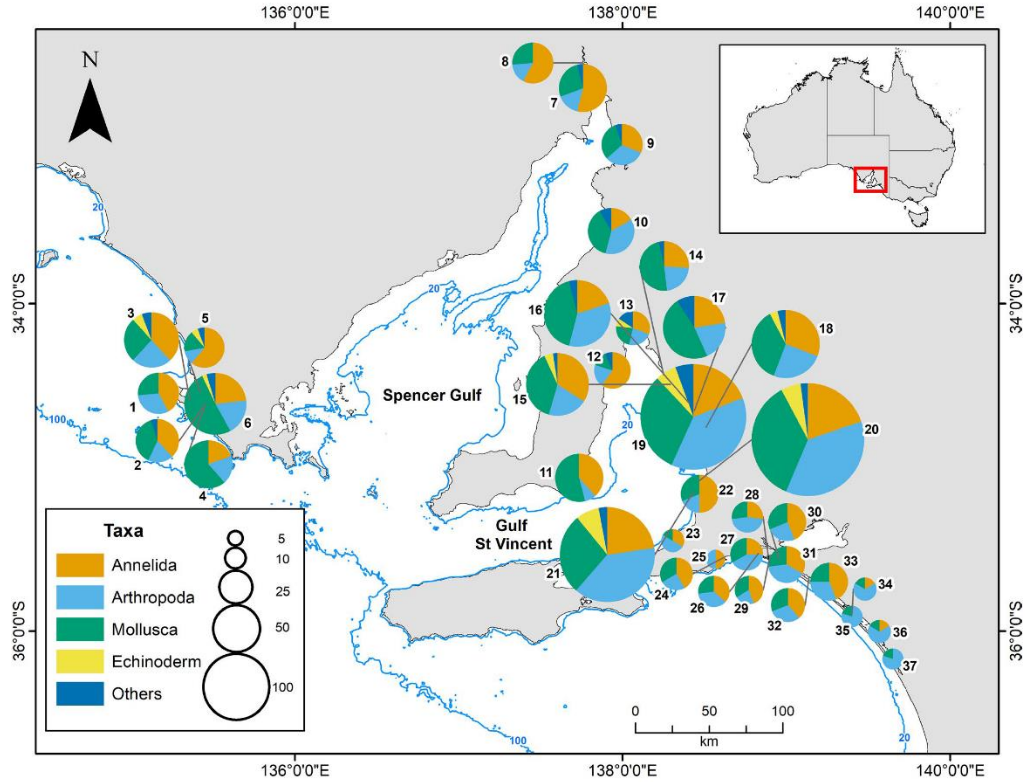
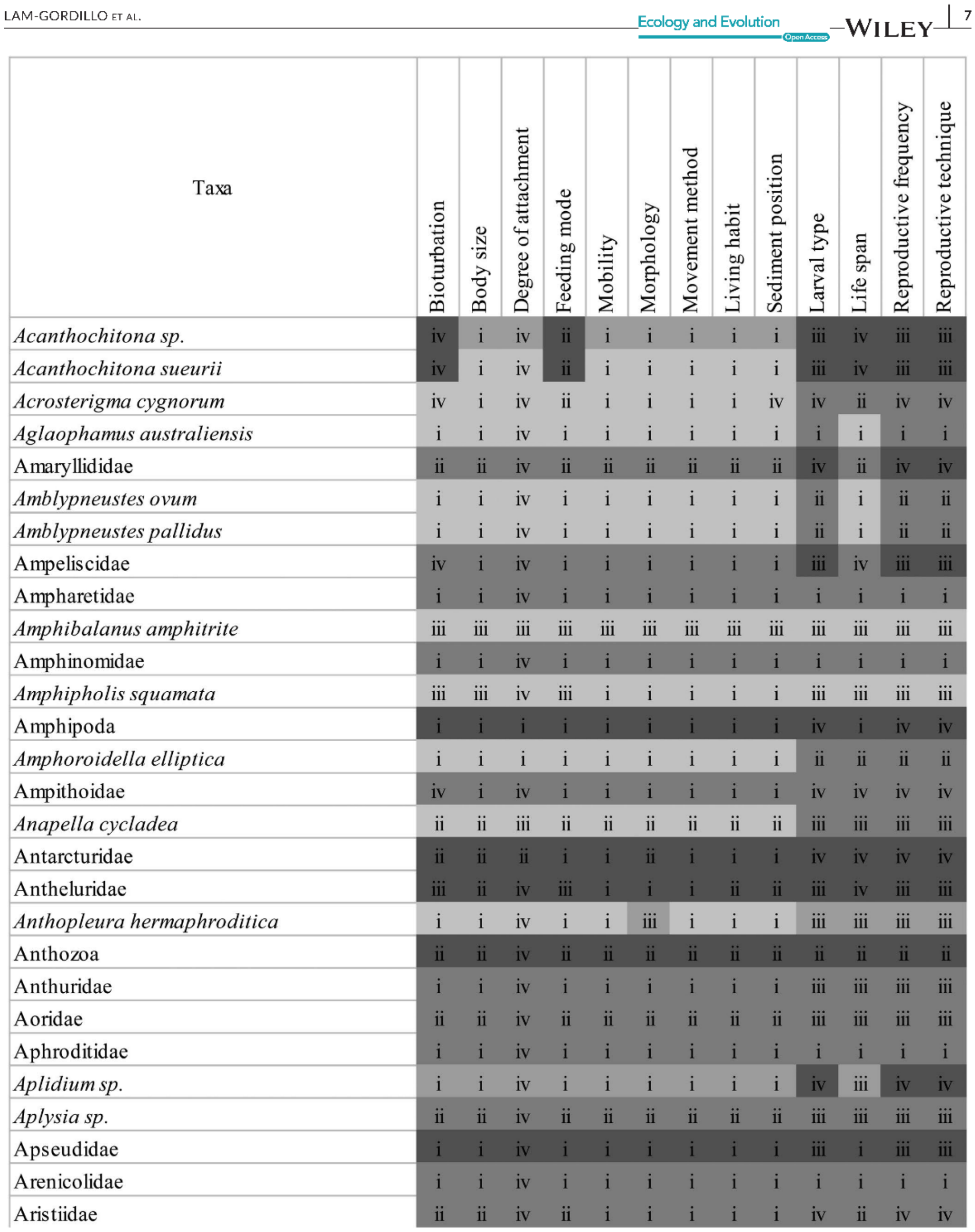


FIGURE 2 Number of taxa per locality of South Australia. Circle size is proportional to the number of taxa. (1) Port Douglas; (2) Eely Point; (3) Mount Dutton Bay; (4) Long Beach; (5) Crinoline Point; (6) Kellidie Bay; (7) Blanche Harbor; (8) Curlew Point; (9) Port Germain; (10) Fisherman Bay; (11) Coobowie; (12) Tiddy Widdy; (13) Port Arthur; (14) Port Parham; (15) Thompson's Beach; (16) Middle Beach; (17) Port Gawler; (18) Section Bank; (19) Glenelg; (20) Port Stanvac; (21) Port Noarlunga; (22) Onkaparinga; (23) Normanville; (24) Hindmarsh River; (25) Inman River; (26) Monument Rd; (27) Tarni Warra; (28) Hunters Creek; (29) Mundoo Channel; (30) Ewe Island; (31) Pelican Point; (32) Mulbin Yerrok; (33) Noonameena; (34) Parnka Point; (35) Villa de Yumpa; (36) Jack Point; (37) Loop Rd



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Taxa	Bioturbation	Body size	Degree of attachment	Feeding mode	Mobility	Morphology	Movement method	Living habit	Sediment position	Larval type	Life span	Reproductive frequency	Reproductive technique
Acanthochitona sp.	iv	i	iv	ii	i	i	i	i	i	iii	iv	iii	iii
Acanthochitona sueurii	iv	i	iv	ii	i	i	i	i	i	iii	iv	iii	iii
Acrosterigma cygnorum	iv	i	iv	ii	i	i	i	i	iv	iv	ii	iv	iv
Aglaophamus australiensis	i	i	iv	i	i	i	i	i	i	i	i	i	i
Amaryllididae	ii	ii	iv	ii	ii	ii	ii	ii	ii	iv	ii	iv	iv
Amblypneustes ovum	i	i	iv	i	i	i	i	i	i	ii	i	ii	ii
Amblypneustes pallidus	i	i	iv	i	i	i	i	i	i	ii	i	ii	ii
Ampeliscidae	iv	i	iv	i	i	i	i	i	i	iii	iv	iii	iii
Ampharetidae	i	i	iv	i	i	i	i	i	i	i	i	i	i
Amphibalanus amphitrite	iii	iii	iii	iii	iii	iii	iii	iii	iii	iii	iii	iii	iii
Amphinomidae	i	i	iv	i	i	i	i	i	i	i	i	i	i
Amphipholis squamata	iii	iii	iv	iii	i	i	i	i	i	iii	iii	iii	iii
Amphipoda	i	i	i	i	i	i	i	i	i	iv	i	iv	iv
Amphoroidella elliptica	i	i	i	i	i	i	i	i	i	ii	ii	ii	ii
Ampithoidae	iv	i	iv	i	i	i	i	i	i	iv	iv	iv	iv
Anapella cycladea	ii	ii	iii	ii	ii	ii	ii	ii	ii	iii	iii	iii	iii
Antarcturidae	ii	ii	ii	i	i	ii	i	i	i	iv	iv	iv	iv
Antheluridae	iii	ii	iv	iii	i	i	i	ii	ii	iii	iv	iii	iii
Anthopleura hermaphroditica	i	i	iv	i	i	iii	i	i	i	iii	iii	iii	iii
Anthozoa	ii	ii	iv	ii	ii	ii	ii	ii	ii	ii	ii	ii	ii
Anthuridae	i	i	iv	i	i	i	i	i	i	iii	iii	iii	iii
Aoridae	ii	ii	iv	ii	ii	ii	ii	ii	ii	iii	iii	iii	iii
Aphroditidae	i	i	iv	i	i	i	i	i	i	i	i	i	i
Aplidium sp.	i	i	iv	i	i	i	i	i	i	iv	iii	iv	iv
Aplysia sp.	ii	ii	iv	ii	ii	ii	ii	ii	ii	iii	iii	iii	iii
Apseudidae	i	i	iv	i	i	i	i	i	i	iii	i	iii	iii
Arenicolidae	i	i	iv	i	i	i	i	i	i	i	i	i	i
Aristiidae	ii	ii	iv	ii	i	i	i	i	i	iv	ii	iv	iv

FIGURE 3 Screenshot of a section of the Traits information sources table. Roman numerals indicate sources' origin, and cell shading specify the taxonomic level of the information. i: South Australian literature; ii: Australian literature; iii: Overseas literature; iv: online resources. Species level; Genus level; Family level; Order/Class level. Full table available in https://doi.org/10.6084/m9.figshare.12763154

TABLE 2 Test results from univariate one-way fixed factor PERMANOVA to compare trait expression of bioturbator, body size, feeding mode, morphology, living habit, and sediment position across regions. Significant results are shown in bold

	df	MS	Pseudo-F	*p* (perm)
Bioturbator				
Region	3	995.08	8.3728	**.0009**
Residual	21	118.85		
Body size				
Region	3	1,635.6	9.8249	**.0011**
Residual	21	166.47		
Feeding mode				
Region	3	818.11	7.4907	**.0035**
Residual	21	109.22		
Morphology				
Region	3	1,115.00	7.0205	**.0023**
Residual	21	158.82		
Living habitat				
Region	3	1,136.70	9.0705	**.001**
Residual	21	125.32		
Sediment position				
Region	3	744.96	7.6826	**.0022**
Residual	21	96.97		

Australian literature, and 13% from overseas literature. The remaining 10% of information was obtained from reputable resources online (Table 2). However, the source of trait information varied between types of traits (Figure 4a). Across taxonomic levels, most of the trait information was available at the family (42%) and species (38%) levels, with proportionally less at the order/class and genus levels (11% and 9% respectively; Figure 4b). It also emerged that the traits larval type, life span, reproductive frequency, and technique are less studied for the macrobenthic fauna from Australia (Figure 4).

3.3 | The South Australian Macrobenthic Traits (SAMT) database

Functional trait information (i.e., traits and fuzzy coding classification) for the 277 macrobenthic taxa analyzed from the South Australian region is the basis for the SAMT database, which is available as an accessible resource at "https://doi.org/10.6084/m9.figshare.12763154" (see Figure 5 for a screenshot of the SAMT database). Along with the database resource, version 1.0.0 of the SAMT R package is provided for assistance in using and analyzing the SAMT database. The SAMT v1.0.0 R package is currently available on the repository https://github.com/OrlandoLam/SAMT (see Appendix 1 for SAMT package user guide). The SAMT database is intended to progress with regular updates of new data by researchers conducting work across southern Australia for easy downloading and sharing.

To illustrate the utility of the SAMT database, we developed a flow chart showing the step-by-step process for assessing the contribution of macrobenthic fauna to ecosystem functioning (Figure 6). The first steps are to compile macrobenthic data from diverse sources (e.g., surveys, field sampling, collections, and online databases) and allocate the respective trait information to each taxon. The SAMT database reduces the time needed for gathering and finding the taxa-trait information and provides the information in one place. Macrobenthic abundance data can be added to the database at any time, and the R package provided within SAMT database can be used for compiling a trait x sample matrix (LQ). Depending on the aim of the study, and with all the matrices compiled, different analyses can be performed using different software (e.g., R, PRIMER), from measuring trait patterns (LQ), relationships between species-traits and the environment, or modeling the interactions between species-traits and the environment (RQL), to calculating functional diversity as a proxy for assessing ecosystem functioning (Figure 6).

3.4 | Case study using SAMT database: Preliminary functional perspectives for South Australia waters

The analysis of data from the SAMT database included, on average, 47 of the 54 trait-modalities across all taxa, analyzed across the 37 South Australian localities. However, based on the traits and localities analyzed, some trait-modalities were expressed more than others due to the different number of taxa present in each locality. Based on effect traits, and grouping the localities into regions (e.g., Coffin Bay, Spencer Gulf, Gulf St. Vincent, and Coorong), the majority of the taxa recorded were surface modifiers and bioirrigators (Figure 7a), with large body size (Figure 7b) and were deposit feeders (Figure 7c). The most common morphology was irregular and fragile/soft bodies (Figure 7d). The most common living habit was free living/surface crawler and burrower (Figure 7e), and most of the organisms inhabited demersal habitats (Figure 7f).

Trait expression (i.e., the number of taxa that exhibit a determined trait) differed significantly across the regions ($p < .01$, Table 2). Considering the six effect traits analyzed (e.g., bioturbator, body size, feeding mode, morphology, living habit, and sediment position), Coffin Bay, Spencer Gulf, and Gulf St Vincent were significantly different in the number of traits present compared to the Coorong region ($p < .01$, Table 3). Greater similarities in terms of trait expression were found between Coffin Bay, Spencer Gulf, and Gulf St Vincent (Table 3).

The relationship between the macrobenthic fauna (biodiversity) and trait expression (ecosystem functioning) was asymptotic, showing a decreasing effect of adding new species to the ecosystem (Figure 8a). Taxonomic and trait richness were significantly different across regions ($p < .01$, Table 4; Figure 8b). The pairwise tests revealed significant differences in taxa richness across all regions except for the pairing of the Gulf St Vincent and Coorong regions ($p < .01$, Table 5), while differences in trait richness were only

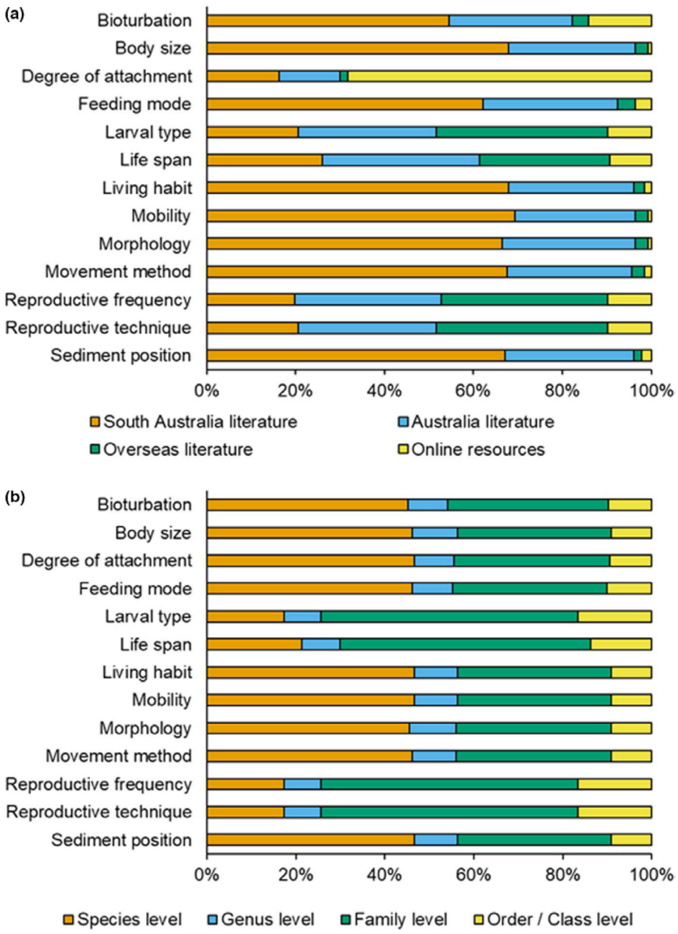


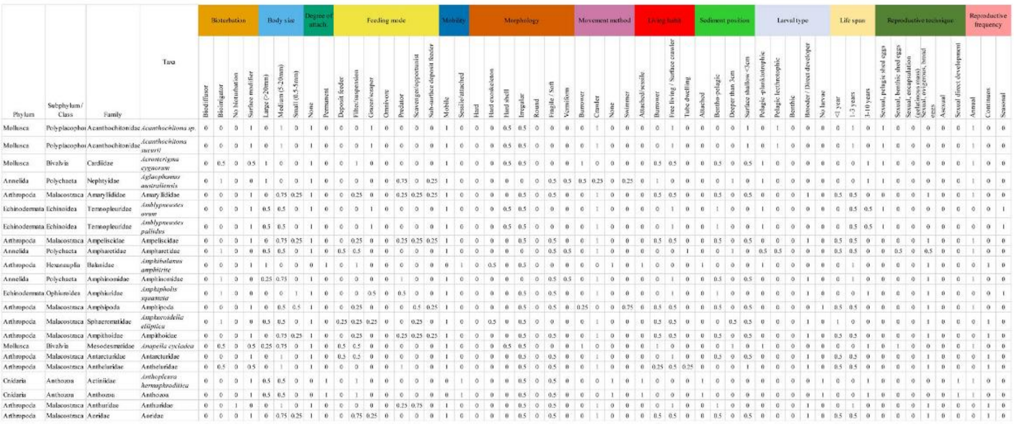
FIGURE 4 Stacked bar graphs showing (a) the cumulative percentage of trait information sources, and (b) the cumulative percentage of trait information by taxonomic level

identified between Coffin Bay and the other three regions ($p < .01$, Table 5). The example reveals that trait richness can show greater similarity, whereas macrobenthic fauna assemblages were taxonomically different between regions.

Diversity, measured using the Simpson Index (Figure 8c), revealed significant differences for taxa and traits across regions ($p < .01$, Table 4). Coffin Bay was the most significantly different region compared to the other regions based on both taxa and traits (Table 5). Based on traits, the Simpson Index was similar between Gulf St Vincent and Spencer Gulf. Based on taxa, the Simpson Index was significantly different between most region pairs except for the Gulf St Vincent and Coorong (Table 5). Functional diversity was also significantly different between regions ($p < .01$, Table 4, Figure 8d). In pairwise comparisons, functional diversity was different in Spencer Gulf compared to the other three regions, and in Gulf St Vincent compared to the Coorong ($p < .05$, Table 5). The case study demonstrated the usefulness of the SAMT database for elucidating functional similarities for taxonomically different benthic assemblages across regions.

4 | DISCUSSION

Functional approaches have become a requisite for studying ecosystem functioning (e.g., Bolam et al., 2016; Bremner et al., 2003, 2006; Degen et al., 2018), yet, functional assessments remain hindered by a lack of taxa-specific trait data (Lam-Gordillo et al., 2020). Compiling trait information of marine macrobenthic fauna is often considered time-consuming and difficult, due to knowledge gaps on the biology and ecology of many species, the lack of identification keys, as well as the scarcity of relevant data (Beauchard et al., 2017; Degen et al., 2018; Verissimo et al., 2012).



				Bioturbation				Body size			Degree of attach.		Feeding mode							Mobility		Morphology							Movement method				Living habit				Sediment position				Larval type					Life span			Reproductive technique						Reproductive frequency		
Phylum	Subphylum/ Class	Family	Taxa	Biodiffusor	Bioirrigator	No bioturbation	Surface modifier	Large (>20mm)	Medium (5-20mm)	Small (0.5-5mm)	None	Permanent	Deposit feeder	Filter/suspension	Grazer/scraper	Omnivore	Predator	Scavenger/opportunist	Sub-surface deposit feeder	Mobile	Sessile/attached	Hard	Hard exoskeleton	Hard shell	Irregular	Round	Fragile / Soft	Vermiform	Burrower	Crawler	None	Swimmer	Attached/sessile	Burrower	Free living / Surface crawler	Tube dwelling	Attached	Bentho-pelagic	Deeper than 3cm	Surface shallow <3cm	Pelagic -planktotrophic	Pelagic lecithotrophic	Benthic	Brooder / Direct developer	No larvae	<1 year	1-3 years	3-10 years	Sexual, pelagic shed eggs	Sexual, benthic shed eggs	Sexual, encapsulation (gelatinous mass)	Sexual, ovigerous, brood eggs	Asexual	Sexual direct development	Annual	Continuos	Seasonal
Mollusca	Polyplacophor	Acanthochitonidae	*Acanthochitona sp.*	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0.5	0.5	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Mollusca	Polyplacophor	Acanthochitonidae	*Acanthochitona sueurii*	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0.5	0.5	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Mollusca	Bivalvia	Cardiidae	*Acrosterigma cygnorum*	0	0.5	0	0.5	1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0.5	0.5	0	0	0	1	0	0	0	0	0.5	0.5	0	0	0.5	0	0.5	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Annelida	Polychaeta	Nephtyidae	*Aglaophamus australiensis*	0	1	0	0	1	0	0	1	0	0	0	0	0	0.75	0	0.25	1	0	0	0	0	0	0	0.5	0.5	0.5	0.25	0	0.25	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Arthropoda	Malacostraca	Amaryllididae	Amaryllididae	0	0	0	1	0	0.75	0.25	1	0	0	0.25	0	0	0.25	0.25	0.25	1	0	0	0	0	0.5	0	0.5	0	0	1	0	0	0	0.5	0.5	0	0	0.5	0	0.5	0	0	0	1	0	0.5	0.5	0	0	0	0	1	0	0	1	0	0
Echinodermata	Echinoidea	Temnopleuridae	*Amblypneustes ovum*	0	0	0	1	0.5	0.5	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0.5	0.5	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0.5	0.5	1	0	0	0	0	0	0	0	1
Echinodermata	Echinoidea	Temnopleuridae	*Amblypneustes pallidus*	0	0	0	1	0.5	0.5	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0.5	0.5	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0.5	0.5	1	0	0	0	0	0	0	0	1
Arthropoda	Malacostraca	Ampeliscidae	Ampeliscidae	0	0	0	1	0	0.75	0.25	1	0	0	0.25	0	0	0.25	0.25	0.25	1	0	0	0	0	0.5	0	0.5	0	0	1	0	0	0	0.5	0.5	0	0	0.5	0	0.5	0	0	0	1	0	0.5	0.5	0	0	0	0	1	0	0	1	0	0
Annelida	Polychaeta	Ampharetidae	Ampharetidae	0	1	0	0	0.5	0.5	0	1	0	0.5	0.5	0	0	0	0	0	1	0	0	0	0	0	0	0.5	0.5	0	1	0	0	0	0	0	1	0	0	1	0	0.5	0.5	0	0	0	0.5	0.5	0	0	0.5	0	0.5	0	0	1	0	0
Arthropoda	Hexanauplia	Balanidae	*Amphibalanus amphitrite*	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0.5	0	0.5	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0
Annelida	Polychaeta	Amphinomidae	Amphinomidae	0	1	0	0	0.25	0.75	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0.5	0.5	0	1	0	0	0	0	1	0	0	0.5	0	0.5	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0
Echinodermata	Ophiuroidea	Amphiuridae	*Amphipholis squamata*	0	1	0	0	0	0	1	1	0	0	0	0.5	0	0.5	0	0	1	0	0	0	0	0.5	0	0.5	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1
Arthropoda	Malacostraca	Amphipoda	Amphipoda	0	0	0	1	0	0.5	0.5	1	0	0	0.25	0	0	0	0.5	0.25	1	0	0	0	0	0.5	0	0.5	0	0.25	0	0	0.75	0	0.5	0.5	0	0	0.5	0	0.5	0	0	0	0	1	0.5	0.5	0	0	0	0	1	0	0	1	0	0
Arthropoda	Malacostraca	Sphaeromatidae	*Amphoroidella elliptica*	0	1	0	0	0.5	0.5	0	1	0	0.25	0.25	0.25	0	0	0.25	0	1	0	0	0.5	0	0.5	0	0	0	0	1	0	0	0	0.5	0.5	0	0	0	0.5	0.5	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0
Arthropoda	Malacostraca	Ampithoidae	Ampithoidae	0	0	0	1	0	0.75	0.25	1	0	0	0.25	0	0	0.25	0.25	0.25	1	0	0	0	0	0.5	0	0.5	0	0	1	0	0	0	0.5	0.5	0	0	0.5	0	0.5	0	0	0	1	0	0.5	0.5	0	0	0	0	1	0	0	0	1	0
Mollusca	Bivalvia	Mesodesmatidae	*Anapella cycladea*	0	0.5	0	0.5	0.25	0.75	0	1	0	0.5	0.5	0	0	0	0	0	1	0	0	0	0.5	0.5	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Arthropoda	Malacostraca	Antarcturidae	Antarcturidae	0	0	0	1	0	1	0	1	0	0.5	0.5	0	0	0	0	0	1	0	0	0	0	0.5	0	0.5	0	0	1	0	0	0	0	1	0	0	0.5	0	0.5	0	0	0	1	0	0.5	0.5	0	0	0	0	1	0	0	0	1	0
Arthropoda	Malacostraca	Antheluridae	Antheluridae	0	0.5	0	0.5	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0.5	0	0.5	0	0	1	0	0	0	0.25	0.5	0.25	0	0	0	1	0	0	0	1	0	0.5	0.5	0	0	0	0	1	0	0	0	1	0
Cnidaria	Anthozoa	Actiniidae	*Anthopleura hermaphroditica*	0	0	0	1	0.5	0.5	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0.5	0	0.5	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0
Cnidaria	Anthozoa	Anthozoa	Anthozoa	0	0	0	1	0.5	0.5	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0.5	0	0.5	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0
Arthropoda	Malacostraca	Anthuridae	Anthuridae	0	0	1	0	0	1	0	1	0	0	0	0	0	0.25	0.75	0	1	0	0	0	0	0.5	0	0.5	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0
Arthropoda	Malacostraca	Aoridae	Aoridae	0	0	0	1	0	0.75	0.25	1	0	0	0.75	0.25	0	0	0	0	1	0	0	0	0	0.5	0	0.5	0	0	1	0	0	0	0.5	0.5	0	0	0.5	0	0.5	0	0	0	1	0	0.5	0.5	0	0	0	0	1	0	0	0	1	0

FIGURE 5 Screenshot of a section of the SAMT database (South Australia Macrobenthic Traits database). Traits are differentiated by colours. Phylum, Subphylum/ Class, Family and Taxa tabs are displayed for easy sorting and searching. Full table available in https://doi.org/10.6084/m9.figshare.12763154

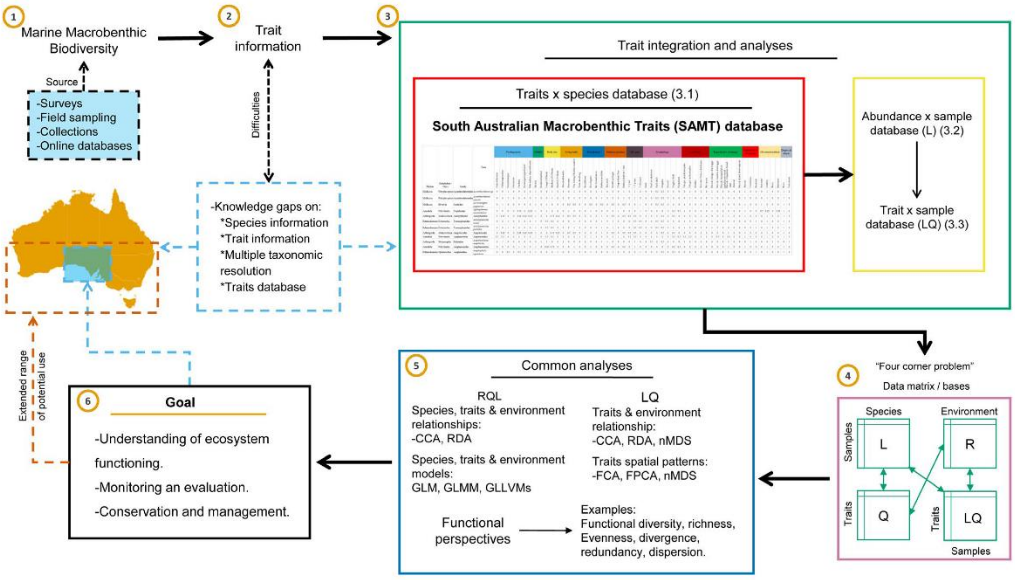


FIGURE 6 Flow chart showing step-by-step processes for assessing ecosystem functioning. Solid colored boxes (green, pink, blue, and black) represent the separate task for analyzing trait data, and black arrows indicate the logical order for the steps. Red box highlights the essential step for having a macrobenthic fauna trait database for southern Australia. Yellow box shows the complementary information needed. Blue dotted box and arrows show the information provided in this study, and the brown dotted box and arrow show the range of potential use of the information provided

The SAMT database we present here aims to close the information gap by enabling a comprehensive assessment of traits for the South Australian macrobenthic fauna. SAMT, and the accompanying R package, will facilitate and enhance further research addressing ecosystem functioning and functional perspectives. The SAMT database provides trait information for 277 macrobenthic taxa and a trait classification for South Australian temperate marine waters. This first iteration of the SAMT database can be

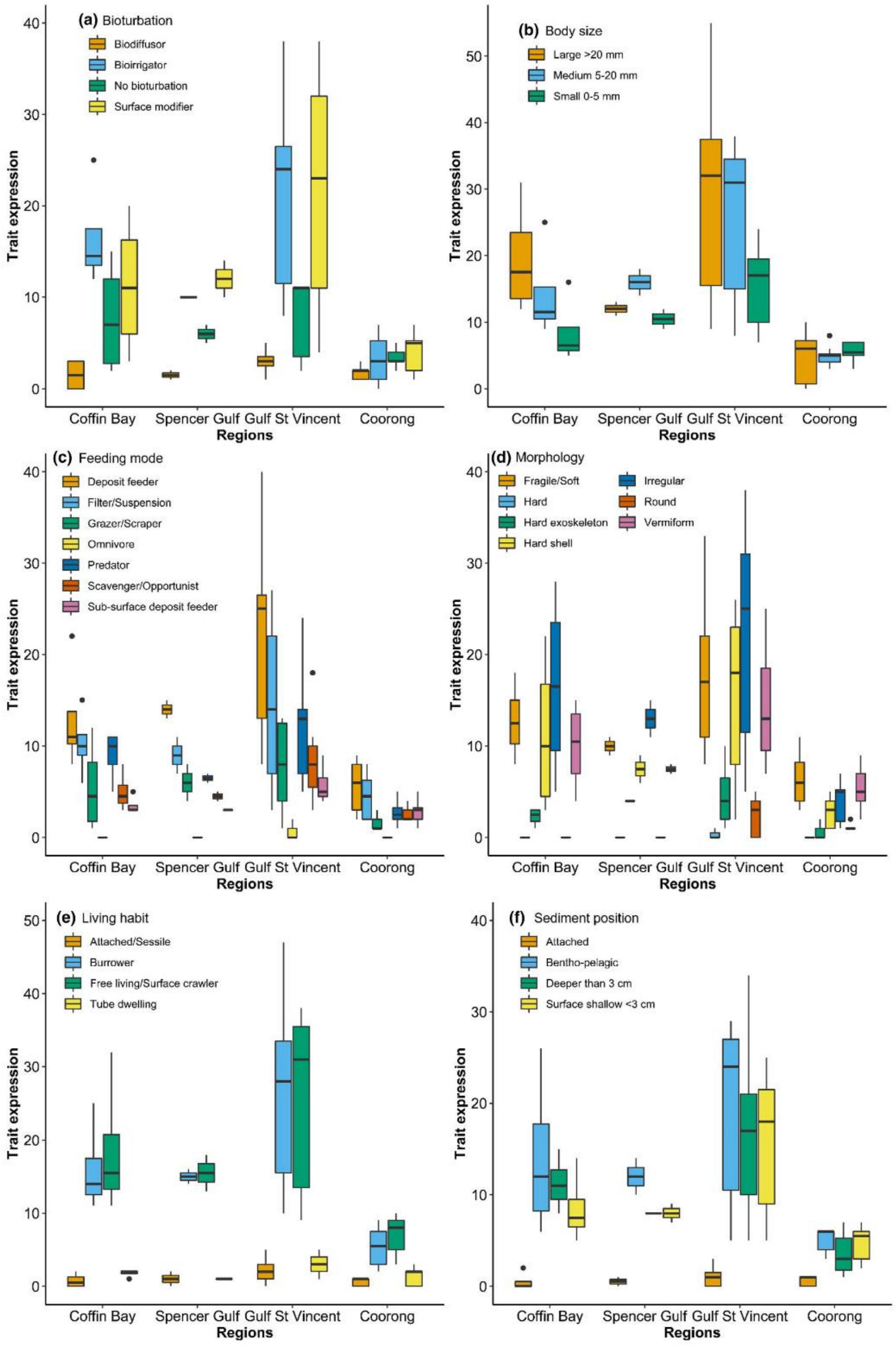


FIGURE 7 Expressed traits across four regions (Coffin Bay, Spencer Gulf, Gulf St. Vincent, and Coorong Lagoon) in South Australia. Median, percentiles, upper/lower bounds, and outliers are shown. Traits shown: (a) bioturbation, (b) body size, (c) feeding mode, (d) morphology, (e) living habit, and (f) sediment position

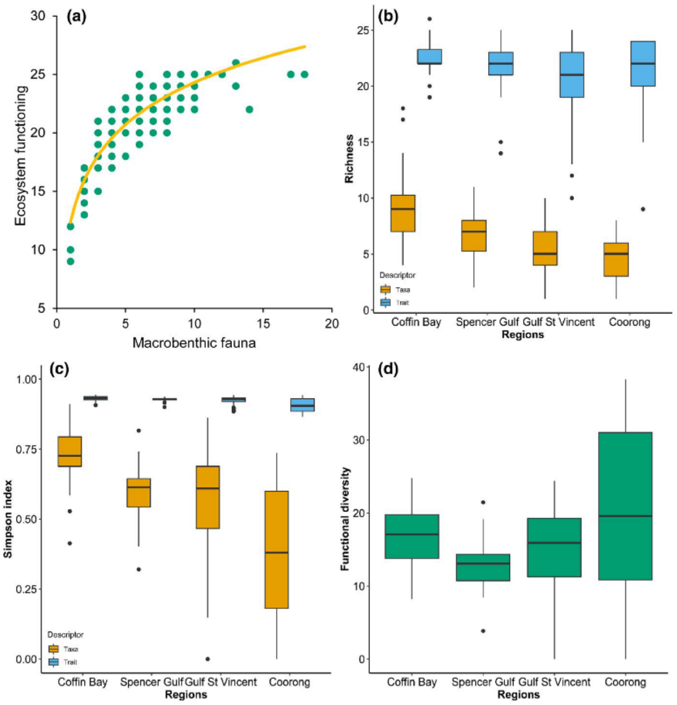
TABLE 3 Results from univariate pairwise test of bioturbator, body size, feeding mode, morphology, living habit, and sediment position across regions. Significant results are shown in bold

Pairwise test	t	*p* (perm)
Bioturbator		
Coffin Bay, Spencer Gulf	0.77	.6047
Coffin Bay, Gulf St Vincent	1.11	.2997
Coffin Bay, Coorong	4.39	**.001**
Spencer Gulf, Gulf St Vincent	1.09	.3659
Spencer Gulf, Coorong	4.14	**.0106**
Gulf St Vincent, Coorong	4.78	**.0002**
Body size		
Coffin Bay, Spencer Gulf	0.85	.7364
Coffin Bay, Gulf St Vincent	1.32	.2027
Coffin Bay, Coorong	4.44	**.0006**
Spencer Gulf, Gulf St Vincent	1.22	.3086
Spencer Gulf, Coorong	4.35	**.0109**
Gulf St Vincent, Coorong	5.16	**.0001**
Feeding mode		
Coffin Bay, Spencer Gulf	0.42	.9292
Coffin Bay, Gulf St Vincent	1.17	.2447
Coffin Bay, Coorong	3.81	**.0006**
Spencer Gulf, Gulf St Vincent	0.93	.4901
Spencer Gulf, Coorong	3.81	**.0113**
Gulf St Vincent, Coorong	4.49	**.0002**
Morphology		
Coffin Bay, Spencer Gulf	0.57	.7966
Coffin Bay, Gulf St Vincent	0.86	.4178
Coffin Bay, Coorong	3.69	**.0003**
Spencer Gulf, Gulf St Vincent	1.07	.359
Spencer Gulf, Coorong	3.47	**.0114**
Gulf St Vincent, Coorong	4.50	**.0003**
Living habit		
Coffin Bay, Spencer Gulf	0.38	.9319
Coffin Bay, Gulf St Vincent	1.18	.2785
Coffin Bay, Coorong	4.32	**.0005**
Spencer Gulf, Gulf St Vincent	1.07	.3793
Spencer Gulf, Coorong	4.43	**.0105**
Gulf St Vincent, Coorong	5.01	**.0001**
Sediment position		
Coffin Bay, Spencer Gulf	0.50	.9332
Coffin Bay, Gulf St Vincent	1.13	.281
Coffin Bay, Coorong	3.91	**.0009**
Spencer Gulf, Gulf St Vincent	1.12	.3662
Spencer Gulf, Coorong	3.61	**.0111**
Gulf St Vincent, Coorong	4.61	**.0003**

used as a part of the framework provided in this paper, with the aim to facilitate functional assessments along Australia's south coast.

The SAMT database is available for easy downloading, sharing, and using. However, as in any trait classification, several limitations need to be considered: (a) The structure of the database represents

FIGURE 8 (a) Correlation and trend line between the macrobenthic fauna (number of taxa) and ecosystem functioning (trait expression) in the main four regions of South Australia. (b) Boxplots of the taxonomic and trait richness, (c) Simpson index, and (d) functional diversity across the four study regions



the current taxonomic classification at the time of the analysis, (b) the taxa included reflect the sampling design (e.g., effort, habitats sampled) of the projects from which the information was retrieved; and (c) the SAMT database is an ongoing project, with continuous updates and refinements as additional taxa and trait information becomes available, resulting in up to date versions of functional trait classifications.

We identified several knowledge gaps in the literature while building the SAMT database. For example, the majority of the information included for "Larval type" (58%, 160 of 277 taxa), "Reproduction technique" (58%, 160 of 277 taxa), "Reproduction frequency" (58%, 160 of 277 taxa), and "Life span" (56%, 156 of 277 taxa) were based on the family level taxonomic classification, highlighting that basic knowledge about macrobenthic fauna that inhabit southern Australian waters is still very limited in many cases.

The exemplary use of the SAMT database found an asymptotic pattern between the macrobenthic fauna taxa and trait expression (ecosystem functioning), which could be explained by redundancy in these regions. Redundancy can be due to (a) different species performing the same functioning in the ecosystem, and (b) adding species to the ecosystem until all functionality (functional traits) is represented (van der Linden et al., 2012; Loreau et al., 2002; Schulze & Mooney, 1993). Taxa and trait differences were found in terms of richness and diversity using the Simpson index across all regions, but

TABLE 4 Test results from univariate one-way fixed factor PERMANOVA to compare Richness (S), Simpson index (1-Lambda'), and functional diversity (FD) of macrobenthic fauna across regions. Significant results are shown in bold

	df	MS	Pseudo-*F*	*p* (perm)
Richness (S)				
Taxa				
Region	3	140.32	23.803	**.0001**
Residual	203	5.89		
Trait				
Region	3	45.45	4.0587	**.0094**
Residual	203	11.20		
Simpson index				
Taxa				
Region	3	144.64	23.782	**.0001**
Residual	203	6.08		
Trait				
Region	3	0.004	21.85	**.0001**
Residual	203	0.0002		
Functional diversity				
Region	3	352.66	6.9265	**.0003**
Residual	202	50.91		

TABLE 5 Results from univariate pairwise test of richness (S), Simpson index (1-Lambda'), and functional diversity (FD). Only significant differences are shown

Pairwise test	t	*p* (perm)
Richness (S)		
Taxa		
Coffin Bay, Spencer Gulf	3.15	.0028
Coffin Bay, Gulf St Vincent	7.34	.0001
Coffin Bay, Coorong	6.47	.0001
Spencer Gulf, Gulf St Vincent	3.04	.0036
Spencer Gulf, Coorong	3.51	.0010
Trait		
Coffin Bay, Spencer Gulf	2.34	.021
Coffin Bay, Gulf St Vincent	3.46	.001
Coffin Bay, Coorong	2.42	.017
Simpson index (1-Lambda')		
Taxa		
Coffin Bay, Spencer Gulf	3.15	.0017
Coffin Bay, Gulf St Vincent	7.34	.0001
Coffin Bay, Coorong	6.48	.0001
Spencer Gulf, Gulf St Vincent	3.08	.0024
Spencer Gulf, Coorong	3.52	.0004
Trait		
Coffin Bay, Gulf St Vincent	2.30	.0232
Coffin Bay, Coorong	5.46	.0001
Spencer Gulf, Coorong	4.52	.0001
Gulf St Vincent, Coorong	6.09	.0001
Functional diversity (FD)		
Coffin Bay, Spencer Gulf	4.04	.0001
Spencer Gulf, Gulf St Vincent	2.06	.0400
Spencer Gulf, Coorong	3.01	.0038
Gulf St Vincent, Coorong	3.28	.0014

for comparing particular regions, taxonomically indices varied more than those based on traits across all regions.

Functional diversity (FD), as Rao's quadratic entropy metric, was significantly different across regions, highlighting greater FD in the Coorong and the lowest FD in Spencer Gulf. This pattern could be explained by the Coorong region having the greatest abundance of individuals and the most similar community compared to the other regions, aligning with the properties of the Rao's quadratic entropy metric, that bases its calculations on the proportion of the abundance of taxa present and the measure of dissimilarities between them (Botta-Dukát, 2005; Rao, 1982). The case study represents an example of the usefulness to combine both taxa and trait perspectives, as they give complementary insight to ecosystem functioning assessment and identify further research needs. Future targeted studies with consistent design can apply the database and framework presented here to demonstrate the ecological importance of effect traits and advance the understanding of the functionality of ecosystems along the southern Australian coast.

5 | CONCLUSION

To date, this is the first study providing a comprehensive assessment of traits for the southern Australian macrobenthic fauna. We highlight that the South Australia Macrobenthic Traits (SAMT) database presented here is a valuable tool to enhance further research on trait-based approaches within southern temperate Australia. The structure of the SAMT database includes 277 macrobenthic taxa so far, is very intuitive and was created for easy downloading, sharing, and using by researchers working on southern temperate benthic ecosystems. The newly developed R package for using and analyzing the SAMT database that can be applied more broadly to link trait and species data. A theoretical framework detailing the step-by-step process for assessing ecosystem functioning is introduced, illustrating the need for taxa-trait information and the use of SAMT database.

The use of the SAMT database should be approached with awareness of its limitations of available taxonomic and trait-based information, as well as ongoing changes to taxonomic nomenclature, traits information, and trait classification as the database evolves. The structure of the SAMT database will remain as simple as possible, avoiding complexity, redundancy, and duplication between traits as it expands to include more taxa, traits, and regions. The SAMT database is an ongoing project, where adding more taxa and traits will be continued with expansion into other regions within southern Australia.

6 | CODE AVAILABILITY

Code is available on figshare (https://doi.org/10.6084/m9.figshare.12763154) and on the GitHub repository (https://github.com/OrlandoLam/SAMT).

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CONFLICT OF INTEREST

No potential conflict of interest was reported by the authors.

AUTHOR CONTRIBUTION

Orlando Lam-Gordillo: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Software (lead); Validation (equal); Writing-original draft (lead); Writing-review & editing (equal). **Ryan Baring:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Supervision (lead); Validation (supporting); Writing-original draft (supporting); Writing-review & editing (equal). **Sabine Dittmann:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Supervision (lead); Validation (supporting); Writing-original draft (supporting); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

Data are available on figshare (https://doi.org/10.6084/m9.figshare.12763154).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Appendix C. Supplementary information for Chapter 4.

Table S1. Summary of the variance inflation factor (VIF), cut-off <3 for measuring the amount of multicollinearity in the set of environmental conditions analysed. All environmental conditions were retained for performing the analyses.

Variable	**VIF**
Chlorophyll *a* (mg.m^3)	1.15
Organic matter (%)	1.52
D50 (µm)	1.61
Sorting (σG)	1.66
pH	1.51
Salinity	1.14
Temperature (°C)	1.19
Nitrate (mg/L)	1.12
Nitrite (mg/L)	1.35
Ammonia (mg/L)	2.83
Phosphate (mg/L)	2.59

Table S2. Summary of the different generalized linear latent variable models (GLLVMs) performed. Four models were tested (Mod_1 – Mod_4), resulting in the Negative Binomial as the best fit model. Individual GLLVMs Negative Binomial were performed for each of the combinations: all dataset, summer dataset, winter dataset, datasets by site, and by site and season.

ID	Variables	Season	Family	AIC	AICc	BIC	Time elapsed
Mod_1	Species+enviromental+traits	Both	Poisson	20230.18	18280.49	22148.01	14.28 min
Mod_2	Species+enviromental+traits	Both	ZIP	17405.37	15378.17	19580.77	1.12 hours
Mod_3	Species+enviromental+traits	Both	Gaussian	32924.89	30897.68	35100.29	16.31 min
Mod_4	Species+enviromental+traits	Both	Negative Binomial	15672.30	13645.09	17847.69	10.10 min
Mod_all	Species+enviromental+traits	Both	Negative Binomial	15672.30	13645.09	17847.69	10.10 min
Mod_all_s	Species+enviromental+traits	Summer	Negative binomial	8818.64	7377.17	10404.73	3.10 min
Mod_all_w	Species+enviromental+traits	Winter	Negative binomial	6482.08	5107.09	7967.81	2.18 min
Mod_LB_both	Species+envi+traits	Both	Negative binomial	1831.74	893.48	2444.06	15 sec
Mod_KB_both	Species+envi+traits	Both	Negative binomial	2579.34	1593.31	3225.29	11 sec
Mod_PG_both	Species+envi+traits	Both	Negative binomial	1401.12	526.49	1968.61	6 sec
Mod_FB_both	Species+envi+traits	Both	Negative binomial	1737.40	823.01	2332.91	7 sec
Mod_PPa_both	Species+envi+traits	Both	Negative binomial	1666.96	736.65	2273.67	7 sec
Mod_MB_both	Species+envi+traits	Both	Negative binomial	2044.87	1034.96	2707.64	13 sec
Mod_PP_both	Species+envi+traits	Both	Negative binomial	2146.30	1335.24	2668.95	9 sec
Mod_N_both	Species+envi+traits	Both	Negative binomial	1823.67	1004.67	2351.92	5 sec
Mod_LB_s	Species+envi+traits	Summer	Negative binomial	1118.91	293.86	1400.05	5 sec
Mod_KB_s	Species+envi+traits	Summer	Negative binomial	1497.97	592.97	1807.38	5 sec
Mod_PG_s	Species+envi+traits	Summer	Negative binomial	1081.14	272.02	1356.57	5 sec
Mod_FB_s	Species+envi+traits	Summer	Negative binomial	1223.97	406.86	1502.24	5 sec

Mod_PPa_s	Species+envi+traits	Summer	Negative binomial	1174.56	349.46	1455.66	5 sec
Mod_MB_s	Species+envi+traits	Summer	Negative binomial	1328.92	407.94	1644.00	5 sec
Mod_PP_s	Species+envi+traits	Summer	Negative binomial	1274.99	505.80	1536.26	5 sec
Mod_N_s	Species+envi+traits	Summer	Negative binomial	1367.93	598.75	1629.20	5 sec
Mod_LB_w	Species+envi+traits	winter	Negative binomial	1178.47	289.45	1482.22	5 sec
Mod_KB_w	Species+envi+traits	winter	Negative binomial	1408.16	511.16	1714.75	5 sec
Mod_PG_w	Species+envi+traits	winter	Negative binomial	898.20	129.02	1159.47	5 sec
Mod_FB_w	Species+envi+traits	winter	Negative binomial	1026.50	209.40	1304.72	5 sec
Mod_PPa_w	Species+envi+traits	winter	Negative binomial	1024.26	199.16	1305.35	5 sec
Mod_MB_w	Species+envi+traits	winter	Negative binomial	1130.03	264.98	1425.28	5 sec
Mod_PP_w	Species+envi+traits	winter	Negative binomial	1286.84	533.63	1542.45	5 sec
Mod_N_w	Species+envi+traits	winter	Negative binomial	898.71	153.49	1151.48	5 sec

Table S3. Summary of the environmental conditions recorded in the eight sites along the southern Australian coast in two seasons. Mean values and standard deviations are shown. Chl *a*: chlorophyll *a*; OM: organic matter; D50: median grain size.

Site	Season	Chl *a* (mg.m^{3})		OM (%)		D50 (µm)		Sorting (σG)		pH		Salinity		Temperature (°C)	
		Mean	± SE	Mean	± SE	Mean	± SE	Mean	± SE	Mean	± SE	Mean	± SE	Mean	± SE
Long Beach	Summer	1.20	0.15	1.99	0.13	245.89	1.52	1.59	0.03	7.86	0.03	43.33	0.44	24.81	0.40
	Winter	0.71	0.08	2.17	0.08	248.04	2.96	1.77	0.08	7.73	0.07	36.11	0.97	13.10	0.17
Kellidie Bay	Summer	1.49	0.11	2.91	0.31	215.88	8.03	2.16	0.22	7.88	0.09	34.58	2.37	24.15	0.42
	Winter	0.70	0.08	2.94	0.22	254.06	28.89	2.80	0.34	8.37	0.06	34.54	0.89	16.10	0.20
Port Germein	Summer	0.52	0.06	1.77	0.06	224.27	6.70	2.05	0.11	7.46	0.06	45.17	0.76	26.43	0.35
	Winter	0.31	0.02	2.18	0.05	167.46	8.04	2.25	0.05	7.88	0.11	56.91	1.06	13.83	0.38
Fisherman Bay	Summer	0.83	0.10	3.08	0.07	384.02	8.74	3.75	0.17	7.90	0.10	51.40	5.61	22.90	0.31
	Winter	0.57	0.04	3.17	0.10	378.08	11.19	2.28	0.17	8.16	0.04	43.44	0.10	6.23	0.33
Port Parham	Summer	0.51	0.04	2.26	0.06	197.29	10.39	2.18	0.11	8.04	0.11	46.32	1.46	30.44	0.88
	Winter	0.21	0.02	2.30	0.12	240.07	11.33	2.25	0.12	8.11	0.03	40.68	0.45	11.65	0.31
Middle Beach	Summer	1.23	0.21	3.33	0.13	438.69	25.69	2.81	0.22	7.97	0.12	41.93	0.28	30.63	0.60
	Winter	0.78	0.14	2.96	0.12	652.66	38.97	3.48	0.25	7.87	0.04	40.31	0.19	13.89	0.22
Pelican Point	Summer	2.10	0.27	1.41	0.09	320.12	4.96	2.36	0.09	7.93	0.12	27.49	0.48	18.95	0.43
	Winter	0.97	0.10	0.91	0.12	346.66	16.32	1.79	0.07	7.53	0.10	35.65	2.67	11.01	0.14
Noonameena	Summer	1.85	0.16	0.99	0.04	227.82	5.42	1.69	0.01	8.08	0.01	65.86	0.63	24.96	0.17
	Winter	0.62	0.06	0.82	0.04	198.06	2.92	1.58	0.01	8.18	0.03	34.10	0.64	11.74	0.18

Table S3. Continued

Site	Season	Nitrate (mg/L)		Nitrite (mg/L)		Ammonia (mg/L)		Phosphate (mg/L)	
		Mean	± SE	Mean	± SE	Mean	± SE	Mean	± SE
Long Beach	Summer	0.07	0.02	0.12	0.01	0.47	0.04	0.19	0.04
	Winter	0.04	0.02	0.41	0.19	0.46	0.13	0.18	0.03
Kellidie Bay	Summer	0.02	0.01	0.17	0.01	0.27	0.01	0.00	0.00
	Winter	0.20	0.14	0.66	0.21	0.19	0.02	0.09	0.01
Port Germein	Summer	0.01	0.01	0.28	0.01	1.34	0.47	0.02	0.01
	Winter	1.04	0.64	0.68	0.03	1.21	0.22	0.29	0.02
Fisherman Bay	Summer	0.09	0.02	0.28	0.01	0.01	0.00	0.00	0.00
	Winter	0.07	0.02	0.73	0.05	0.46	0.02	0.27	0.02
Port Parham	Summer	0.05	0.01	0.26	0.01	0.35	0.03	0.01	0.00
	Winter	0.02	0.01	0.64	0.06	0.37	0.03	0.20	0.01
Middle Beach	Summer	0.00	0.00	0.11	0.01	0.84	0.41	0.12	0.08
	Winter	0.02	0.01	0.53	0.03	0.26	0.03	0.18	0.02
Pelican Point	Summer	0.13	0.01	0.42	0.01	0.61	0.20	0.05	0.04
	Winter	0.94	0.80	1.00	0.25	5.23	1.97	2.17	0.97
Noonameena	Summer	0.01	0.01	0.36	0.01	0.49	0.00	0.03	0.01
	Winter	0.18	0.04	0.75	0.01	0.51	0.08	0.35	0.05

Table S4. Macrobenthic fauna abundances recorded in the eight sites surveyed across the southern Australian coast in two seasons. Major taxonomical groups, mean and error standard values are shown.

Site	Season	Total number of species	Mean total abundance (ind.m^2)	Annelida		Arthropoda		Bivalvia	
				Mean (ind.m^2)	± SE	Mean (ind.m^2)	± SE	Mean (ind.m^2)	± SE
Long Beach	Summer	17	2496.40	1416.23	256.67	72.01	15.71	480.08	85.27
	Winter	25	3592.57	1736.28	419.51	208.03	76.33	184.03	38.61
Kellidie Bay	Summer	27	14330.29	3120.50	1130.93	2224.36	1178.50	3968.63	756.85
	Winter	26	14210.27	1400.22	93.46	152.02	32.01	3928.63	502.48
Port Germein	Summer	15	4632.74	1352.22	286.77	232.04	86.44	2816.45	587.49
	Winter	10	2320.37	128.02	27.39	32.01	18.40	480.08	136.09
Fisherman Bay	Summer	16	15818.53	1256.20	409.42	312.05	55.93	1696.27	314.91
	Winter	16	1904.30	480.08	49.69	144.02	42.55	64.01	28.37
Port Parham	Summer	17	13194.11	1280.20	244.47	56.01	19.83	640.10	156.56
	Winter	17	2152.34	920.15	127.05	32.01	14.18	112.02	34.08
Middle Beach	Summer	29	13498.16	5480.88	1198.51	216.03	56.42	680.11	230.61
	Winter	22	3872.62	1648.26	741.65	1128.18	445.20	432.07	143.83
Pelican Point	Summer	10	49399.90	17858.86	1356.66	1472.24	301.01	27452.39	4588.10
	Winter	8	52592.41	13234.12	2919.97	16794.69	6394.36	21707.47	3221.71
Noonameena	Summer	11	87486.00	68626.98	4455.75	18122.90	1732.13	600.10	143.93
	Winter	7	10489.68	8905.42	1142.94	1568.25	491.44	8.00	8.00

Table S4. Continued.

Site	Season	Cnidaria		Echinodermata		Gastropoda		Nemertea	
		Mean (ind.m^2)	± SE	Mean (ind.m^2)	± SE	Mean (ind.m^2)	± SE	Mean (ind.m^2)	± SE
Long Beach	Summer	0.00	0.00	0.00	0.00	528.08	115.24	0.00	0.00
	Winter	0.00	0.00	0.00	0.00	1464.23	511.91	0.00	0.00
Kellidie Bay	Summer	0.00	0.00	24.00	12.83	4992.80	830.51	0.00	0.00
	Winter	0.00	0.00	0.00	0.00	8729.40	1737.72	8.00	8.00
Port Germein	Summer	0.00	0.00	0.00	0.00	232.04	78.10	16.00	10.90
	Winter	0.00	0.00	0.00	0.00	1680.27	285.22	0.00	0.00
Fisherman Bay	Summer	0.00	0.00	0.00	0.00	12554.01	2208.26	0.00	0.00
	Winter	8.00	8.00	0.00	0.00	1208.19	169.52	8.00	8.00
Port Parham	Summer	0.00	0.00	0.00	0.00	11217.79	2656.55	24.00	17.37
	Winter	0.00	0.00	0.00	0.00	1088.17	165.42	0.00	0.00
Middle Beach	Summer	64.01	25.84	0.00	0.00	7057.13	1604.30	40.01	19.13
	Winter	0.00	0.00	0.00	0.00	664.11	116.46	8.00	8.00
Pelican Point	Summer	0.00	0.00	0.00	0.00	2616.42	646.45	0.00	0.00
	Winter	0.00	0.00	0.00	0.00	856.14	256.04	0.00	0.00
Noonameena	Summer	0.00	0.00	0.00	0.00	136.02	46.66	0.00	0.00
	Winter	0.00	0.00	0.00	0.00	8.00	8.00	0.00	0.00

Table S5. Taxa list of the macrobenthic fauna recorded in the eight sites surveyed across the southern Australian.

Phylum	**Class**	**Order**	**Family**	**Species**
Annelida	Polychaeta	Eunicida	Onuphidae	
Annelida	Polychaeta	Phyllodocida	Goniadidae	
Annelida	Polychaeta	Phyllodocida	Nephtyidae	*Aglaophamus australiensis*
Annelida	Polychaeta	Phyllodocida	Nephtyidae	
Annelida	Polychaeta	Phyllodocida	Nereididae	*Australonereis ehlersi*
Annelida	Polychaeta	Phyllodocida	Nereididae	*Simplisetia aequisetis*
Annelida	Polychaeta	Phyllodocida	Nereididae	
Annelida	Polychaeta	Phyllodocida	Syllidae	
Annelida	Polychaeta	Sabellida	Sabellidae	*Euchone variabilis*
Annelida	Polychaeta	Spionida	Spionidae	*Boccardiella limnicola*
Annelida	Polychaeta	Spionida	Spionidae	
Annelida	Polychaeta	Terebellida	Cirratulidae	
Annelida	Polychaeta		Arenicolidae	
Annelida	Polychaeta		Capitellidae	
Annelida	Polychaeta		Opheliidae	
Annelida	Polychaeta		Orbiniidae	
Annelida	Polychaeta		Paraonidae	
Arthropoda	Hexanauplia	Sessilia	Balanidae	*Amphibalanus amphitrite*
Arthropoda	Hexanauplia	Sessilia	Chthamalidae	*Chamaesipho tasmanica*
Arthropoda	Insecta	Diptera	Ceratopogonidae	
Arthropoda	Insecta	Diptera	Chironomidae	
Arthropoda	Insecta	Diptera	Dolichopodidae	
Arthropoda	Malacostraca	Amphipoda	Corophiidae	
Arthropoda	Malacostraca	Amphipoda		
Arthropoda	Malacostraca	Cumacea	Bodotriidae	*Cyclaspis spilotes*
Arthropoda	Malacostraca	Decapoda	Callianassidae	*Arenallianassa arenosa*
Arthropoda	Malacostraca	Decapoda	Callichiridae	*Neocallichirus angelikae*
Arthropoda	Malacostraca	Decapoda	Leucosiidae	*Bellidilia laevis*
Arthropoda	Malacostraca	Decapoda	Paguridae	*Lophopagurus nanus*
Arthropoda	Malacostraca	Decapoda	Penaeidae	*Penaeus latisulcatus*
Arthropoda	Malacostraca	Decapoda	Portunidae	*Portunus pelagicus*
Arthropoda	Malacostraca	Decapoda	Varunidae	*Brachynotus spinosus*
Arthropoda	Malacostraca	Isopoda	Cirolanidae	*Cirolana cranchii australiensis*
Arthropoda	Malacostraca	Isopoda	Idoteidae	*Euidotea bakeri*
Arthropoda	Malacostraca	Isopoda	Janiridae	
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Exosphaeroma alii*
Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Platynympha longicaudata*
Arthropoda	Malacostraca	Leptostraca	Nebaliidae	

Arthropoda	Malacostraca	Mysida	Mysidae	
Arthropoda	Malacostraca	Tanaidacea	Apseudidae	*Carpoapseudes austroafricanus*
Cnidaria	Anthozoa	Actiniaria	Actiniidae	*Anthopleura hermaphroditica*
Echinodermata	Holothuroidea	Holothuriida	Holothuriidae	
Mollusca	Bivalvia	Cardiida	Psammobiidae	*Hiatula alba*
Mollusca	Bivalvia	Cardiida	Tellinidae	*Tellina margaritinus*
Mollusca	Bivalvia	Cardiida	Tellinidae	*Tellina sp.*
Mollusca	Bivalvia	Galeommatida	Lasaeidae	*Arthritica semen*
Mollusca	Bivalvia	Mytilida	Mytilidae	*Brachidontes rostratus*
Mollusca	Bivalvia	Mytilida	Mytilidae	*Xenostrobus inconstans*
Mollusca	Bivalvia	Venerida	Mactridae	*Spisula trigonella*
Mollusca	Bivalvia	Venerida	Mesodesmatidae	*Anapella cycladea*
Mollusca	Bivalvia	Venerida	Mesodesmatidae	*Atactodea cuneata*
Mollusca	Bivalvia	Venerida	Veneridae	*Dosinia sp.*
Mollusca	Bivalvia	Venerida	Veneridae	*Katelysia peronii*
Mollusca	Bivalvia	Venerida	Veneridae	*Katelysia rhytiphora*
Mollusca	Bivalvia	Venerida	Veneridae	*Katelysia scalarina*
Mollusca	Gastropoda	Caenogastropoda	Batillariidae	*Zeacumantus diemenensis*
Mollusca	Gastropoda	Caenogastropoda	Batillariidae	*Zeacumantus plumbeus*
Mollusca	Gastropoda	Cephalaspidea	Bullidae	*Bulla quoyii*
Mollusca	Gastropoda	Cephalaspidea	Haminoeidae	*Liloa brevis*
Mollusca	Gastropoda	Cephalaspidea	Philinidae	*Philine angasi*
Mollusca	Gastropoda	Littorinimorpha	Hydrobiidae	
Mollusca	Gastropoda	Littorinimorpha	Littorinidae	*Bembicium vittatum*
Mollusca	Gastropoda	Littorinimorpha	Naticidae	*Conuber conicum*
Mollusca	Gastropoda	Littorinimorpha	Rissoinidae	*Rissoina fasciata*
Mollusca	Gastropoda	Neogastropoda	Buccinidae	*Cominella lineolata*
Mollusca	Gastropoda	Neogastropoda	Fasciolariidae	*Propefusus australis*
Mollusca	Gastropoda	Neogastropoda	Nassariidae	*Nassarius pyrrhus*
Mollusca	Gastropoda	Neogastropoda	Terebridae	*Duplicaria kieneri*
Mollusca	Gastropoda	Neogastropoda	Volutomitridae	*Peculator porphyria*
Mollusca	Gastropoda	Trochida	Trochidae	*Austrocochlea constricta*
Mollusca	Gastropoda	Trochida	Trochidae	*Phasianotrochus eximius*
Mollusca	Gastropoda		Amphibolidae	*Salinator fragilis*
Mollusca	Gastropoda		Lottiidae	*Notoacmea flammea*
Nemertea	Pilidiophora	Heteronemertea	Lineidae	*Notospermus sp.*

Table S6. Summary of the Pairwise test by expressed trait. P-values are presented, and significant differences are shown in bold. LB: Long Beach; KB: Kellidie Bay; MB: Middle Beach; PPa: Port Parham; PG: Port Germein, FB: Fisherman Bay; PP: Pelican Point; N: Noonameena.

Groups / Traits modalities	Biodiffusor		Bioirrigator		No bioturbation		Surface modifier		Large (>20mm)		Medium (5-20mm)		Small (0.5-5mm)	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
LB, KB	**0.0002**	**0.0030**	**0.0078**	0.0624	0.1996	**0.0033**	0.6748	0.1605	**0.0001**	0.2434	**0.0001**	0.2364	**0.0042**	0.4195
LB, MB	**0.0001**	**0.0009**	**0.001**	0.3565	0.0291	0.0179	0.2569	0.6427	**0.0001**	**0.0001**	**0.0001**	**0.0006**	**0.0032**	**0.0034**
LB, PPa	**0.0001**	**0.0001**	**0.0093**	0.0207	0.9781	**0.0001**	0.1606	0.7580	**0.0001**	**0.0001**	**0.0001**	0.0338	**0.0001**	**0.0001**
LB, PG	**0.0002**	**0.0001**	**0.0061**	0.0855	0.8253	**0.0001**	0.0101	0.4507	**0.0001**	**0.0015**	**0.0001**	**0.0006**	**0.0001**	0.3512
LB, FB	**0.0001**	**0.0003**	**0.0001**	0.2641	**0.0001**	0.4752	0.4385	0.3571	**0.0001**	**0.0015**	**0.0001**	0.0149	**0.0001**	**0.0032**
LB, PP	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0004**	**0.0005**	**0.0002**	0.4099	**0.0001**	**0.0001**	**0.0001**	**0.0005**	**0.0001**	**0.0001**
LB, N	**0.0001**	0.0149	0.5324	**0.0001**	0.3103	**0.0001**	**0.0077**	0.5934	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
KB, MB	0.0137	0.2250	0.1742	**0.0093**	0.1725	0.8824	0.3290	0.0258	0.6411	**0.0037**	0.6554	0.0165	0.7683	**0.0088**
KB, PPa	**0.0001**	**0.0006**	0.7508	0.6525	0.2217	**0.0001**	0.1580	0.2998	0.0827	**0.0072**	0.1208	0.3475	0.2306	**0.0001**
KB, PG	**0.0001**	**0.0001**	0.3821	**0.0051**	0.4626	**0.0007**	**0.0015**	0.3444	**0.0007**	0.0521	**0.0001**	0.0176	**0.0016**	0.8196
KB, FB	**0.0001**	0.1518	**0.0002**	0.0104	**0.0020**	0.0246	0.5721	0.5447	0.0140	0.0779	**0.0026**	0.3835	0.8335	0.0105
KB, PP	**0.0001**	**0.0001**	**0.0001**	**0.0001**	0.0102	0.1329	**0.0001**	**0.0015**	**0.0001**	**0.0001**	0.2432	0.0747	**0.0001**	**0.0001**
KB, N	0.5387	**0.0001**	0.0143	**0.0001**	0.6469	**0.0001**	**0.0003**	0.0167	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
MB, PPa	**0.0095**	0.4021	0.3208	**0.0029**	0.0277	**0.0004**	0.8889	0.4250	0.027	0.8771	0.0823	0.1406	0.0870	0.2212
MB, PG	**0.0001**	**0.0002**	0.8318	0.2237	0.0900	**0.0084**	**0.0007**	0.1228	**0.0001**	0.1699	**0.0006**	0.8685	**0.0001**	0.0186
MB, FB	0.1455	0.8156	0.038	0.7222	0.2849	0.0627	0.5670	0.0999	**0.006**	0.0933	**0.0017**	0.0388	0.5560	0.3972
MB, PP	**0.0001**	**0.0002**	**0.0087**	**0.0003**	0.7433	0.3448	**0.0058**	0.6493	**0.0001**	**0.0001**	0.6333	0.1911	**0.0001**	**0.0001**
MB, N	0.1533	**0.0001**	**0.0022**	**0.0003**	0.0820	**0.0001**	0.2256	0.9145	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
PPa, PG	**0.0001**	**0.0002**	0.5518	**0.0016**	0.8159	0.4953	**0.0003**	0.7237	**0.0073**	0.2442	0.0406	0.1241	**0.0071**	**0.0002**
PPa, FB	0.1723	0.0578	**0.0028**	**0.0046**	**0.0001**	**0.0001**	0.3844	0.5886	0.2169	0.1265	0.0727	0.8011	0.1967	0.0125
PPa, PP	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0003**	**0.0003**	**0.0020**	0.2283	**0.0001**	**0.0001**	**0.0095**	0.5549	**0.0001**	**0.0001**
PPa, N	**0.0002**	**0.0001**	0.0198	**0.0001**	0.3296	**0.0001**	0.1633	0.3806	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**

PG, FB	**0.0001**	**0.0001**	0.0441	0.3316	**0.002**	**0.0001**	**0.0008**	0.7849	0.1155	0.7349	0.8674	0.0383	**0.0005**	0.0324
PG, PP	**0.0001**	0.1576	0.0158	0.2787	0.0109	0.0228	**0.0001**	**0.0053**	0.0435	**0.0001**	**0.0001**	0.1762	**0.0001**	**0.0001**
PG, N	**0.0001**	**0.0001**	0.0124	0.2516	0.6376	**0.0001**	**0.0001**	0.0925	**0.005**	**0.0001**	0.0257	**0.0001**	**0.0033**	**0.0001**
FB, PP	**0.0001**	**0.0001**	0.8944	**0.0024**	0.2251	**0.0021**	**0.0001**	0.0154	**0.0001**	**0.0001**	**0.0003**	0.2138	**0.0001**	**0.0001**
FB, N	**0.0023**	**0.0001**	**0.0001**	**0.0031**	**0.0005**	**0.0001**	**0.0076**	0.0821	**0.0001**	**0.0001**	0.0220	**0.0001**	**0.0001**	**0.0001**
PP, N	**0.0001**	**0.0001**	**0.0001**	0.8665	**0.0009**	**0.0001**	**0.0030**	0.7678	**0.0089**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**

Table S6. Continued.

Groups / Traits modalities	Deposit feeder		Filter/suspension		Grazer/scraper		Predator		Scavenger / Opportunist		Sub-surface deposit feeder	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
LB, KB	**0.0002**	**0.0001**	0.0184	0.0904	0.0127	0.4008	**0.001**	**0.0001**	0.3814	0.0564	**0.0021**	**0.0002**
LB, MB	0.8874	0.2462	0.0129	0.0618	**0.0002**	0.3549	0.5510	0.6595	0.3267	0.3380	**0.0082**	**0.0021**
LB, PPa	**0.0001**	**0.0001**	**0.0001**	**0.0003**	**0.0001**	0.9141	0.3829	0.0189	0.0339	**0.0093**	0.1082	**0.0001**
LB, PG	0.0893	**0.0001**	0.0117	0.0904	**0.0013**	0.1477	0.4671	**0.0002**	0.0390	**0.0001**	0.2844	0.0502
LB, FB	**0.0071**	**0.0002**	0.0365	**0.0120**	**0.0001**	0.3148	0.2148	0.7341	**0.0033**	0.0682	**0.0001**	0.1859
LB, PP	**0.0010**	**0.0001**	0.0223	0.1157	0.3202	0.0456	**0.0002**	**0.0005**	0.1279	0.2813	0.3902	**0.0001**
LB, N	**0.0001**	0.4916	**0.0001**	**0.0001**	**0.0018**	**0.0011**	**0.0001**	**0.0001**	**0.0048**	**0.0001**	**0.0001**	**0.0001**
KB, MB	**0.0002**	**0.0001**	0.6719	0.6073	0.0212	**0.0073**	**0.0030**	**0.0002**	0.9538	0.0177	0.9655	**0.0001**
KB, PPa	0.2974	0.0562	**0.0001**	**0.0040**	0.0336	0.1044	0.0148	**0.0001**	0.1492	0.4381	0.3050	**0.0001**
KB, PG	**0.0067**	0.9523	**0.0001**	0.9424	**0.0001**	0.3368	**0.0045**	0.7062	0.1689	**0.0015**	0.0552	0.1350
KB, FB	**0.0023**	**0.0005**	0.7296	0.1568	**0.0006**	0.8156	0.0241	**0.0001**	0.0155	0.9857	0.0296	0.0117
KB, PP	**0.0095**	**0.0001**	0.8687	0.6096	0.0137	**0.0002**	0.1590	**0.0001**	**0.0043**	**0.0006**	**0.0045**	**0.0001**
KB, N	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	0.1276	**0.0026**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
MB, PPa	**0.0005**	**0.0004**	**0.0026**	0.0604	0.2939	0.1327	0.7275	0.1106	0.1080	**0.0047**	0.3573	0.0677
MB, PG	0.1077	**0.0001**	**0.0001**	0.6795	**0.0001**	**0.0005**	0.2550	**0.0018**	0.1306	**0.0003**	0.0990	**0.0004**
MB, FB	0.0215	0.0132	0.4883	0.4705	0.4498	**0.0030**	0.4760	0.8846	**0.0054**	0.0199	0.0960	**0.0006**
MB, PP	**0.0045**	0.0305	0.5798	0.3615	**0.0003**	0.0589	**0.0052**	**0.0053**	**0.0012**	0.7976	0.0194	**0.0002**

MB, N	**0.0010**	0.4459	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0002**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
PPa, PG	0.0374	0.0764	**0.0001**	0.0114	**0.0001**	0.0113	0.1938	0.0136	0.9175	**0.0004**	0.5130	**0.0001**
PPa, FB	0.0168	0.0228	**0.0001**	0.1901	**0.0096**	0.0413	0.7593	0.0373	0.2059	0.4919	0.0103	**0.0001**
PPa, PP	0.0701	**0.0008**	**0.0001**	**0.0003**	**0.0001**	**0.0001**	0.0496	0.0862	**0.0002**	**0.0001**	0.2685	0.0308
PPa, N	**0.0001**	**0.0001**	**0.0001**	0.0166	**0.0001**	**0.0001**	**0.0002**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
PG, FB	0.7531	**0.0009**	**0.0001**	0.2066	**0.0001**	0.4172	0.1244	**0.0005**	0.1676	**0.0002**	**0.0006**	0.5153
PG, PP	0.3347	**0.0002**	**0.0001**	0.6051	**0.0001**	**0.0001**	0.0101	0.0987	**0.0001**	**0.0001**	0.6530	**0.0001**
PG, N	**0.0001**	**0.0001**	0.2849	**0.0002**	0.4752	**0.0001**	**0.0003**	0.0655	**0.0001**	**0.0001**	**0.0001**	**0.0001**
FB, PP	0.2624	0.2679	0.8544	0.0426	**0.0001**	**0.0001**	0.0792	**0.0004**	**0.0001**	**0.0009**	**0.0001**	**0.0001**
FB, N	**0.0001**	**0.0004**	**0.0001**	**0.0008**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
PP, N	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0007**	**0.0001**	**0.0001**	**0.0099**	**0.0001**	**0.0001**	**0.0001**

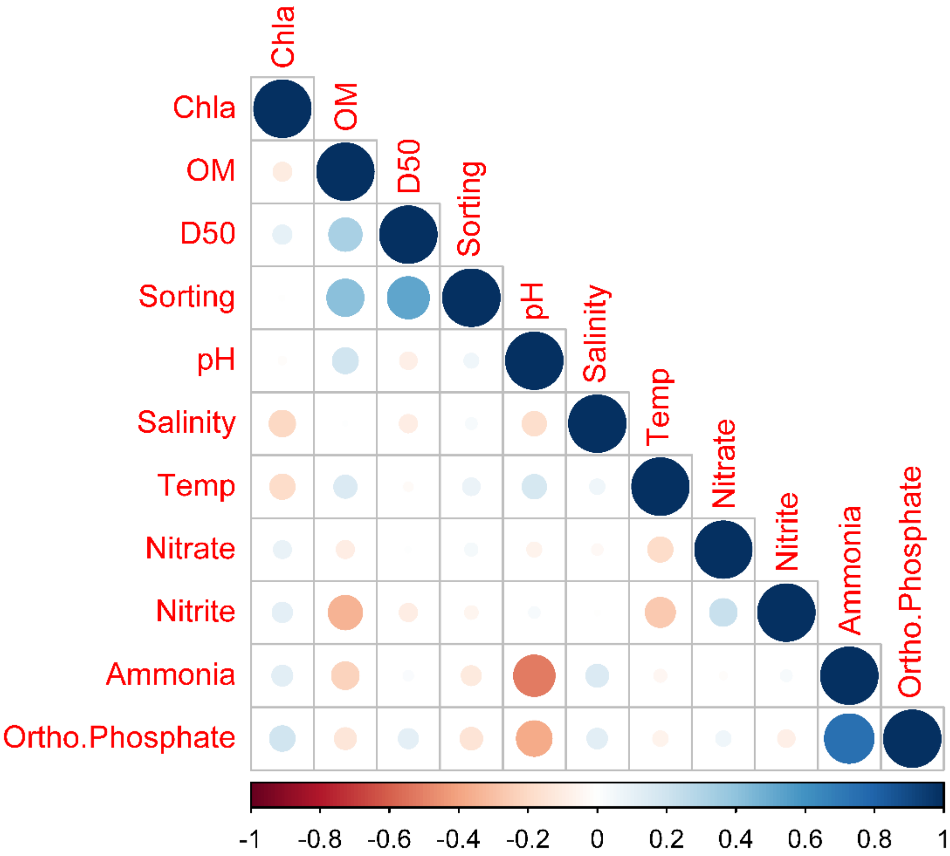


Figure S1. Spearman correlation plot for measuring collinearity among the environmental conditions recorded at the eight sites across the southern Australian coast. All environmental conditions were retained for the analyses performed. Chl *a*: chlorophyll *a*; OM: organic matter; DO: dissolved oxygen, Temp: Temperature.

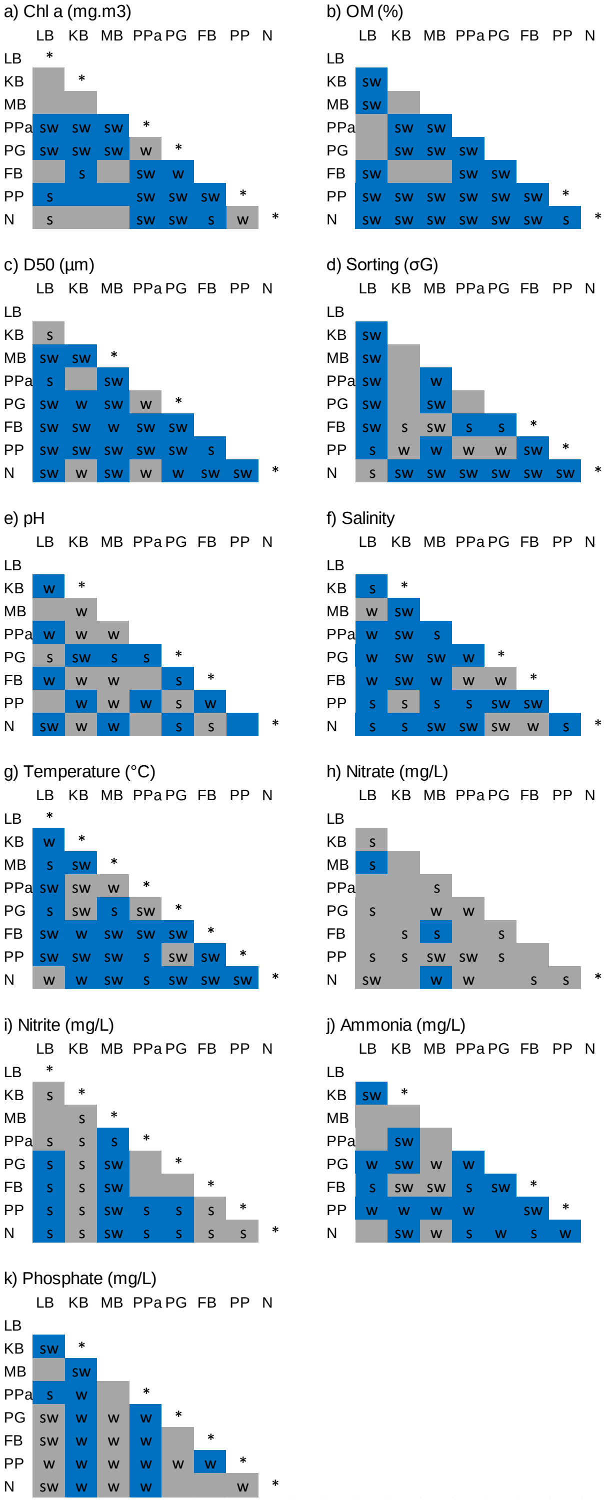
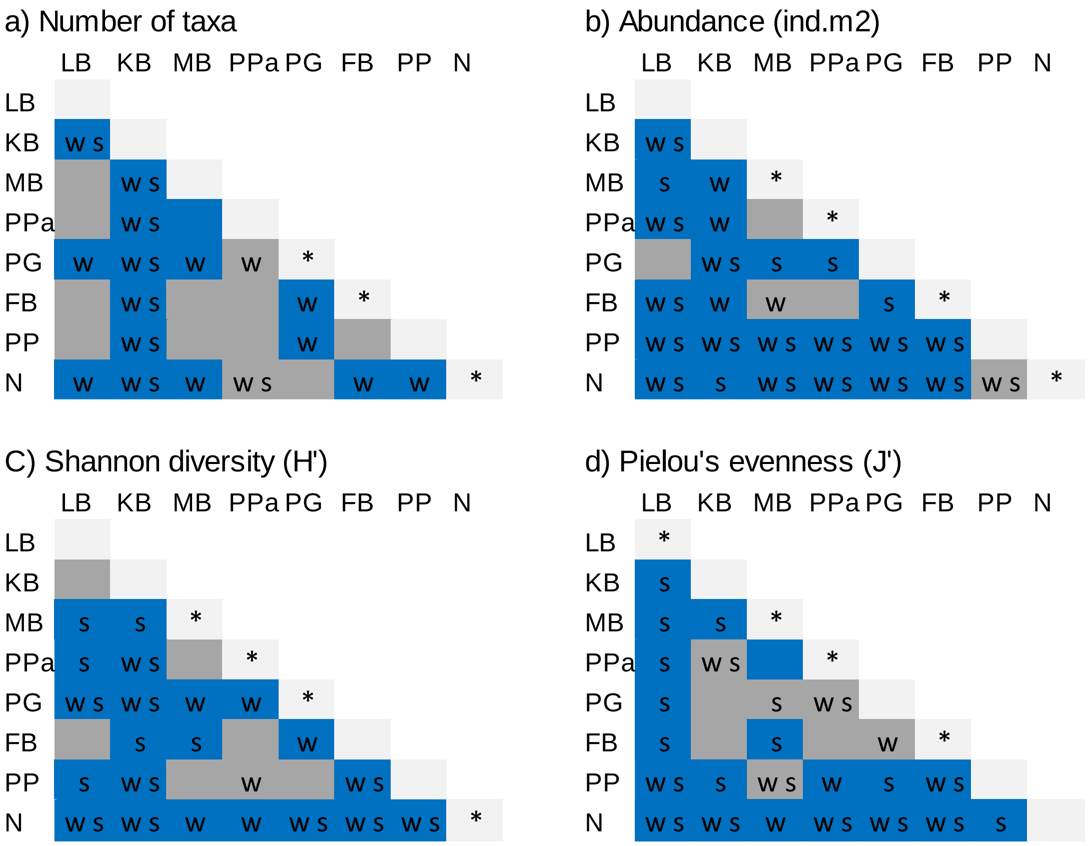


Figure S2. Visual summary of PERMANOVA Pairwise test outcomes for taxa. Season: Blue= significant difference p<0.01; Grey= not significant difference p>0.01. Site x Season interaction: *= significant difference p<0.01 between seasons by site; s= significant difference p<0.01 in summer season; w= significant difference p<0.01 in winter season. LB: Long Beach; KB: Kellidie

Bay; MB: Middle Beach; PPa: Port Parham; PG: Port Germein, FB: Fisherman Bay; PP: Pelican Point; N: Noonameena.



a) Number of taxa

	LB	KB	MB	PPa	PG	FB	PP	N
LB								
KB	w s							
MB		w s						
PPa		w s						
PG	w	w s	w	w	*			
FB		w s			w	*		
PP		w s			w			
N	w	w s	w	w s		w	w	*

b) Abundance (ind.m2)

	LB	KB	MB	PPa	PG	FB	PP	N
LB								
KB	w s							
MB	s	w	*					
PPa	w s	w		*				
PG		w s	s	s				
FB	w s	w	w		s	*		
PP	w s	w s	w s	w s	w s	w s		
N	w s	s	w s	w s	w s	w s	w s	*

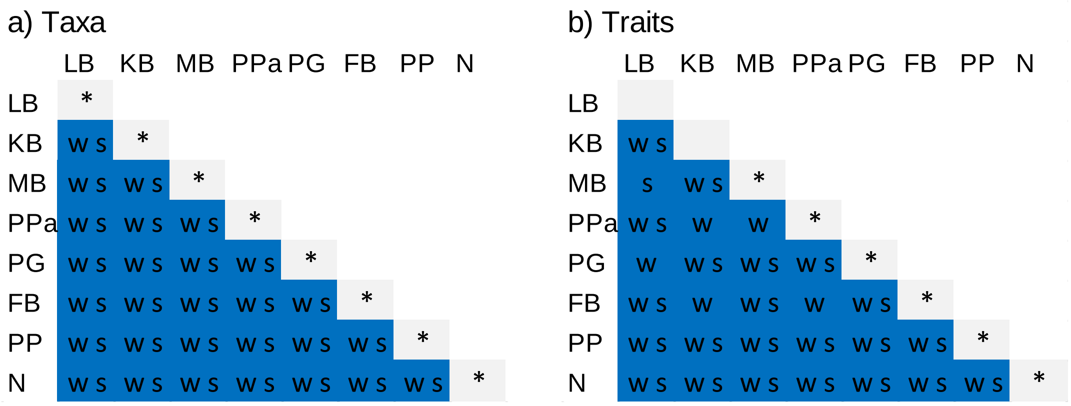
C) Shannon diversity (H')

	LB	KB	MB	PPa	PG	FB	PP	N
LB								
KB								
MB	s	s	*					
PPa	s	w s		*				
PG	w s	w s	w	w	*			
FB		s	s		w			
PP	s	w s		w		w s		
N	w s	w s	w	w	w s	w s	w s	*

d) Pielou's evenness (J')

	LB	KB	MB	PPa	PG	FB	PP	N
LB	*							
KB	s							
MB	s	s	*					
PPa	s	w s		*				
PG	s		s	w s				
FB	s		s		w	*		
PP	w s	s	w s	w	s	w s		
N	w s	w s	w	w s	w s	w s	s	

Figure S3. Visual summary of PERMANOVA Pairwise test outcomes for taxa. Season: Blue= significant difference p<0.01; Grey= not significant difference p>0.01. Site x Season interaction: *= significant difference p<0.01 between seasons by site; s= significant difference p<0.01 in summer season; w= significant difference p<0.01 in winter season. a) Number of taxa, b) Abundance (ind.m2), c) Shannon Index H’, d) Evenness Index J’. LB: Long Beach; KB: Kellidie Bay; MB: Middle Beach; PPa: Port Parham; PG: Port Germein, FB: Fisherman Bay; PP: Pelican Point; N: Noonameena.



a) Taxa

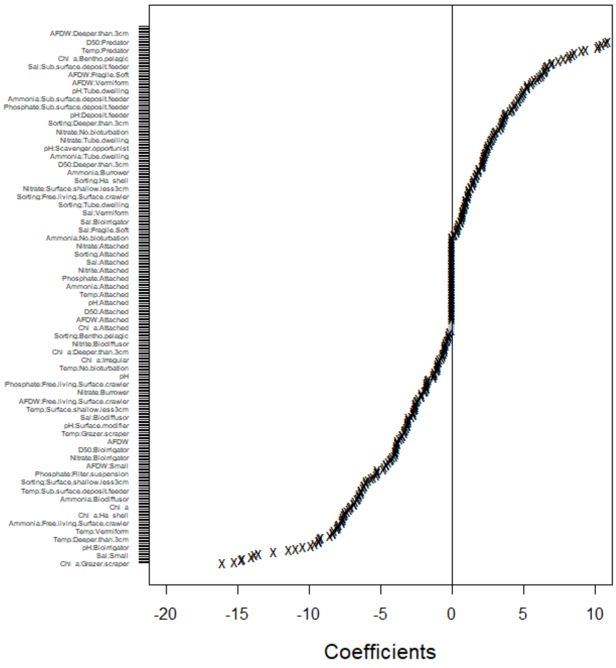
	LB	KB	MB	PPa	PG	FB	PP	N
LB	*							
KB	w s	*						
MB	w s	w s	*					
PPa	w s	w s	w s	*				
PG	w s	w s	w s	w s	*			
FB	w s	w s	w s	w s	w s	*		
PP	w s	w s	w s	w s	w s	w s	*	
N	w s	w s	w s	w s	w s	w s	w s	*

b) Traits

	LB	KB	MB	PPa	PG	FB	PP	N
LB								
KB	w s							
MB	s	w s	*					
PPa	w s	w	w	*				
PG	w	w s	w s	w s	*			
FB	w s	w	w s	w	w s	*		
PP	w s	w s	w s	w s	w s	w s	*	
N	w s	w s	w s	w s	w s	w s	w s	*

Figure S4. Visual summary of PERMANOVA Pairwise test outcomes for traits. Season: Blue= significant difference p<0.01; Grey= not significant difference p>0.01. Site x Season interaction: *= significant difference p<0.01 between seasons by site; s= significant difference p<0.01 in summer season; w= significant difference p<0.01 in winter season. LB: Long Beach; KB: Kellidie Bay; MB: Middle Beach; PPa: Port Parham; PG: Port Germein, FB: Fisherman Bay; PP: Pelican Point; N: Noonameena.

a) Long Beach summer



b) Long Beach winter

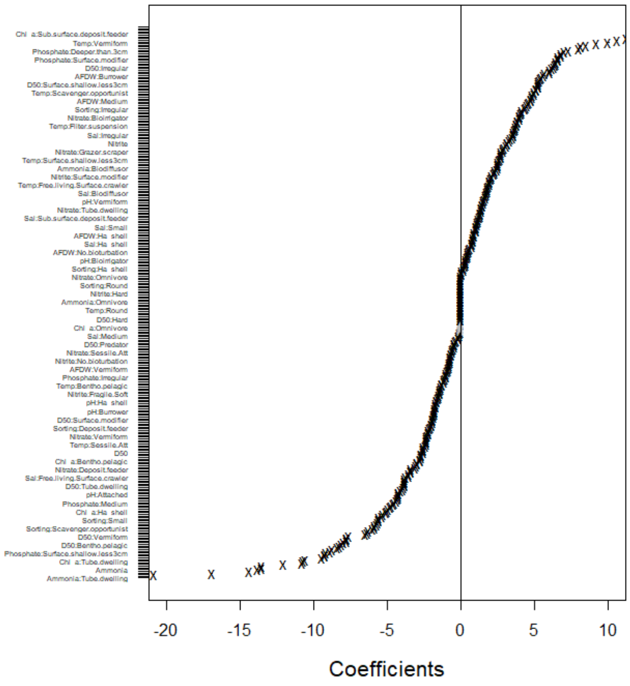
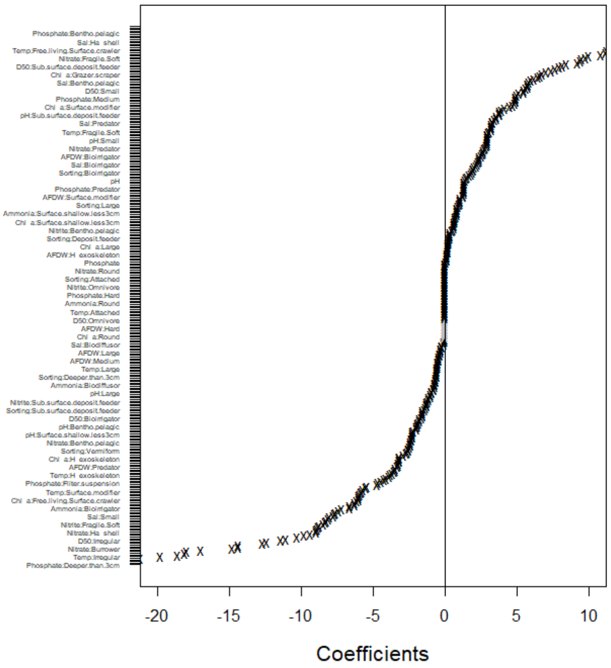


Figure S5. Estimated coefficients for predictors and their confidence intervals for the fourth corner interaction (taxa abundance, traits, and environmental conditions) using NB-GLLVM by site by season: a) Long Beach summer, b) Long Beach winter. Lines represented their 95% confidence interval, black dots denoted intervals not containing zeros (evidence of association between environmental conditions, traits, and taxa abundance), while grey dots denoted intervals containing zeros (no associations).

a) Kellidie Bay summer



b) Kellidie Bay winter

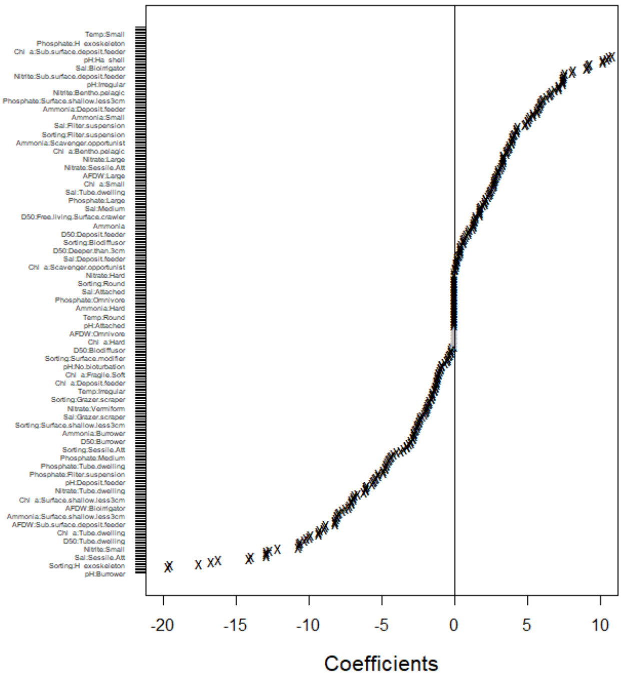
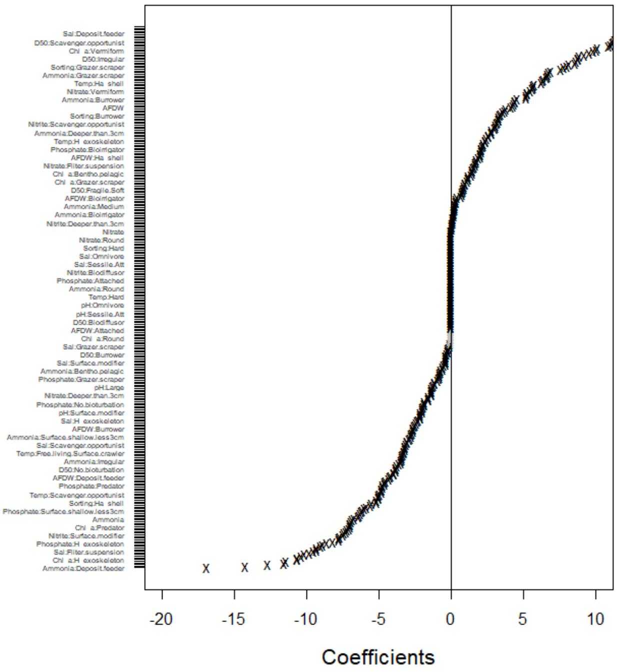


Figure S6. Estimated coefficients for predictors and their confidence intervals for the fourth corner interaction (taxa abundance, traits, and environmental conditions) using NB-GLLVM by site by season: a) Kellidie Bay summer, b) Kellidie Bay winter. Lines represented their 95% confidence interval, black dots denoted intervals not containing zeros (evidence of association between environmental conditions, traits, and taxa abundance), while grey dots denoted intervals containing zeros (no associations).

a) Port Germein summer



b) Port Germein winter

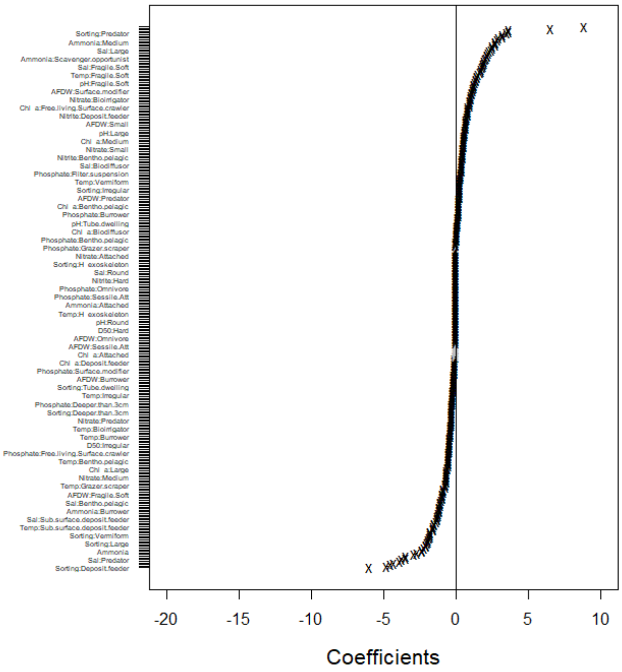
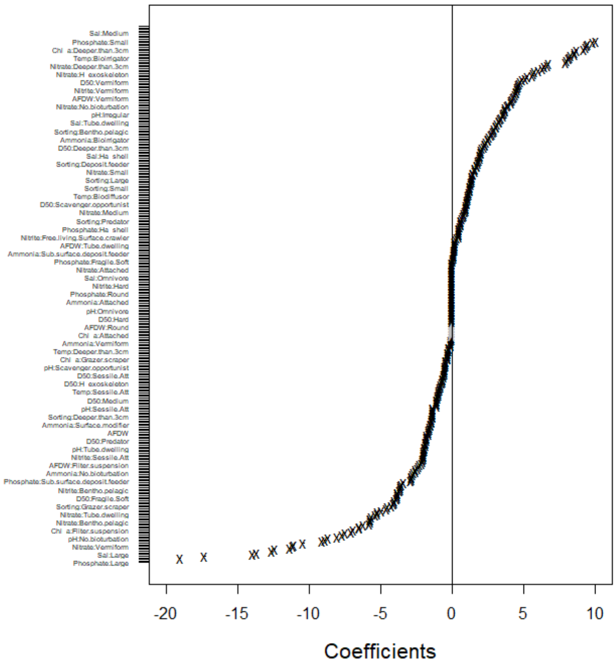


Figure S7. Estimated coefficients for predictors and their confidence intervals for the fourth corner interaction (taxa abundance, traits, and environmental conditions) using NB-GLLVM by site by season: a) Port Germein summer, b) Port Germein winter. Lines represented their 95% confidence interval, black dots denoted intervals not containing zeros (evidence of association between environmental conditions, traits, and taxa abundance), while grey dots denoted intervals containing zeros (no associations).

a) Fisherman Bay summer



b) Fisherman Bay winter

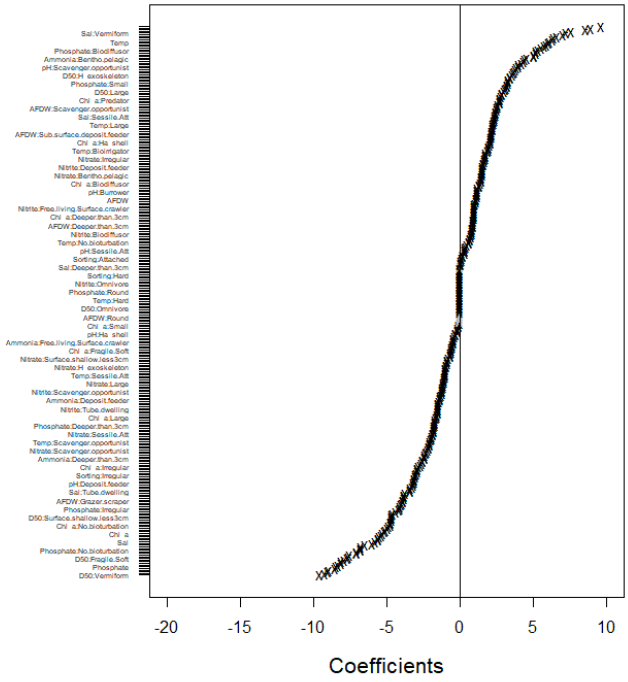
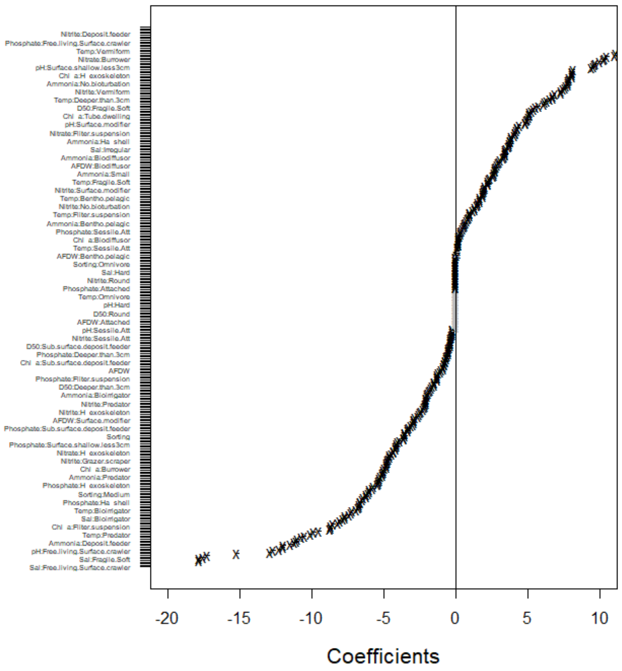


Figure S8. Estimated coefficients for predictors and their confidence intervals for the fourth corner interaction (taxa abundance, traits, and environmental conditions) using NB-GLLVM by site by season: a) Fisherman Bay summer, b) Fisherman Bay winter. Lines represented their 95% confidence interval, black dots denoted intervals not containing zeros (evidence of association between environmental conditions, traits, and taxa abundance), while grey dots denoted intervals containing zeros (no associations).

a) Port Parham summer



b) Port Parham winter

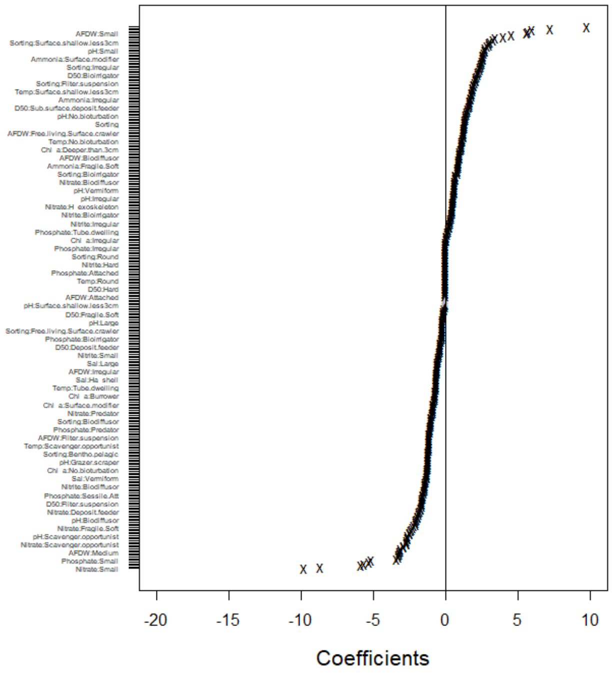
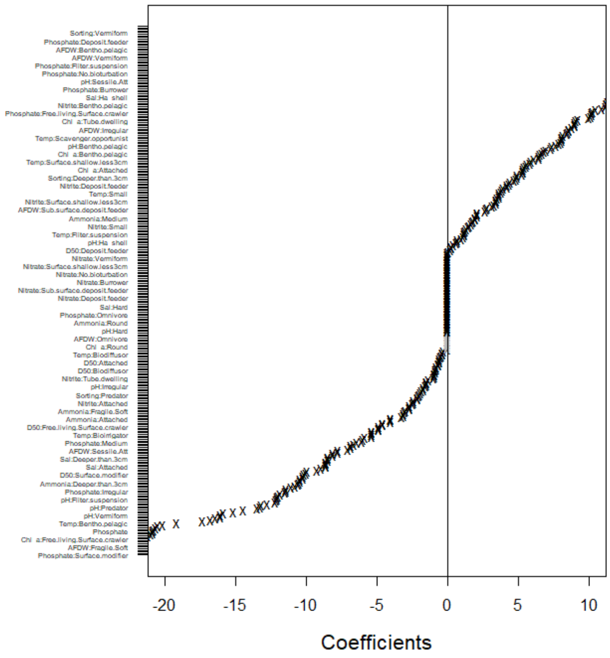


Figure S9. Estimated coefficients for predictors and their confidence intervals for the fourth corner interaction (taxa abundance, traits, and environmental conditions) using NB-GLLVM by site by season: a) Port Parham summer, b) Port Parham winter. Lines represented their 95% confidence interval, black dots denoted intervals not containing zeros (evidence of association between environmental conditions, traits, and taxa abundance), while grey dots denoted intervals containing zeros (no associations).

a) Middle Beach summer



b) Middle Beach winter

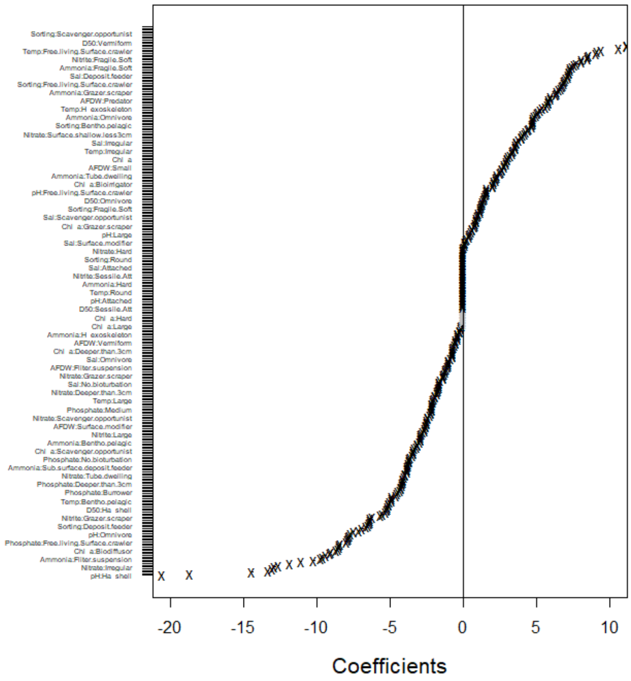
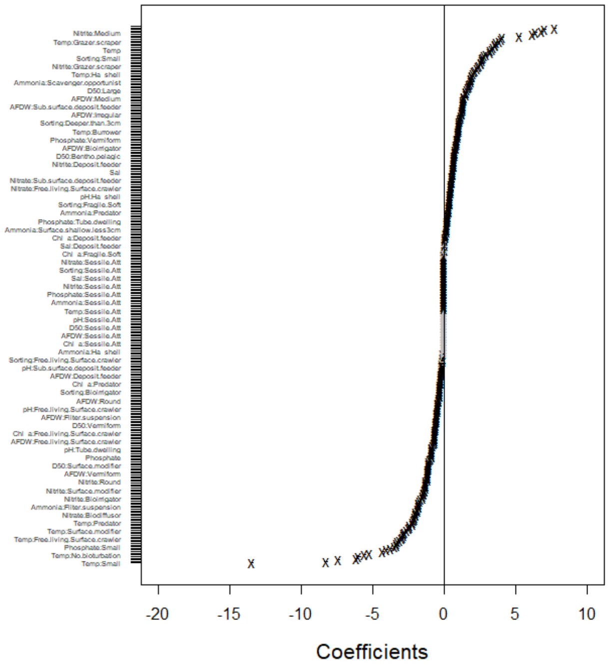


Figure S10. Estimated coefficients for predictors and their confidence intervals for the fourth corner interaction (taxa abundance, traits, and environmental conditions) using NB-GLLVM by site by season: a) Middle Beach summer, b) Middle Beach winter. Lines represented their 95% confidence interval, black dots denoted intervals not containing zeros (evidence of association between environmental conditions, traits, and taxa abundance), while grey dots denoted intervals containing zeros (no associations).

a) Pelican Point summer



b) Pelican Point winter

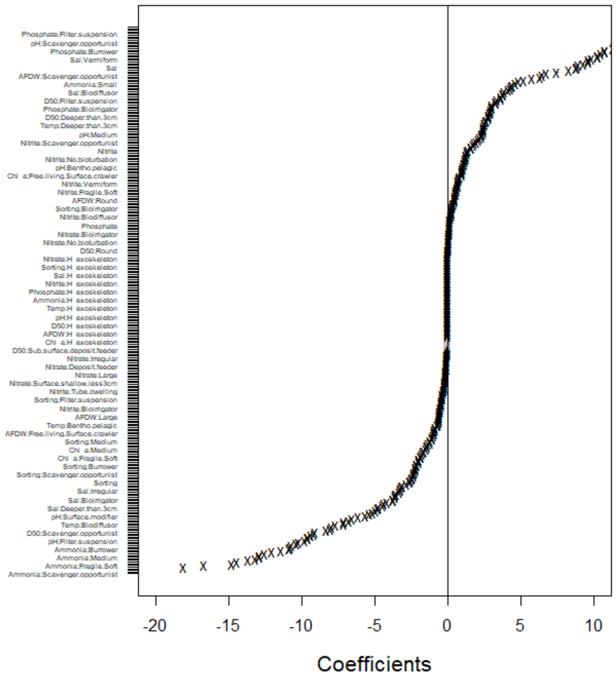
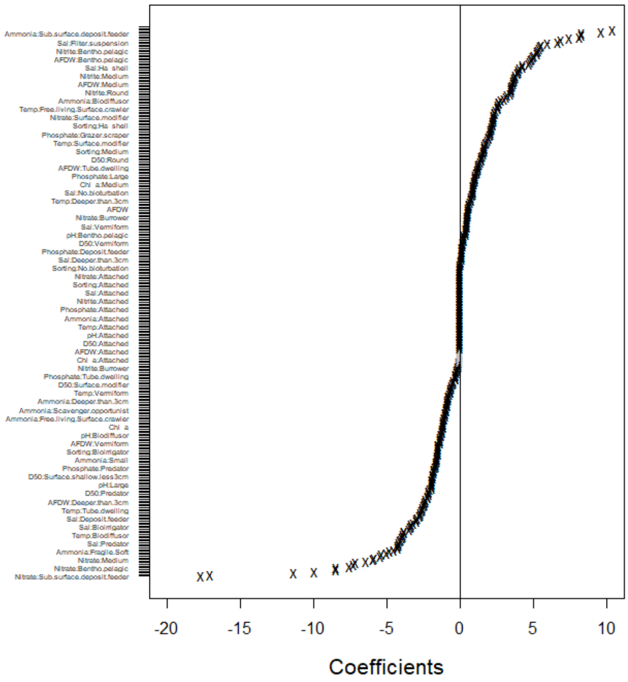


Figure S11. Estimated coefficients for predictors and their confidence intervals for the fourth corner interaction (taxa abundance, traits, and environmental conditions) using NB-GLLVM by site by season: a) Pelican Point summer, b) Pelican Point winter. Lines represented their 95% confidence interval, black dots denoted intervals not containing zeros (evidence of association between environmental conditions, traits, and taxa abundance), while grey dots denoted intervals containing zeros (no associations).

a) Noonameena summer



b) Noonameena winter

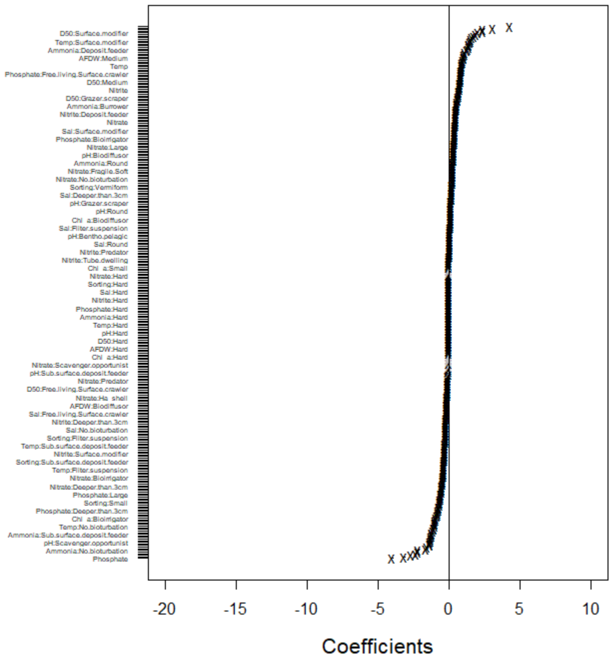


Figure S12. Estimated coefficients for predictors and their confidence intervals for the fourth corner interaction (taxa abundance, traits, and environmental conditions) using NB-GLLVM by site by season: a) Noonameena summer, b) Noonameena winter. Lines represented their 95% confidence interval, black dots denoted intervals not containing zeros (evidence of association between environmental conditions, traits, and taxa abundance), while grey dots denoted intervals containing zeros (no associations).

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Taxonomic and Functional Patterns of Benthic Communities in Southern Temperate Tidal Flats

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Coastal ecosystems are vulnerable to anthropogenic disturbances which can cause loss of benthic macrofauna and their ecosystem functioning. Despite the importance of functional assessments for conservation and management, knowledge gaps persist on the generality of how the diversity and functional traits of benthic communities influence ecosystem functioning. We investigated eight sites in three different habitats across ~1,260 km of coastline, to evaluate patterns between taxonomic and functional diversity of benthic macrofauna, and the relationship between benthic macrofauna, functional traits and environmental conditions. A total of 74 benthic macrofauna taxa were identified. Significant differences across sites and season were found for metrics based on taxonomic and functional traits. Multivariate analysis revealed spatial-temporal differences, which were more evident based on taxa than functional traits. Functional diversity also showed spatial and temporal differences and was positively correlated with the number of taxa. The dominant functional traits modalities were deposit feeders, with large (>20 mm) body size, burrowers, bioirrigators, deeper than 3 cm in sediments, and irregular morphology. Novel Generalized Linear Latent Variable Models (GLLVM) uncovered several site-dependent relationships between taxa, traits and environmental conditions. Functional redundancy was lowest in a highly modified lagoon, and highest in a more pristine embayment. The outcomes from this study showed site-dependent patterns of benthic communities based on either taxonomic or functional metrics, highlighting that both perspectives are complementary to obtain a holistic understanding of the functioning in marine sediments under environmental change.

Keywords: Australia, functional traits, ecosystem functioning, macroinvertebrates, GLLVM

INTRODUCTION

Benthic macrofauna are major providers of ecosystem functioning in marine habitats. They modify soft-sediment habitats through biological processes such as ingestion, digestion, excretion, and bioturbation, which facilitates microbial recycling of nutrients, detoxification of pollutants, and organic matter remineralization (Snelgrove et al., 2014; Shojaei et al., 2015; Caswell et al., 2018; Wyness et al., 2021). Benthic macrofauna also represent a connection between benthic and pelagic ecosystems, and plays an important role in energy transfer to different trophic levels (Pearson and Rosenberg, 1978; Kristensen et al., 2014; Murillo et al., 2020). Furthermore, benthic macro-organisms are often used as bioindicators to assess ecosystem "health" due to their sensitivity to natural and anthropogenic disturbances (Borja et al., 2000; Tweedley et al., 2015).

Descriptive and experimental approaches have highlighted that benthic communities are structured by environmental factors (e.g., temperature, water depth, salinity, sediment type, habitat complexity), biological processes (e.g., competition, predation, bioturbation), and ecosystem engineering by benthic macrofauna (e.g., Reise, 1985; Honkoop et al., 2006; Meadows et al., 2012). These traditional taxonomic-based studies laid the base for functional assessments of benthic fauna (Snelgrove, 1997; Thrush et al., 2006; Snelgrove et al., 2014), which allow the understanding of how changes in benthic biodiversity influence the functioning of an ecosystem. Functional approaches have been increasingly explored to comprehensively understand effects of the alarming loss of biodiversity in terrestrial and marine ecosystems (de Juan et al., 2015; Degen et al., 2018; Gammal et al., 2019; van der Plas, 2019). For benthic communities, the use of functional approaches is a powerful tool to investigate Biodiversity and Ecosystem Functioning relationships (BEF), and how these relationships vary spatially and temporally, or under specific environmental conditions (Baldrighi et al., 2017; Beauchard et al., 2017).

Ecosystem functioning, defined as the combined effects of all natural processes that sustain an ecosystem (Reiss et al., 2009; Gladstone-Gallagher et al., 2017; Degen et al., 2018), is commonly analyzed by using Functional Diversity (FD) measurements. Functional Diversity considers the variation of functional traits occurring across ecological communities of a given ecosystem based on the activities of organisms (e.g., movement, behavior, feeding and reproduction; Díaz and Cabido, 2001; Reiss et al., 2009; Beauchard et al., 2017; Degen et al., 2018). Several indices have been used to quantify functional diversity, however, there is a lack of consensus on which index is the most appropriate (Mason et al., 2005; Villeger et al., 2008; Mouchet et al., 2010; Lam-Gordillo et al., 2020a).

Functional diversity is usually split into at least three components: functional richness, evenness, and divergence (Mason et al., 2005; Villeger et al., 2008), with several other components recently added (e.g., functional dispersion and functional redundancy) (Laliberté and Legendre, 2010; van der Linden et al., 2012; Gammal et al., 2020). Functional diversity, and all its main components, are based on the analysis of functional traits and their modalities (e.g., bioturbation, body size, feeding mode, morphology, living habit, sediment position), where species are clustered into groups with shared physiological and morphological attributes (Bremner et al., 2003, 2006). The functional traits and their modalities studied can be selected in accordance with the processes of interest, the ecosystem type, and the spatial and temporal scale of study (Hooper et al., 2005; Wright et al., 2006; Bremner, 2008; Beauchard et al., 2017).

Functional metrics, which are based on functional traits, can be more important to explain ecological processes and ecosystem functioning than taxonomic metrics (Belley and Snelgrove, 2016; Mestdagh et al., 2020). Yet, considering both approaches can provide a more robust and holistic knowledge about the structure of benthic communities and functioning of ecosystems. Recent investigations have applied a combination of taxonomic and functional approaches to understand the influence of benthic macrofauna on ecosystem functioning and support management and conservation efforts (e.g., Hajializadeh et al., 2020; Delfan et al., 2021; Nunes de Souza et al., 2021; Shojaei et al., 2021). Results from taxonomic and functional approaches have been similar (e.g., van der Linden et al., 2012; Wong and Dowd, 2015; Hajializadeh et al., 2020), but distinct patterns based on either taxonomic or functional diversity emerged as well (e.g., Emmerson et al., 2001; Kraan et al., 2013; Frid and Caswell, 2015; Gladstone-Gallagher et al., 2017). These different patterns could result from highly variable relationships between taxonomic and functional diversity subject to the environmental context (Gladstone-Gallagher et al., 2017; Thrush et al., 2017; Gammal et al., 2019), and from presence of key benthic macrofauna functional groups, that is often more important than species diversity *per se* (Norkko et al., 2013; Thomas et al., 2020).

Despite the importance of functional assessments for conservation strategies (Miatta et al., 2021) and to inform policy and management to ensure healthy coastal ecosystems, several uncertainties still persist in the interpretation and potential use of the outcomes from trait-based and functional approaches in future scenarios of biodiversity loss in coastal ecosystems. Such uncertainties can be reduced with greater understanding of how taxonomic diversity and functional traits present in benthic communities influence ecosystem functioning across different habitats. For example, low functional redundancy can be used to indicate habitats vulnerable to functional loss.

To contribute to the knowledge on patterns of taxonomic and functional diversity and their links with ecosystem functioning (e.g., Gammal et al., 2019; Taupp and Wetzel, 2019; Shojaei et al., 2021), this study investigated benthic communities in soft sediments along the southern temperate coast of South Australia, where traits of benthic fauna have been recently compiled (Lam-Gordillo et al., 2020b), which enabled a comparative assessment of taxonomic and functional perspectives. The aims of this field study were to (i) assess the taxonomic and functional diversity of benthic communities across contrasting habitats (coastal embayment, gulfs, and lagoon), each representing a typical habitat of the southern temperate Australian coastline, and (ii) evaluate the relationships between benthic macrofauna, functional traits and environmental conditions across these habitats. Over two seasons, benthic macrofauna, their functional traits and environmental conditions were assessed in each habitat to provide a comprehensive analysis on their patterns and relationships. It was predicted that (1) taxonomic and functional patterns are distinct across the studied habitats, (2) functional diversity is greater within habitats with a greater number of taxa, and (3) the relationships between taxa, traits and environmental conditions are habitat-specific.

MATERIALS AND METHODS

Study Area

The southern Australian coast is the longest east-west temperate coastline in the southern hemisphere, and harbors diverse sedimentary habitats (Short, 2020). The benthic sampling was conducted across eight sites in South Australia, covering three contrasting habitats of this coastline: a coastal embayment (Coffin Bay: Long Beach—LB, Kellidie Bay—KB), gulfs

(Spencer Gulf: Port Germein—PG, Fisherman Bay—FB, Gulf St Vincent: Port Parham—PPa, Middle Beach—MB), and lagoon (Coorong: Pelican Point—PP, Noonameena—N) (**Figure 1**; **Table 1**).

Data Collection and Laboratory Procedures

Benthic samples were collected in July 2019 (Austral winter) and January 2020 (Austral summer) at the eight tidal flat sites. South

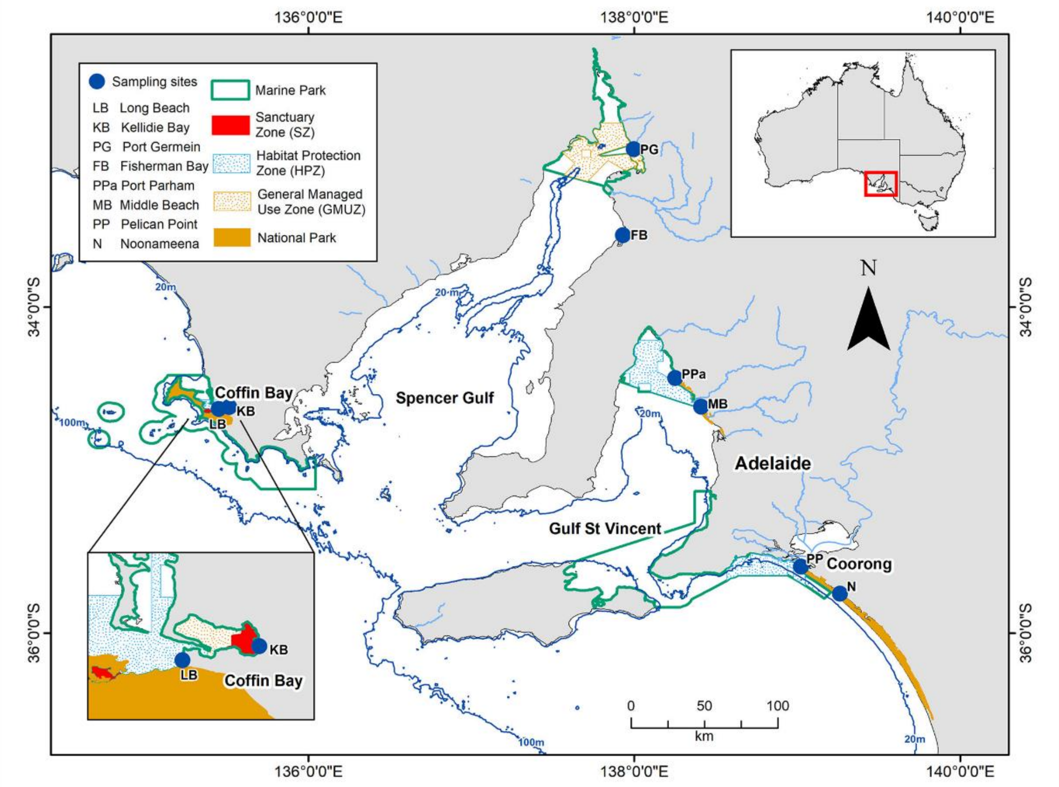

FIGURE 1 | Map of the study area showing the eight sites across South Australia from where benthic macrofauna samples were collected. The dark blue lines indicate depths at 20 and 100 m, and the light blue lines indicate the rivers.

TABLE 1 | Main habitat characteristics of the eight sampling sites across southern Australia.

Site	Habitat (Geomorphology)	Protection status	Region	Sediment description	Width (m)
Long Beach	Coastal embayment	Habitat Protection Zone	Coffin Bay	Fine sand, moderately well-sorted	~100
Kellidie Bay	Coastal embayment	Sanctuary Zone	Coffin Bay	Fine sand, poorly sorted	~100
Port Germein	Gulf	General Managed Use Zone	Upper Spencer Gulf	Fine sand, poorly sorted	~1000
Fisherman Bay	Gulf	None	Upper Spencer Gulf	Medium sand, poorly sorted	~200
Port Parham	Gulf	Habitat Protection Zone	Upper Gulf St Vincent	Fine sand, poorly sorted	~500
Middle Beach	Gulf	Habitat Protection Zone	Upper Gulf St Vincent	Coarse sand, poorly sorted	~500
Pelican Point	Lagoon	Habitat Protection Zone / National Park / Ramsar site	Coorong	Medium sand, poorly sorted	~200
Noonameena	Lagoon	National Park / Ramsar site	Coorong	Fine sand, moderately sorted	~500

Sediment description based on Folk and Ward (1957) geometric description. Width (m) refers to the extension of the mudflats from high to low tide mark.

Australia has a Mediterranean climate, with dry summers and winter rain. January is the warmest month of the year with an average air maximum temperature of 29.6°C, while the coldest month is July with a minimum temperature average of 7.6°C (Bureau of Meteorology, 2021). All sampling occurred at low tide when tidal flats were exposed and accessible from shore. Tides in South Australia are of a unique mixed tidal pattern with tidal range varying from micro-tidal (Coffin Bay, Coorong) to mesotidal (gulfs). The samples for benthic macrofauna were taken using a handheld PVC corer (83.32 cm^2 surface area), pushed it into the sediment up to 20 cm depth, with 15 replicates haphazardly taken per site. All sediment samples were sieved through 500 µm mesh size in the field and preserved in 70% ethanol until further processing. In the laboratory, samples were sorted and all benthic macrofauna were identified to the lowest possible taxonomic level (i.e., 66.2% to Species, 4.1% to Genus, 28.4% to Family, and 1.4% to Order), and counted.

At each sampling site, environmental conditions known for influencing the abundance, composition and distribution of benthic communities were measured (Hillebrand and Matthiessen, 2009; Dutertre et al., 2013; Dittmann et al., 2015; Shojaei et al., 2015). Water temperature (°C), salinity, and pH were recorded in the water overlying the mudflat, using a Hannah HI98194 multiparameter meter. Sediment samples were taken for analyzing Chlorophyll-*a* (g/m^3), total organic matter content (OM%) and sediment grain size. In addition, sediment pore water was collected for analyzing nutrients (Nitrate, Nitrite, Ammonium and Phosphate). Fifteen replicate samples for each environmental parameter were taken at each site within the same area where the sediment samples for benthic fauna were collected.

Chlorophyll-*a* (g/m^3) was determined using a spectrophotometer (Thermo Scientific, Spectronic 200) following the protocols described by Ritchie (2008). The organic matter (OM%) content in sediment was determined by loss on ignition, first drying the sediment to constant weight, followed by burning in a furnace at 450°C for 5 h. Grain size was determined by laser diffraction using a particle size analyser (Malvern Mastersizer 2000). Average values for grain size fractions for each site were entered into the GRADISTAT program v8.0 (Blott and Pye, 2001) to obtain the median (D50 µm) and coefficient (sorting σG). Nutrient concentrations (mg/L) of Nitrate (NO_3-), Nitrite (NO_2-), Ammonium (NH_3) and Phosphate (PO_4^{3}-) were determined using a Skalar SAN ++ SFA segmented flow analyser.

Data Analysis

Environmental Data Analysis

Environmental data were square root transformed as needed to approximate normality (except OM, pH and salinity), and then normalized prior to multivariate analysis (Clarke et al., 2014). Spearman correlation (**Supplementary Figure 1**) and variance inflation factors with a cut-off <3 (VIF) (**Supplementary Table 1**) were analyzed for collinearity among variables and, as no redundant environmental variable was identified, all were included in the analyses. To test for differences between sites and season, univariate PERMutational ANalysis Of VAriance (PERMANOVA) and multiple pair-wise tests were conducted, using Euclidean distance for the single variables in PRIMER v7 with PERMANOVA+ add on software (Anderson et al., 2008). Principal Component Analyses (PCA) were performed separately for summer and winter data to explore spatial and temporal patterns. R software (R Core Team, 2017) and the packages "corrplot" (Wei and Simko, 2017), "fmsb" (Nakazawa, 2019), "vegan" (Oksanen et al., 2019), were used for conducting the analyses.

Selection of Traits and Trait Information

A suite of six functional traits and 29 trait-modalities (**Table 2**) were selected. The functional traits selected describe behavioral, morphological, and physiological attributes of benthic macrofauna, and are considered as effects traits as they are directly or indirectly related to several ecosystem functions including nutrient cycling and sediment transport (Lam-Gordillo et al., 2020a). Trait information was obtained from the South Australia Macrobenthic Trait (SAMT) database (Lam-Gordillo et al., 2020b). The SAMT database applied a fuzzy

TABLE 2 | Traits and traits-modalities selected.

Traits	Traits modalities	Acronym
Bioturbator	Biodiffusor	Bdiff
	Bioirrigator	Birrig
	No bioturbation	Nbio
	Surface modifier	Surmo
Body size	Large (>20 mm)	Lar
	Medium (5–20 mm)	Med
	Small (0.5–5 mm)	Sma
Feeding mode	Deposit feeder	Defe
	Filter/suspension	Fisus
	Grazer/scraper	Graz/Sc
	Omnivore	Omn
	Predator	Pred
	Scavenger/opportunist	Scav
	Sub-surface deposit feeder	Ssdefe
Morphology	Hard	Hard
	Hard exoskeleton	Haexosk
	Hard shell	Hashell
	Irregular	Irreg
	Round	Round
	Soft / Fragile	Frag/Sof
	Vermiform	Verm
Living habit	Attached/Sessile	Att/S
	Burrower	Burr
	Free living / Surface crawler	Free
	Tube dwelling	Tubdw
Sediment position	Attached	Att
	Bentho-pelagic	Be-pel
	Deeper than 3 cm	Deep
	Surface shallow <3 cm	Surfsh

Acronyms are used in ***Figure 4****.*

coding procedure assigning scores from 0 to 1, with 0 being no affinity and 1 being high affinity to a trait (for details see Lam-Gordillo et al., 2020b). This resulted in the compilation of three data matrices (1) "taxa abundance by site matrix," in this case the data collected from our surveys; (2) "taxa by traits matrix," obtained from the SAMT database; and (3) the combinations of the previous two: "traits by site matrix" (Bremner et al., 2006; Bremner, 2008).

Taxonomic and Functional Analysis

The benthic macrofauna was analyzed for traditional diversity metrics, including the analysis of taxonomic richness (S), Shannon index (H'; log e) and Pielou's evenness (J') for each site and season using the package "vegan" (Oksanen et al., 2019). For the functional diversity (FD) analyses, the benthic abundance data (taxa abundance by site matrix) were log $(1 + x)$ transformed to reduce the influence of dominant taxa without losing the abundance effect. To compare the FD across sites and seasons, the following functional metrics were calculated as a proxy of FD. (i) Functional Richness (FRic), provides the amount of functional space occupied by a community (Mason et al., 2005), i.e., the quantity of traits that are expressed in a habitat. (ii) Functional Evenness (FEve), describes how consistently the taxa abundance is distributed across the expressed traits (Mason et al., 2005). (iii) Functional Redundancy (FR), describes the ratio between FD and H', when the ratio decreases, FR increases and *vice versa* (van der Linden et al., 2012), providing information on how common the expressed traits are within a habitat. In addition, community-level weighted means of trait values (CWM) were calculated to compare trait expression across the sites and seasons. Functional metrics and CWM were calculated using the package "FD" (Laliberté et al., 2014) in R software (R Core Team, 2017).

Statistical Analysis

To elucidate spatial (sites) and temporal (seasons) patterns for each taxonomic (e.g., S, abundance, H', J'), functional metric (FRic, FEve, Fdis, FR) and CWM, univariate PERMANOVA were used with Euclidean distance for the single variables, permutation of residuals under a reduced model, sums of squares type III and 9999 permutations (Anderson et al., 2008). In addition, multiple pair-wise tests were conducted if fixed factors (sites, seasons) or interactions (sites x season) were significant to identify which groupings contributed to differences from PERMANOVA main tests. To assess community structure differences between sites and seasons, Principal Coordinates Ordination (PCO) were performed for the taxonomic and trait data. Species density (taxa abundance) was fourth root transformed, and in both taxa and trait data, a Bray-Curtis similarity resemblance was applied. To assess the relationship between functional metrics and environmental conditions, non-parametric multiple regressions were performed with the DISTLM routine, using Euclidean distances and 9999 permutations (McArdle and Anderson, 2001). PERMANOVA, pair-wise tests, PCO and DISTLM analysis were carried out using PRIMER v7 with PERMANOVA add on. To elucidate the direction of the relationships, multiple Spearman correlation analyses were performed using the R package "ggpubr" (Kassambara, 2020).

For assessing the response of benthic taxa and functional traits to the environmental predictor variables (fourth corner analysis), several generalized linear latent variable models (GLLVMs) were performed with the R package "gllvm" (Niku et al., 2020). GLLVM extends the basic GLM, handles overdispersion data, includes latent variables to capture the correlation between species, and considers fourth-corner terms to account for species-traits- environment- interactions (Niku et al., 2020, 2021).

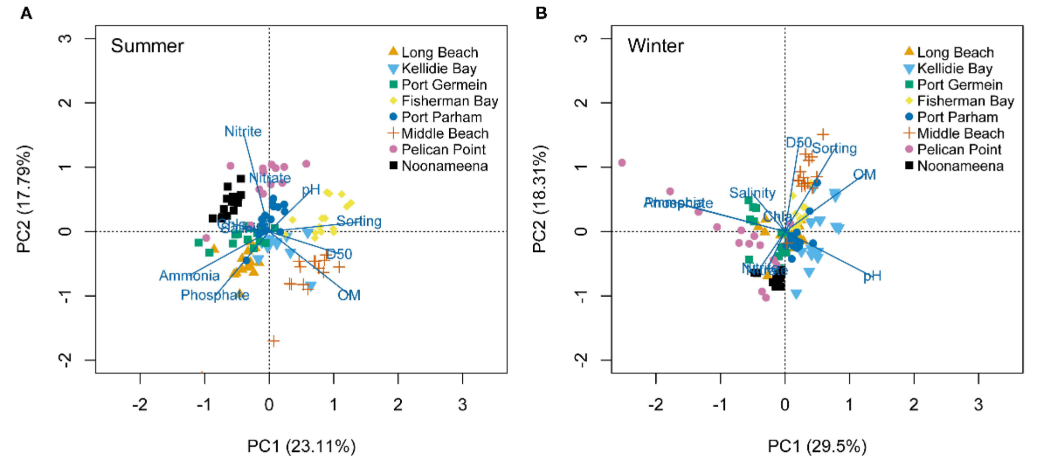

FIGURE 2 | Principal Component Analysis (PCA) on the environmental conditions measured at the eight sites across South Australia, in the seasons: **(A)** Summer, and **(B)** Winter.

Further, the fourth-corner approach includes regression of the multivariate abundance against the function of the trait and environment association (Niku et al., 2019). GLLVMs were constructed for fitting multivariate data using a negative binomial distribution as the best fit model (lowest Akaike information criterion—AIC; **Supplementary Table 2**) (Niku et al., 2019). Level plots were performed for visualizing the interactions between taxa-traits and environmental variables obtained with the GLLVMs using the R package "lattice" (Sarkar, 2008).

RESULTS

Environmental Conditions

The environmental conditions varied across sites and seasons (PERMANOVA $p < 0.01$, **Supplementary Figure 2**; **Supplementary Table 3**). In general, hypersaline conditions were recorded at the gulfs (PG, FB) and lagoon (N) habitats in summer. Sediment grain size (D50 and sorting) was mostly characterized by fine sand at the coastal embayment (LB, KB) and lagoon (N), while the gulfs (FB, MB) had medium to coarse sand. The PCA analyses showed spatial and temporal variation (summer: 40.9%, winter: 47.81% of variability explained by the first two axes) (**Figure 2**). In summer, porewater nutrients separated the lagoon habitat located in the Coorong (N, PP) based on Nitrate and Nitrite, and LB and PG based on Ammonium and Phosphate. MB had larger sediment grain size (D50, sorting) and higher sediment organic matter (**Figure 2A**). In winter, higher porewater nutrient concentrations also separated sites from the Coorong (PP, N due to nitrous oxides), and MB was separated again by sediment grain size (D50, Sorting) and organic matter (**Figure 2B**).

Abundance of Benthic Macrofauna

The average abundance recorded was 18,255 (±1,676 SE) ind.m^{-2} across the sampling sites in South Australia. Annelida was the phylum with the greatest abundance overall (44%), followed by Mollusca (41%) and Arthropoda (15%) (**Supplementary Table 4**). The most abundant polychaete families were Capitellidae (mean: 5,588 ind.m^{-2} ± 1,091 SE) and Nereididae (mostly *Simplisetia aequisetis* mean: 1,340 ind.m^{-2} ± 291 SE). *Arthritica semen* (mean: 3,104 ind.m^{-2} ± 628 SE) and *Salinator fragilis* (mean: 2,205 ind.m^{-2} ±288 SE) contributed most to the abundance of Mollusca, while the most abundant arthropods were amphipods (1,536 ind.m^{-2} ± 466 SE). The total individual densities were significantly different across sites and seasons (PERMANOVA $p = 0.0001$; **Table 3**), with significantly higher individual densities at the Coorong lagoon (PP and N), compared to the other six sites ($p < 0.01$; **Supplementary Table 4**; **Supplementary Figure 3B**).

Taxonomic and Functional Assessment of Benthic Macrofauna

In total, 74 taxa were found across eight sites in South Australia, belonging to six different phyla. Mollusca was the phylum with the highest number of taxa (42%, 31 taxa), followed by Arthropoda (31%, 23 taxa), and Annelida (23%, 17 taxa), while Cnidaria, Echinodermata and Nemertea were represented by only one taxon each (1.4%) (**Supplementary Table 5**). The taxonomic metrics (species richness, H', J') showed the highest mean values in the coastal embayment habitats (LB, KB) at Coffin Bay, and the lowest mean values in the lagoon (PP, N) at the Coorong (**Figure 3**). Significant differences between sites and seasons (i.e., the warmest and coldest moth) were found for all three taxonomic metrics (PERMANOVA $p = 0.0001$; **Table 3**). The number of taxa was higher in summer than winter at all the sites (**Figure 3A**). In pairwise comparisons between sites, significant differences in the number of taxa were found for PG and N compared to the other five sites, but only in winter ($p < 0.01$; **Supplementary Figure 3A**). The Shannon diversity index ranged from 0 to 1.99, with greater values in summer at the coastal embayment habitats (LB, KB), and one site in

TABLE 3 | Test results from univariate one-way fixed factor PERMANOVA to compare number of taxa (richness), abundance, Shannon diversity index (H'), Pielou's evenness index (J'), Functional: Richness, Evenness, and Redundancy across sites and seasons.

	df	MS	Pseudo-*F*	*P*-value
Number of taxa				
Site	7	61.75	21.47	**0.0001**
Season	1	234.04	81.35	**0.0001**
Site x Season	7	21.54	7.49	**0.0001**
Residual	224	2.88		
Abundance (ind.m^{2})				
Site	7	1.19E + 10	87.46	**0.001**
Season	1	1.13E + 10	83.03	**0.001**
Site x Season	7	5.19E + 09	38.22	**0.001**
Residual	224	1.36E + 08		
H'				
Site	7	2.79	34.83	**0.0001**
Season	1	0.25	3.08	0.0828
Site x Season	7	0.86	10.72	**0.0001**
Residual	224	0.08		
J'				
Site	7	0.46	29.56	**0.0001**
Season	1	0.35	22.56	**0.0001**
Site x Season	7	0.17	11.12	**0.0001**
Residual	224	0.02		
Functional Richness				
Site	1	374.48	14.39	**0.0001**
Season	7	2589.50	99.52	**0.0001**
Site x Season	7	26.01	6.99	**0.0001**
Residual	224	26.018		
Functional Evenness				
Site	1	0.36	8.65	**0.0001**
Season	7	0.13	3.19	0.0761
Site x Season	7	0.26	6.32	**0.0001**
Residual	224	0.04		
Functional Redundancy				
Site	1	309.42	21.04	**0.0001**
Season	7	118.34	8.04	**0.0018**
Site x Season	7	110.34	7.50	**0.0001**
Residual	224	14.70		

Significant differences are shown in bold.

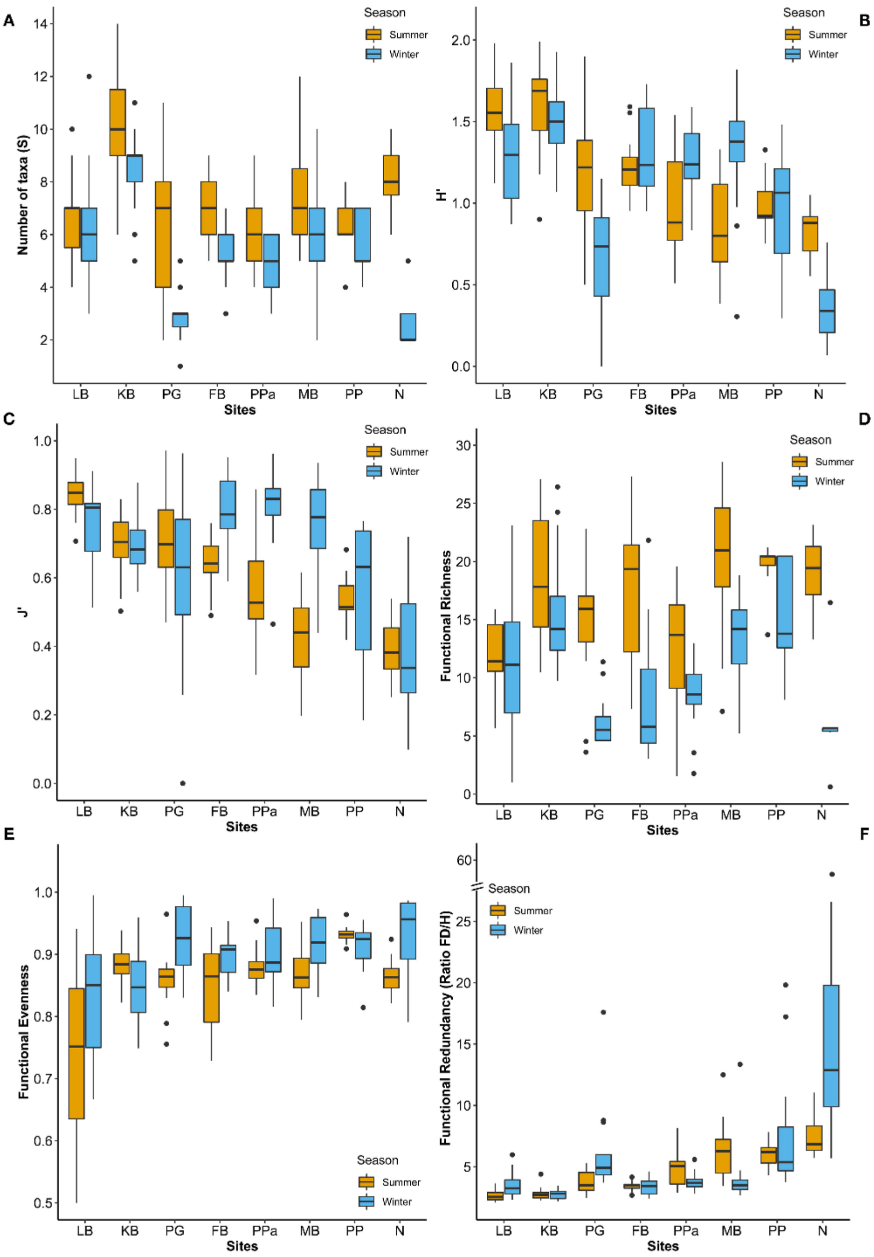

FIGURE 3 | Box plots of **(A)** number of taxa (S), **(B)** Shannon diversity index (H'), **(C)** Pielou's evenness index (J'), **(D)** Functional Richness, **(E)** Evenness, and **(F)** Redundancy across sites and seasons. LB, Long Beach; KB, Kellidie Bay; MB, Middle Beach; PPa, Port Parham; PG, Port Germein, FB, Fisherman Bay; PP, Pelican Point; N, Noonameena.

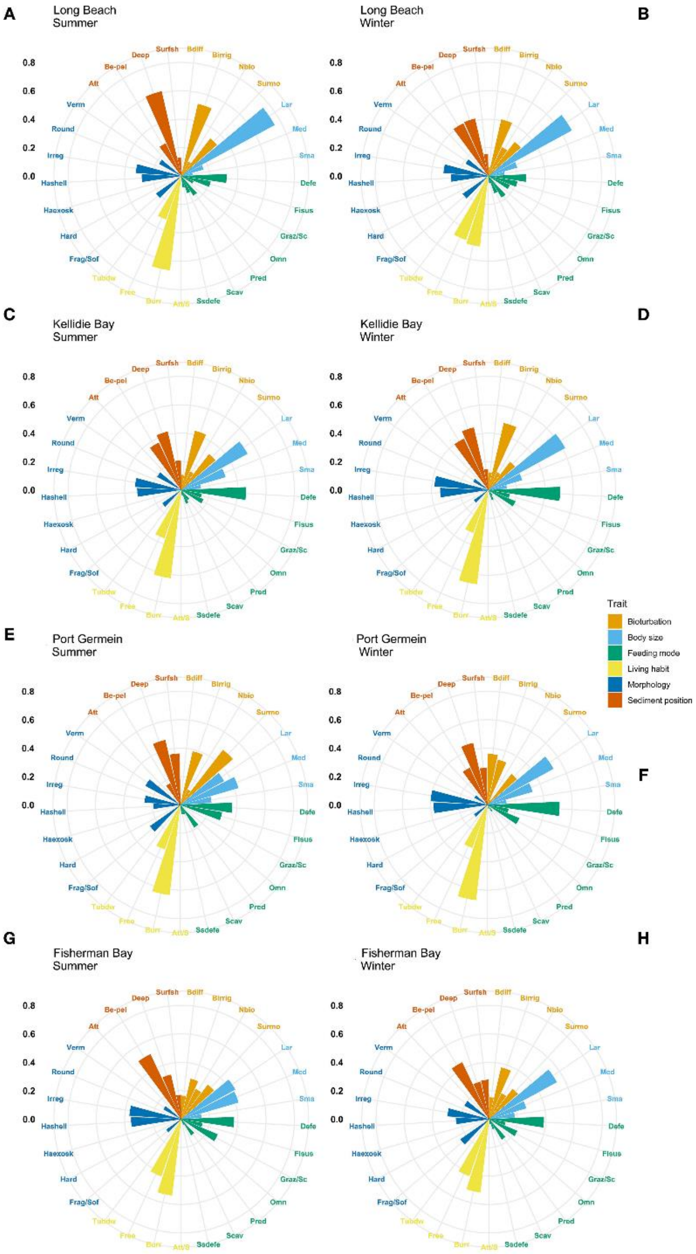

FIGURE 4 | Community-weighted means (CWM) of trait-modalities expression. Scale represents the percentage contribution to CWM. Trait modalities labels (acronyms) are defined in **Table 2**. Long Beach **(A)** summer, **(B)** winter; Kellidie Bay **(C)** summer, **(D)** winter; Port Germein **(E)** summer, **(F)** winter; Fhiserman Bay **(G)** summer, **(H)** winter.

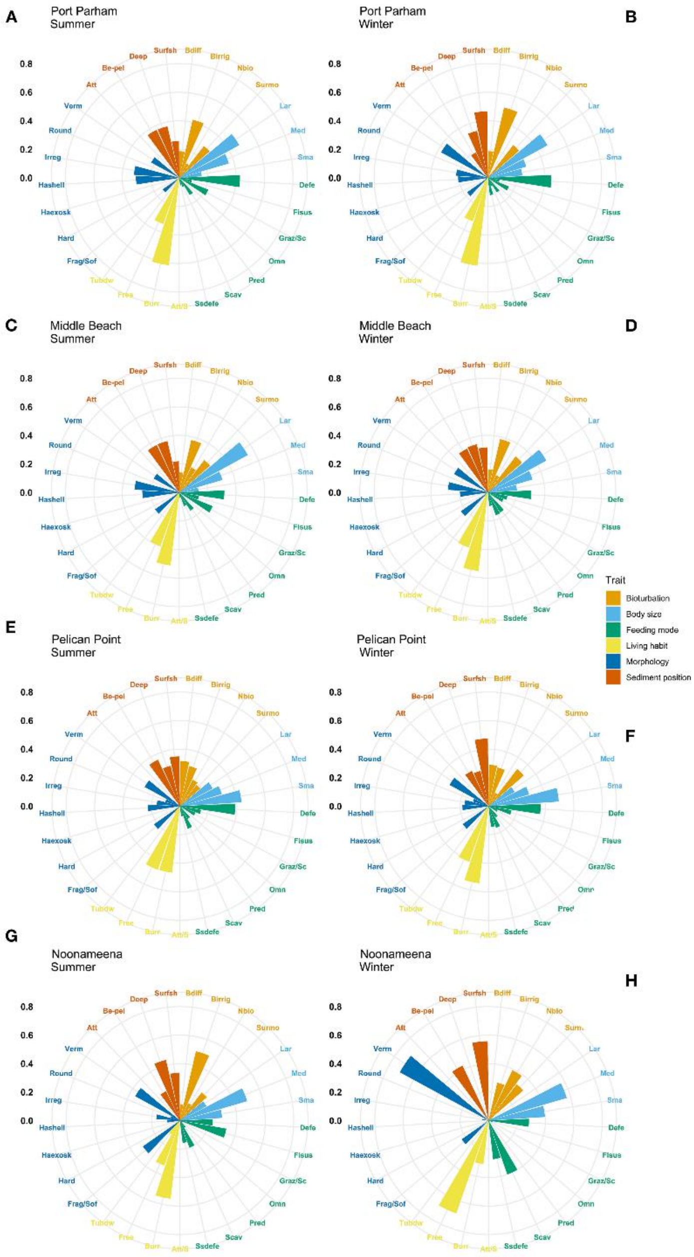

FIGURE 5 | Community-weighted means (CWM) of trait-modalities expression. Scale represents the percentage contribution to CWM. Trait modalities labels (acronyms) are defined in Table 2. Port Parham **(A)** summer, **(B)** winter; Middle Beach **(C)** summer, **(D)** winter; Pelican Point **(E)** summer, **(F)** winter; and Noonameena **(G)** summer, **(H)** winter.

the gulfs (PG) and lagoon (N) habitat respectively (**Figure 3B**). In pairwise comparisons, the majority of the sites were distinct from each other ($p < 0.01$; **Supplementary Figure 3C**), apart from the two coastal embayment habitats in Coffin Bay. Pielou's evenness index ranged from 0 and 0.97, following the same patter as H', with greater values at the coastal embayment habitats in summer (**Figure 3C**). In pairwise comparisons, LB and N were significantly different to the other sites ($p < 0.01$; **Supplementary Figure 3D**).

The most expressed functional trait modalities in the studied benthic communities, based on community-level weighted means (CWM) analyses of trait values, were deposit feeder (feeding mode; contribution: 0.37%), large (>20 mm) body size (contribution: 0.44%), burrower (living habit; contribution: 0.56%), bioirrigator (bioturbation; contribution: 0.56%), sediment position of deeper than 3 cm (contribution: 0.36%), and irregular morphology (contribution: 0.27%) (**Figure 4**). The CWM values of each compiled functional trait varied significatively across all sites and seasons (**Table 4; Figures 4, 5**). Most of the CWM trait modalities showed significant differences across sites, except for the trait modalities omnivore and hard exoskeleton. In contrast, significant differences across seasons were less evident for trait modalities (**Table 4**). In pairwise comparisons, significant differences in CWM trait modalities were also observed among sites and seasons (**Figures 4, 5; Table 5**, **Supplementary Table 6**). For example, the functional trait feeding mode showed significant differences in all the trait-modalities at the lagoon habitat (N) compared to all other sites (**Supplementary Table 6**), and the trait modality sub-surface deposit feeder (feeding mode) and surface shallow <3 cm (Sediment position) were significantly different in summer and winter in six of the eight sites analyzed (**Table 5**).

Functional Richness (FRic), Functional Evenness (FEve), and Functional Redundancy (FR) varied significantly across sites (PERMANOVA $p = 0.0001$; **Table 3**). However, FEve was the only metric not significantly different across season (**Table 3**). The greatest FRic values were found in summer at all sites, with greatest FRic values in the gulf habitat at Upper Gulf St Vincent (**Figure 3D**). In contrast, the greatest values of FEve were found in winter at the gulf (PG, PPa), and lagoon (N) habitats. In terms of FR (ratio FD/H'), the greatest values were recorded at the two lagoon habitats in the Coorong, showing the lowest functional redundancy (**Figures 3E,F**). Functional diversity, as FRic, was significant and positively correlated with the number of taxa ($R^2 = 0.64$, $p < 0.01$, **Figures 6A,B**). The ratio of FD/H' (i.e., FR) showed a significant but weak negative relationship with the number of taxa ($R^2 = 0.13$, $p < 0.01$, **Figures 6C,D**). Also, a significant but weak, positive relationship was identified between FEve and the number of taxa ($R^2 = 0.17$, $p < 0.01$, **Figures 6E,F**). DISTLM analyses revealed that FRic, FEve and FR were mostly influenced by Ammonium, Chlorophyll *a*, sediment grain size (D50), sorting, sediment organic matter content, Nitrite and temperature (**Table 6**).

Community Analyses of Benthic Macrofauna and Functional Traits

Significant community differences were detected between sites and seasons for both taxa and functional traits (PERMANOVA $p = 0.0001$, **Table 7**). The PCO analysis revealed distinct communities across sites and seasons with 47.7% of the variability in taxa composition, and 64.3% of the variability in trait composition (**Figure 7**). Based on taxa, sites in the Coorong lagoon (PP, N) were separated from other sites, while the gulfs habitats were more closely grouped. A separation according to season was found in KB, FB and PG (**Figure 7A, Supplementary Figure 4A**). Less distinction emerged based on traits with the most evident seasonal separation in PG and N (**Figure 7B, Supplementary Figure 4B**).

TABLE 4 | Summary of the test results from univariate one-way fixed factor PERMANOVA to CWM trait modalities across sites and seasons.

Trait	Trait modality	Site	Season	Site x Season
Bioturbator	Biodiffusor	**0.0001**	**0.0001**	**0.0001**
	Bioirrigator	**0.0001**	0.0964	**0.0001**
	No bioturbation	**0.0001**	0.8628	**0.0001**
	Surface modifier	**0.0001**	0.3006	**0.0001**
Body size	Large (>20 mm)	**0.0001**	0.8339	**0.0001**
	Medium (5–2 0mm)	**0.0001**	**0.0002**	**0.0001**
	Small (0.5–5 mm)	**0.0001**	**0.0001**	**0.0001**
Feeding mode	Deposit feeder	**0.0001**	0.0109	**0.0001**
	Filter/suspension	**0.0001**	**0.0010**	**0.0001**
	Grazer/scraper	**0.0001**	0.8023	**0.0001**
	Omnivore	0.5601	0.2277	0.7073
	Predator	**0.0001**	**0.0048**	**0.0001**
	Scavenger/opportunist	**0.0001**	**0.0025**	**0.0001**
	Sub-surface deposit feeder	**0.0001**	**0.0001**	**0.0001**
Living habit	Attached/sessile	0.0075	0.7358	**0.0002**
	Burrower	**0.0001**	**0.0096**	**0.0001**
	Free living / Surface crawler	**0.0001**	**0.0001**	**0.0001**
	Tube dwelling	**0.0001**	**0.0001**	**0.0001**
Morphology	Hard	NC	NC	NC
	Hard exoskeleton	0.101	0.0320	0.0639
	Hard shell	**0.0001**	**0.0044**	**0.0001**
	Irregular	**0.0001**	0.0429	**0.0001**
	Round	**0.0001**	**0.0001**	**0.0001**
	Fragile/Soft	**0.0001**	0.1578	**0.0001**
	Vermiform	**0.0001**	**0.0001**	**0.0001**
Sediment position	Attached	NC	NC	NC
	Bentho-pelagic	**0.0001**	0.1985	**0.0001**
	Deeper than 3 cm	**0.0001**	**0.0001**	**0.0001**
	Surface shallow <3 cm	**0.0001**	**0.0001**	**0.0001**

P-values are presented, and significant differences are shown in bold. NC, not computed.

Ecosystem Functioning—Relationship Between Benthic Macrofauna, Functional Traits and Environmental Conditions

Several significant relationships between the benthic taxa, their functional traits and the environmental conditions were identified across sites and season (**Figure 8**, **Supplementary Figures 5–12**). In general, the interactions were stronger in summer than winter. The stronger interactions were identified at the coastal embayment habitats in Coffin Bay, while the lagoon habitats showed the weakest interactions between benthic macrofauna, traits and environmental conditions

TABLE 5 | Summary of PERMANOVA Pair-wise test of CWM trait modalities comparing differences across seasons by sites.

Trait modality	LB	KB	PG	FB	PPa	MB	PP	N
Biodiffusor	0.0808	0.2851	**0.0001**	0.5609	0.9926	0.4877	0.1095	**0.0001**
Bioirrigator	**0.0038**	0.1372	0.2981	0.0209	0.0476	0.857	0.5886	**0.0001**
No bioturbation	**0.0003**	0.8082	0.0246	0.2672	**0.0001**	0.1454	**0.0003**	**0.0001**
Surface modifier	0.4664	0.0155	**0.0001**	0.1987	0.8288	0.364	**0.0001**	**0.0008**
Large (>20 mm)	0.0545	0.0403	**0.0004**	**0.0093**	0.9374	0.0638	**0.0004**	**0.0001**
Medium (5–20 mm)	0.0607	**0.0062**	**0.0078**	**0.0001**	**0.0089**	0.6922	0.5593	**0.0006**
Small (0.5–5 mm)	0.1382	0.6092	**0.0039**	0.0153	**0.0007**	**0.0091**	**0.0001**	**0.0001**
Deposit feeder	0.0500	0.1671	**0.0001**	0.5138	0.4424	0.739	0.0604	**0.0011**
Filter/suspension	0.9546	0.7268	**0.0001**	0.145	0.6975	0.9878	0.3485	**0.0001**
Grazer/scraper	0.1667	0.2035	**0.0001**	0.016	**0.009**	**0.0011**	**0.0061**	0.082
Omnivore	NC	NC	NC	NC	NC	NC	NC	NC
Predator	0.5465	0.0324	**0.0013**	0.1577	0.3533	0.594	0.239	**0.0002**
Scavenger/opportunist	0.9692	0.2551	**0.0012**	0.0933	0.766	0.0744	0.7113	**0.0001**
Sub-surface deposit feeder	**0.0079**	**0.0032**	0.0166	0.0747	**0.0001**	**0.0027**	**0.0001**	**0.0001**
Attached/sessile	0.4852	0.0975	NC	1	1	0.017	NC	NC
Burrower	**0.0006**	0.2789	0.3393	0.4309	0.9166	0.3287	**0.001**	**0.0001**
Free living / Surface crawler	**0.0008**	0.256	0.7733	0.9636	0.5442	0.8337	0.014	**0.0001**
Tube dwelling	0.6939	0.114	**0.0003**	**0.0018**	0.1343	0.5659	**0.0019**	**0.0001**
Hard	NC	NC	NC	NC	NC	NC	NC	NC
Hard exoskeleton	0.3430	**0.0022**	0.2211	0.2039	0.8692	0.5532	NC	NC
Hard shell	0.6447	0.2025	**0.0001**	**0.0001**	**0.0004**	0.0407	**0.0065**	**0.0001**
Irregular	0.8756	**0.01**	**0.0001**	**0.0018**	**0.0006**	0.1223	0.7021	**0.0001**
Round	NC	NC	NC	NC	NC	NC	0.4272	**0.0001**
Fragile/Soft	0.8881	0.0449	**0.0001**	**0.0001**	0.0747	0.4299	0.941	**0.0001**
Vermiform	0.8762	**0.0069**	**0.0001**	0.0318	**0.0002**	0.0236	0.0525	**0.0001**
Attached	NC	NC	NC	NC	NC	NC	NC	NC
Bentho-pelagic	0.0148	0.4107	0.0162	0.0772	**0.0004**	0.5379	**0.0044**	**0.0001**
Deeper than 3 cm	**0.0028**	0.4188	0.7602	0.1183	0.4579	0.5157	0.0688	**0.0001**
Surface shallow <3 cm	0.4770	**0.0088**	0.0577	**0.0022**	**0.0001**	**0.0054**	**0.0001**	**0.0001**

P-values are presented, and significant differences are shown in bold. NC, not computed.

(**Figure 8**). The six functional traits and their modalities showed significant interactions with environmental conditions across all sites irrespective of season. At the coastal embayment habitats, the trait modality of small (<0.5 mm) body size was correlated to sediment grain size (D50), sub-surface deposit feeder with Chl *a*, and hard exoskeleton and hard shell with temperature and salinity (**Figures 8A,B**). The gulfs at the Upper Spencer Gulf showed significant relationships between the trait modalities filter suspension, small and medium body size, and pH, salinity, and sediment grain size (**Figures 8C,D**). In the other gulf habitats at the Upper Gulf St Vincent, significant relationships were found between the trait modalities deposit feeder, hard exoskeleton and Chl *a*, with correlations between large body size and tube dwelling to salinity and temperature, and burrower to Nitrate (**Figures 8E,F**). At the lagoon habitats in the Coorong, the magnitude of the interactions between benthic macrofauna traits and environmental conditions was lower compared to the other sites. In PP interactions between the trait modalities biodiffusor, surface shallow <3cm and temperature were identified, as well as several trait modalities influenced by Ammonium and Phosphate, while for N the feeding modes filter suspension and sub-surface deposit feeder were influenced by Chl *a* and salinity (**Figures 8G,H**).

DISCUSSION

Patterns of Taxonomic and Functional Metrics

Spatial and temporal patterns of benthic communities, based on taxonomic and functional metrics, elucidated variation in benthic macrofauna diversity and functional traits, suggesting differences in ecosystem functioning across habitats and seasons. The theory proposed by various researchers states that greater taxonomic biodiversity will increase the number of expressed traits, resulting in greater functional diversity, and therefore greater effects on ecosystem functioning (Tilman et al., 1996; Loreau et al., 2002; Reiss et al., 2009). However, correlations between taxonomic and functional metrics have yielded highly variable results, often mediated by environmental context and habitat heterogeneity (Hewitt et al., 2008; Strong et al., 2015; Kokarev et al., 2017; Thrush et al., 2017). In this study,

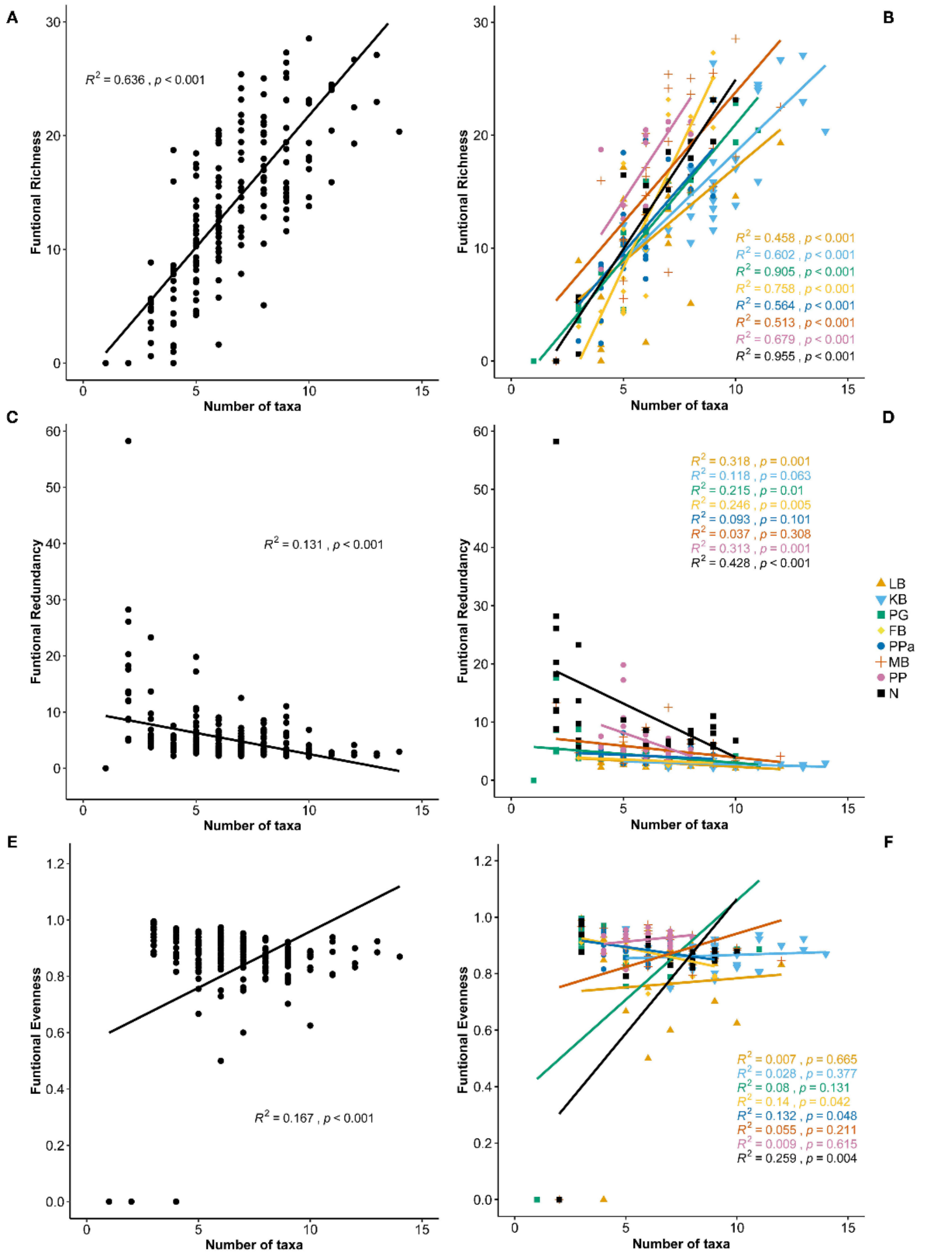

FIGURE 6 | Correlation plots between the number of taxa and **(A)** Functional Richness, **(B)** Functional Richness per site, **(C)** Functional Redundancy, **(D)** Functional Redundancy per site, **(E)** Functional Evenneness, and **(F)** Functional Redundancy per site. LB, Long Beach; KB, Kellidie Bay; MB, Middle Beach; PPa, Port Parham; PG, Port Germein, FB, Fisherman Bay; PP, Pelican Point; N, Noonameena.

TABLE 6 | Result of DISTLM forward analysis.

Variable	R^2	SS (trace)	Pseudo-*F*	P-value	Proportion
Functional Richness	0.35				
Chlorophyll *a*		2172.20	50.979	0.0001	0.176
D50		373.82	7.4517	0.0074	0.030
Sorting		367.52	7.3223	0.0072	0.030
Temperature		2014.50	46.554	0.0001	0.163
Nitrite		488.81	9.8388	0.0015	0.040
Functional Evenness	0.11				
D50		373.82	7.4517	0.0074	0.030
Organic matter		0.54	9.6673	0.0029	0.040
Functional Redundancy	0.21				
Ammonium		385.12	15.366	0.0092	0.060
Organic matter		1000.80	44.37	0.0001	0.157

Only significant ($p < 0.01$) results are shown.

TABLE 7 | Test results from multivariate one-way fixed factor PERMANOVA to compare the community structure of taxa and traits composition across sites and seasons.

	df	MS	Pseudo-*F*	*P*-value
Taxa				
Site	7	61012.00	68.46	**0.0001**
Season	1	19425.00	21.80	**0.0001**
Site x Season	7	13569.00	15.23	**0.0001**
Residual	224	891.23		
Traits				
Site	7	7653.40	63.50	**0.0001**
Season	1	6781.40	56.26	**0.0001**
Site x Season	7	2630.70	21.82	**0.0001**
Residual	224	120.53		

Significant differences are shown in bold.

we identified positive relationships between taxonomic and functional metrics, and ascertained that habitats with greater number of taxa and diversity (H') also showed high Functional Diversity FD (as FRic, FEve and FR), as previously reported in other marine and estuarine systems (e.g., Wong and Dowd, 2015; Hajializadeh et al., 2020; Delfan et al., 2021; Shojaei et al., 2021).

Yet, we also found that taxonomic and functional diversity of benthic communities were site-dependent and varied across the two studied seasons, similar to findings reported in other studies (e.g., Wong and Dowd, 2015; Gladstone-Gallagher et al., 2017; Gammal et al., 2019). The differences of FD (i.e., FRich, FEve, FR) across sites and seasons could be determined by several factors: (i) abundance, diversity and taxa, and (ii) specific environmental conditions and benthic habitat characteristics (e.g. sediment organic matter, grain size, sorting), as described in previous studies (e.g., Hewitt et al., 2008; Shojaei et al., 2015; Henseler et al., 2019; Cappelatti et al., 2020). FRic and FR were greater across all the sites in summer compared to winter, suggesting that the expression of traits was greater in summer. The lower FD in winter could be explained by a temporary decrease of benthic taxa (e.g., bivalves, crustaceans, polychaetes) with specific functional traits modalities or redundant taxa (Loreau et al., 2002), similar to seasonal patterns in cold temperate ecosystems in the Northern hemisphere (e.g., Kröncke et al., 2013; Shojaei et al., 2021).

The two sites at the Coorong lagoon showed a distinctive pattern compared to other habitats, with a low number of taxa but greater FR (ratio FD/H'), indicating low functional redundancy. The low number of taxa could be explained by the habitat characteristics and environmental conditions of the Coorong (e.g., high salinity, eutrophication) (Dittmann et al., 2015; Mosley et al., 2020). Low functional redundancy arising from few taxa occupying the available functional space with few common traits shared, can indicate vulnerability to future functioning loss, as suggested by van der Linden et al. (2012) and Gammal et al. (2020). In this case, 14 taxa accounted for the low functional redundancy across PP and N, and were dominated by the polychaete *Capitella sp.* and the insect larvae Chironomidae, which shared traits related to opportunistic behaviors in disturbed habitats (e.g., free living, scavenger, deposit feeder, surface shallow sediment position).

Functional traits and their modalities also varied across sites and seasons, as a result of changes in the benthic macrofauna. Such spatial and temporal differences in functional traits resulting from environmental conditions and habitat complexity are not uncommon in mudflats (e.g., Wong and Dowd, 2015; Gusmao et al., 2016; Henseler et al., 2019; Hajializadeh et al., 2020; Mestdagh et al., 2020). The multivariate (PCO) analysis for both taxonomic and functional trait composition showed a separation based on the site and season. However, the grouping based on traits was less evident, indicating different patterns of alignment between the two metrics. The functional traits and their modalities were thus more homogenous than the taxonomic composition across sites and seasons. For example, the taxonomic composition of the Coorong lagoon was differentiated from the other habitats, but the multivariate structure of the functional traits in this habitat was similar to the other habitats. Such patterns could result from functional redundancy, when different taxa share few common traits, or new taxa added until all traits are represented, or a combination of both (Schulze and Mooney, 1993; Loreau et al., 2002; van der Linden et al., 2012; Gammal et al., 2020).

Linkages Between Benthic Macrofauna, Functional Traits and Environmental Conditions

In this study, the relationships between benthic macrofauna, functional traits and environmental conditions varied across sites and seasons, potentially indicating that, depending on the benthic composition and trait expression, some ecosystem functioning derived from these relationships may be different across habitats. In the absence of direct measurements, insights into ecosystem functioning can be inferred from knowledge of the linkages between taxa, traits and environmental conditions (Wong and Dowd, 2015; Lam-Gordillo et al., 2020a; Delfan et al., 2021). In our study, the trait modalities bioirrigator, surface modifier ("Bioturbator" trait), burrower, free-living ("Living habit"), deeper than 3 cm and bentho-pelagic ("Sediment position") were commonly expressed. These trait modalities showed strong relationships with the sediment characteristics (D50, sorting) at each habitat, showing that muddy to sandy sediments were most suitable for burrowers and free-living organisms (Liu et al., 2019), which increases sediment oxygenation and nutrient cycling from benthic macrofauna activities (Lam-Gordillo et al., 2020a; Delfan et al., 2021).

The trait "feeding mode" was related with environmental conditions in most of the cases across sites and seasons, as it is fundamental for the structural complexity and trophic status of benthic ecosystems (Pearson and Rosenberg, 1978). In our study, the trait modality of deposit feeder was expressed more in summer. Deposit feeders are generally dominant in muddy sediments (Rhoads and Young, 1970; Hajializadeh et al., 2020), and the sediment grain size (D50 and sorting) was smaller in summer compared to winter. The deposit feeders and grazer trait modalities were also expressed most at sites where high concentrations of Chl *a* were found, as they feed on microphytobenthos (e.g., Wong and Dowd, 2015; Daggers et al., 2020). The relationship of different feeding mode modalities with sediment conditions and primary productivity could also indicate differentiation in the use of resources, food availability, and prey accessibility across sites and seasons (Norkko et al., 2013; Weigel et al., 2016; Sivadas et al., 2020).

The traits for "body size" and "morphology" also varied across sites and seasons, but the trait modalities large body size and irregular body shape were important at almost all sites. Body size is a relevant trait for assessing ecosystem functioning that can be correlated with other traits and provide insight to processes such as nutrient cycling, sediment reworking and energy fluxes (Norkko et al., 2013; Hillman et al., 2020). Large individuals related most to environmental conditions at the studied habitats, however, small and medium body size were the trait modalities most expressed at the lagoon habitats, probably as a result of the large-scale fluctuations in salinity and eutrophic conditions in the Coorong (Dittmann et al., 2015; Mosley et al., 2020).

Environmental conditions correlated most with benthic macrofauna-traits were chlorophyll *a*, organic matter, sediment grain size (D50 and sorting) and concentrations of ammonium. Functional diversity (i.e., FRic, FEve, FR) was also correlated with the environmental conditions Chlorophyll *a*, sediment grain size (D50), sediment organic matter content, temperature, ammonium, and nitrite, supporting the pattern found with the linkages between taxa-traits and environmental conditions. The findings from both perspectives (i.e., correlation between taxa-traits, and environment conditions, and functional diversity), suggest that across the surveyed sites the ecosystem functioning mostly occurring includes nutrient cycling, productivity, and sediment stability and transport (Norkko et al., 2013; Wong and

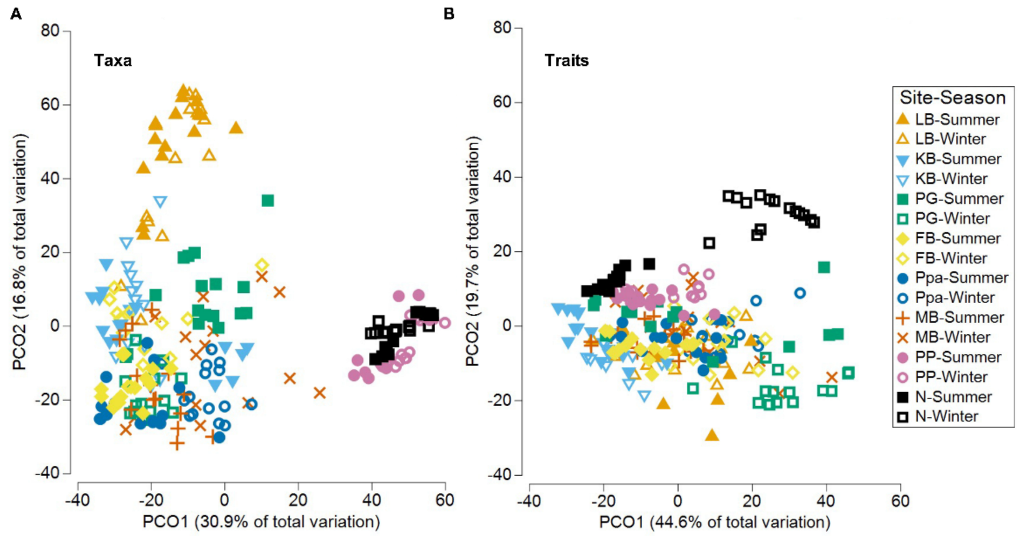

FIGURE 7 | PCO (Principal Coordinates Ordination) plots for benthic assemblages across sites and seasons based on the **(A)** taxonomic and trait **(B)** composition. LB, long beach; KB, kellidie bay; MB, middle beach; PPa, port parham; PG, port germein; FB, fisherman bay; PP, pelican point; N, noonameena.

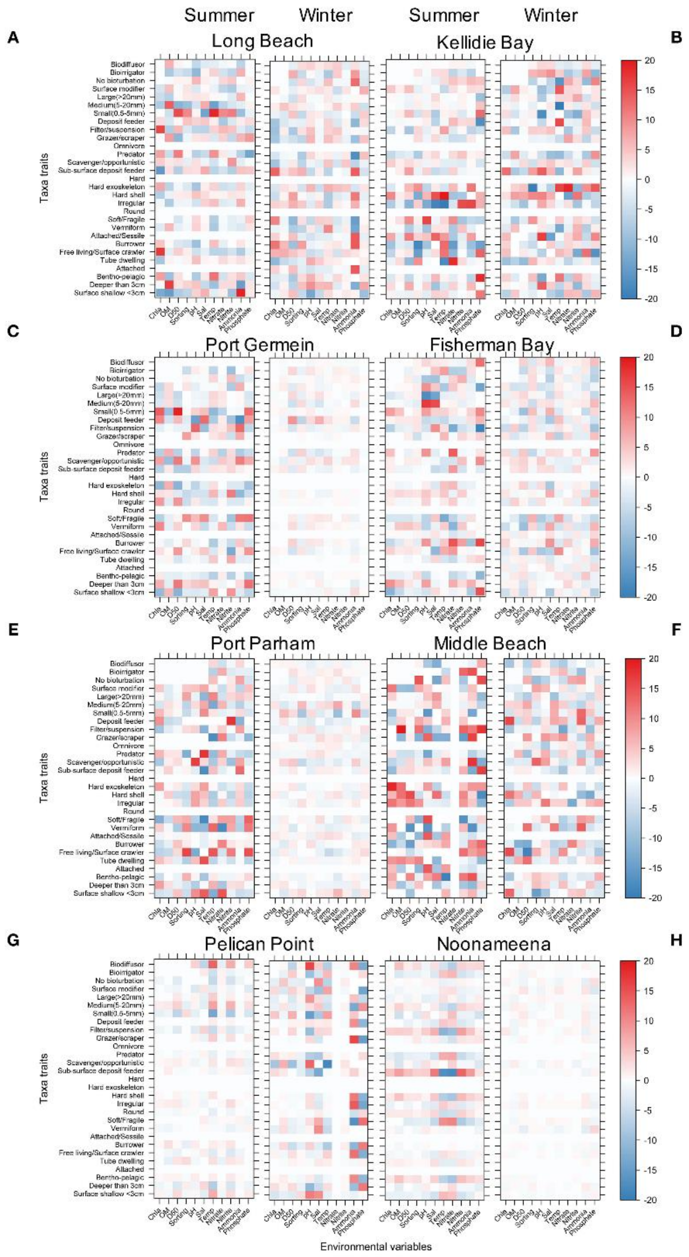

FIGURE 8 | Level plot for the fourth corner interaction (taxa abundance, traits, and environmental conditions) using NB-GLLVM showing the interactions by site and seasons. The colour scale indicates significant interactions and magnitudes of the point estimates. **(A)** Long Beach, **(B)** Kellidie Bay, **(C)** Port Germein, **(D)** Fhiserman Bay, **(E)** Port Parham, **(F)** Middle Beach, **(G)** Pelican Point, and **(H)** Noonameena.

Dowd, 2015, Hajializadeh et al., 2020; Lam-Gordillo et al., 2020a; Delfan et al., 2021).

Implications of Functional Diversity for Conservation and Management

Across the south Australian coast, different patterns in benthic taxa, functional traits and functional diversity were identified, as a result of site-dependent environmental conditions and habitat characteristics. In addition, anthropogenic activities are also shaping the benthic communities and their trait expression. The lagoon showed the lowest functional redundancy compared to other habitats, indicating that the functional traits expressed were less common, and only few taxa occupied the available functional space. It has been proposed that the greater the number of taxa and traits expressed in an ecosystem (i.e., functionality), the greater probability of taxa and traits to persist and maintain ecosystem functioning (van der Linden et al., 2012; Kokarev et al., 2017; Murillo et al., 2020). Our findings could thus indicate that the lagoon is vulnerable to further loss of benthic taxa and structural changes (i.e., ecosystem functioning loss) caused by anthropogenic or natural environmental changes. In contrast, benthic communities in the coastal embayment showed high functional richness and redundancy, suggesting that these sites are more resilient and are more likely to maintain their ecosystem functioning if an event of change (i.e., taxa loss) occurs.

CONCLUSION

This study identified spatial and temporal patterns of benthic communities, based on both taxonomic and functional metrics. Functional diversity and expression of functional traits were site-dependent and different across habitats, which could be explained by the benthic community at each site, the influence of environmental conditions and habitat complexity. Correlations between benthic macrofauna, functional traits and environmental conditions were mostly driven by deposit feeders with large and irregular body organisms, performing bioirrigation and burrowing deep into the sediment. Thus, ecosystem functioning would be most affected by the loss of taxa displaying these traits. Our findings corroborate that using both taxonomic and functional metrics is complementary for conservation and management seeking to maintain biodiversity with the implicit understanding that ecosystem functioning will also be maintained. The outcomes presented here advance the understanding of the relationship between benthic taxa, functional traits and environmental conditions in tidal flats. Understanding those relationships will further enable us to predict how ecosystem functioning changes with biodiversity loss, and could potentially help to improve management to ensure healthy functioning of intertidal benthic ecosystems.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

OL-G and SD conceived the original ideas for the manuscript. OL-G developed the outline, collected, and analyzed the data, prepared the figures and tables and wrote the manuscript with some contributions to drafting from RB and SD and critical refinement by SD. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.723749/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Appendix D. Supplementary information for Chapter 5.

Table S1. Main characteristics of the sampling survey at the seven sites in the Coorong. Historical salinity data was retrieved from Dittmann et al. (2018) and Mosley et al. (2020).

			Field sampling details				
Site	**Salinity range (historical)**	**Salinity**	**Start of anoxic layer**	**Tide**	**Water depth**	**Distance from shore**	**Site photo**
Hunters Creek	0.20 - 45	4.9	5 cm	Low tide - exposed mudflat	0 m	20 m	
Pelican point	0.20 - 40	7.2	3 cm	Low tide - exposed mudflat	0 m	20 m	
Long Point	23 - 61	64.1	3 cm	Low tide - exposed mudflat	0 m	50 m	
Noonameena	41 - 90	70.2	3 cm	Low tide - exposed mudflat	0 m	50 m	
Hells Gate	51 - 108	90	0.5 cm	Low tide - exposed mudflat	0 m	20 m	

Jack point	65 - 125	89	0.2 cm	Low tide - exposed mudflat	0 m	10 m	
Salt Creek	76 - 130	92	0.2 cm	Low tide - exposed mudflat	0 m	50 m	

Table S2. Taxa list of benthic macrofauna recorded across the study sites, x indicates presence. HC: Hunters Creek; PP: Pelican Point; LB: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

Taxa/Site	HC	PP	LP	NM	HG	JP	SC
Australonereis ehlersi				x			
Boccardiela limnicola		x					
Capitellidae		x	x	x			
Euchone variabilis				x			
Simplisetia aequisetis	x	x	x	x			
Arthritica helmsi	x	x	x	x			
Hiatula alba	x						
Spisula trigonella			x				
Hydrobiidae	x	x	x				
Salinator fragilis	x	x	x				
Amphipoda	x	x	x	x	x		
Corophiidae			x	x			
Ostracoda					x	x	
Chironomidae larvae	x	x	x	x	x	x	x
Dolichopodidae larvae					x		
Ceratopogonidae larvae						x	
Stratiomyidae larvae						x	

Table S3. Summary of the different generalized linear latent variable models (GLLVMs) performed. Negative Binomial family was the best fit model. 14 individual GLLVMs Negative Binomial were performed for each of the combinations: each site, porewater nutrients dataset, and sediment conditions dataset.

ID	Variables	Site	Family	AIC	AICc	BIC
M1	Benthic_abundance+porewater_nutrients+functinal_traits	HC	Negative Binomial	332.55	76.21	284.51
M2	Benthic_abundance+Sediment_conditions+functinal_traits	HC	Negative Binomial	384.36	78.08	326.56
M3	Benthic_abundance+porewater_nutrients+functinal_traits	PP	Negative Binomial	342.44	86.10	294.40
M4	Benthic_abundance+Sediment_conditions+functinal_traits	PP	Negative Binomial	393.51	87.23	335.70
M5	Benthic_abundance+porewater_nutrients+functinal_traits	LP	Negative Binomial	-46506.84	-46763.17	-46554.88
M6	Benthic_abundance+Sediment_conditions+functinal_traits	LP	Negative Binomial	368.81	65.53	311.01
M7	Benthic_abundance+porewater_nutrients+functinal_traits	NM	Negative Binomial	287.42	31.08	239.38
M8	Benthic_abundance+Sediment_conditions+functinal_traits	NM	Negative Binomial	337.39	31.11	279.58
M9	Benthic_abundance+porewater_nutrients+functinal_traits	HG	Negative Binomial	257.86	1.52	209.82
M10	Benthic_abundance+Sediment_conditions+functinal_traits	HG	Negative Binomial	307.86	1.58	250.05
M11	Benthic_abundance+porewater_nutrients+functinal_traits	JP	Negative Binomial	253.35	-2.97	205.31
M12	Benthic_abundance+Sediment_conditions+functinal_traits	JP	Negative Binomial	302.95	-3.32	245.14
M13	Benthic_abundance+porewater_nutrients+functinal_traits	SC	Negative Binomial	264.70	8.36	216.66
M14	Benthic_abundance+Sediment_conditions+functinal_traits	SC	Negative Binomial	313.13	6.85	255.33

Table S4. Summary of PERMANOVA Pair-wise test of environmental conditions comparing differences across sites. Significant differences are highlighted in bold. Monte Carlo test ‘P(MC)’ was performed due to the number of unique permutations being <100.

	Overlying water Salinity		**Overlying water pH**		**Sediment Organic matter**		**Sediment Chlorophyll a**		**Sediment size, D50**		**Porewater Nitrite**		**Porewater Nitrate**		**Porewater Ammonium**		**Porewater Phosphate**	
Groups	Perms	P(MC)	Perms	P(MC)	Perms	P(MC)	Perms	P(MC)	Perms	P(MC)	Perms	P(MC)	Perms	P(MC)	Perms	P(MC)	Perms	P(MC)
HC, PP	10	0.0461	54	0.1674	126	0.1929	126	**0.0005**	126	**0.0001**	31	0.4710	13	0.2786	54	0.1376	34	0.1393
HC, LP	9	**0.0001**	57	0.376	126	**0.0053**	126	0.7661	126	**0.0001**	45	0.2805	8	0.3732	81	0.0409	23	0.4477
HC, N	9	**0.0001**	74	0.0549	126	**0.0001**	126	**0.0038**	126	**0.0001**	43	0.6136	13	0.2900	60	0.2098	40	0.1684
HC, HG	20	**0.0001**	68	0.5586	126	**0.0041**	126	**0.0058**	126	**0.0001**	39	0.1427	16	0.2620	56	0.1840	39	0.7522
HC, JP	15	**0.0001**	31	0.7652	126	**0.0014**	126	**0.0006**	126	**0.0001**	57	0.0339	12	0.2236	82	0.3743	35	0.2295
HC, SC	23	**0.0001**	79	0.9053	126	**0.0001**	126	**0.0016**	126	**0.0008**	64	**0.0096**	12	0.2125	81	0.0784	24	0.4675
PP, LP	21	**0.0001**	33	**0.0002**	126	**0.0112**	126	**0.0047**	126	**0.0001**	31	0.3367	7	**0.0005**	78	**0.0011**	22	**0.0007**
PP, NM	24	**0.0001**	40	**0.0001**	126	**0.0001**	126	0.0481	126	**0.0001**	26	0.6392	4	0.3693	43	0.8907	27	0.9317
PP, HG	11	**0.0001**	39	**0.0002**	126	**0.003**	126	0.027	126	**0.0001**	25	**0.0112**	6	0.5803	47	0.9314	33	**0.0001**
PP, JP	23	**0.0001**	22	**0.0001**	126	**0.0002**	126	0.3037	126	**0.0008**	44	**0.0007**	5	**0.0013**	41	0.2156	16	0.2247
PP, SC	30	**0.0001**	61	**0.0042**	126	**0.0001**	126	0.0615	126	**0.0033**	50	**0.0001**	5	**0.0009**	65	**0.0004**	25	**0.0001**
LP, NM	9	**0.0002**	33	**0.0001**	126	0.9101	126	0.0247	126	**0.0014**	40	0.2660	6	**0.0087**	96	**0.0037**	29	0.0629
LP, HG	5	**0.0001**	22	**0.0012**	126	**0.0007**	126	0.0337	126	0.0200	33	0.4677	9	0.0132	85	**0.0027**	21	0.0517
LP, JP	15	**0.0001**	19	**0.0001**	126	**0.0004**	126	**0.0063**	126	**0.0002**	39	0.0369	6	**0.0001**	80	0.8671	24	0.0500
LP, SC	23	**0.0001**	50	0.0462	126	**0.0001**	126	**0.0117**	126	0.6019	50	**0.0017**	6	**0.0001**	58	0.4641	14	0.8710
NM, HG	6	**0.0001**	33	**0.0001**	126	**0.0002**	126	0.6023	126	0.4734	32	0.0318	8	0.3022	61	0.8688	41	0.0092
NM, JP	18	**0.0001**	19	**0.0001**	126	**0.0001**	126	0.0870	126	**0.0001**	51	**0.0024**	7	**0.0017**	76	0.2239	29	0.5407
NM, SC	26	**0.0001**	56	**0.0002**	126	**0.0001**	126	0.4750	126	0.0646	64	**0.0003**	7	**0.0017**	89	**0.0025**	29	0.0494
HG, JP	2	0.1508	17	**0.0001**	126	0.1375	126	0.0448	126	**0.0001**	32	0.0258	2	0.2470	84	0.2150	30	**0.0038**
HG, SC	5	0.1457	27	0.1773	126	0.5368	126	0.2287	126	0.1181	43	**0.0002**	2	0.2469	84	**0.0030**	18	0.0466
JP, SC	9	0.0667	24	0.5763	126	**0.0009**	116	0.1420	126	**0.0003**	31	0.0509	NC	NC	88	0.6947	25	0.0319

Table S4. Continued.

	Sediment Total Phosphorus		**Sediment Total Carbon**		**Sediment Total Nitrogen**		**Sediment Carbon/Nitrogen**	
Groups	Perms	P(MC)	Perms	P(MC)	Perms	P(MC)	Perms	P(MC)
HC, PP	10	**0.0038**	10	**0.0001**	3	0.3462	10	**0.0001**
HC, LP	10	**0.0007**	9	**0.0001**	3	**0.0004**	10	**0.0001**
HC, NM	10	**0.0010**	10	**0.0001**	5	**0.0055**	10	**0.0001**
HC, HG	10	0.0269	10	**0.0003**	6	0.0313	10	0.4151
HC, JP	10	**0.0052**	10	**0.0001**	3	0.0253	10	**0.0001**
HC, SC	10	**0.0072**	10	**0.0006**	5	**0.0069**	10	**0.0007**
PP, LP	10	**0.0011**	10	0.7723	4	0.0414	10	**0.0141**
PP, NM	10	**0.0004**	9	0.0184	4	0.0524	10	0.4594
PP, HG	10	**0.0079**	10	**0.0001**	7	0.0298	10	**0.0042**
PP, JP	10	0.0938	10	**0.0001**	5	0.0473	10	**0.0001**
PP, SC	10	0.0409	10	**0.0001**	6	0.0134	10	**0.0001**
LP, NM	10	**0.0026**	10	**0.0003**	2	0.6425	10	0.0743
LP, HG	10	**0.0009**	10	**0.0001**	4	**0.0030**	10	**0.0064**
LP, JP	10	**0.0003**	10	**0.0001**	3	**0.0001**	10	**0.0001**
LP, SC	10	**0.0017**	10	**0.0006**	4	**0.0001**	10	**0.0001**
NM, HG	10	**0.0003**	9	**0.0001**	7	**0.0042**	10	**0.0064**
NM, JP	10	**0.0001**	10	**0.0001**	5	**0.0016**	10	**0.0001**
NM, SC	10	**0.0007**	10	**0.0001**	6	**0.0015**	10	**0.0001**
HG, JP	10	0.0166	10	**0.0001**	4	0.1340	10	**0.0110**
HG, SC	10	0.1329	10	**0.0018**	4	0.6492	10	0.0224
JP, SC	10	0.1690	10	0.2430	3	0.0669	10	0.3361

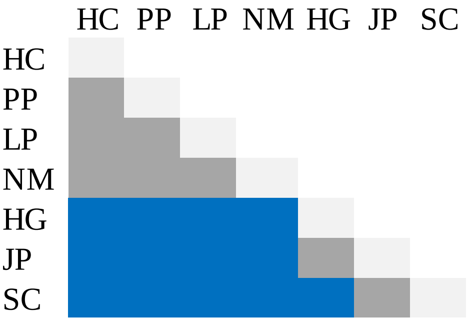
Table S5. Summary of PERMANOVA Pair-wise test of organic matter degradation comparing differences across depths by sites. Significant differences are highlighted in bold. Monte Carlo test ‘P(MC)’ was performed due to the number of unique permutations being <100.

Groups	**Hunters Creek**			**Pelican Point**			**Long Point**			**Noonameena**		
	t	**P(perm)**	**P(MC)**	**t**	**P(perm)**	**P(MC)**	**t**	**P(perm)**	**P(MC)**	**t**	**P(perm)**	**P(MC)**
1-3 cm, 4-7 cm	1.941	0.173	0.0874	1.802	0.046	0.1110	1.930	0.130	0.093	0.686	0.578	0.513
1-3 cm, 8-11 cm	3.556	0.048	**0.0080**	3.184	0.008	0.0120	1.811	0.153	0.110	0.657	0.597	0.530
1-3 cm, 11-15 cm	9.231	0.008	**0.0001**	10.351	0.008	**0.0001**	1.193	0.329	0.266	0.771	0.528	0.462
1-3 cm, 16-19 cm	4.828	0.007	**0.0008**	56.000	0.009	**0.0001**	1.306	0.281	0.232	0.923	0.444	0.382
4-7 cm, 8-11 cm	1.423	0.200	0.1971	1.443	0.216	0.1926	0.316	1.000	0.761	1.445	0.248	0.195
4-7 cm, 11-15 cm	3.036	0.037	0.0149	3.150	0.023	0.0124	0.606	0.691	0.553	1.537	0.214	0.158
4-7 cm, 16-19 cm	2.125	0.069	0.0647	4.677	0.009	**0.0025**	0.728	0.636	0.485	1.692	0.163	0.130
8-11 cm, 11-15 cm	1.040	0.387	0.3361	0.823	0.448	0.4365	0.422	0.839	0.685	0.198	1.000	0.844
8-11 cm, 16-19 cm	0.568	0.567	0.5937	1.762	0.099	0.1206	0.516	0.834	0.615	0.422	0.833	0.681
11-15 cm, 16-19 cm	0.394	0.814	0.7050	2.195	0.090	0.0593	0.000	1.000	1.000	0.200	1.000	0.849

Table S6. Summary of PERMANOVA Pair-wise test of organic matter degradation comparing differences across sites by depth. Significant differences are highlighted in bold. Monte Carlo test ‘P(MC)’ was performed due to the number of unique permutations being <100.

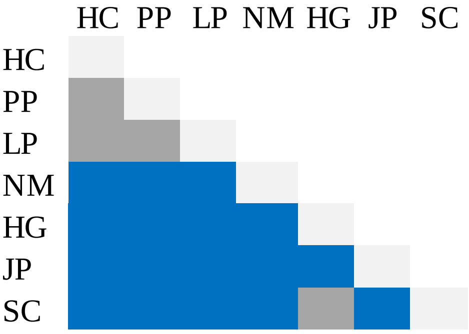
1-3 cm of depth	**t**	**P(perm)**	**Unique perms**	**P(MC)**
Hunters Creek, Pelican Point	0.000			
Hunters Creek, Long Point	16.123	0.008	11	**0.0001**
Hunters Creek, Noonameena	12.758	0.008	15	**0.0001**
Pelican Point, Long Point	16.123	0.008	11	**0.0001**
Pelican Point, Noonameena	12.758	0.009	15	**0.0001**
Long Point, Noonameena	0.468	0.757	10	0.6580
4-7 cm of depth				
Hunters Creek, Pelican Point	0.083	0.953	26	0.9377
Hunters Creek, Long Point	3.552	0.017	24	**0.0084**
Hunters Creek, Noonameena	2.525	0.057	28	0.0381
Pelican Point, Long Point	3.625	0.016	23	**0.0057**
Pelican Point, Noonameena	2.606	0.057	28	0.0297
Long Point, Noonameena	1.757	0.139	11	0.1156
8-11 cm of depth				
Hunters Creek, Pelican Point	0.067	0.928	23	0.9484
Hunters Creek, Long Point	1.162	0.323	19	0.2828
Hunters Creek, Noonameena	1.101	0.378	21	0.3037
Pelican Point, Long Point	0.925	0.452	21	0.3846
Pelican Point, Noonameena	0.875	0.438	23	0.4104
Long Point, Noonameena	0.254	1.000	5	0.7994
11-15 cm of depth				
Hunters Creek, Pelican Point	0.074	1.000	14	0.9444
Hunters Creek, Long Point	0.183	0.968	14	0.8680
Hunters Creek, Noonameena	0.000	1.000	13	1.0000
Pelican Point, Long Point	0.101	1.000	12	0.9210
Pelican Point, Noonameena	0.104	1.000	11	0.9174
Long Point, Noonameena	0.351	0.856	8	0.7396
16-19 cm of depth				
Hunters Creek, Pelican Point	1.524	0.281	12	0.1586
Hunters Creek, Long Point	0.335	0.838	19	0.7430
Hunters Creek, Noonameena	0.502	0.722	18	0.6285
Pelican Point, Long Point	5.422	0.008	11	**0.0006**
Pelican Point, Noonameena	4.648	0.014	10	**0.0019**
Long Point, Noonameena	0.640	0.687	6	0.5297

a) Richness



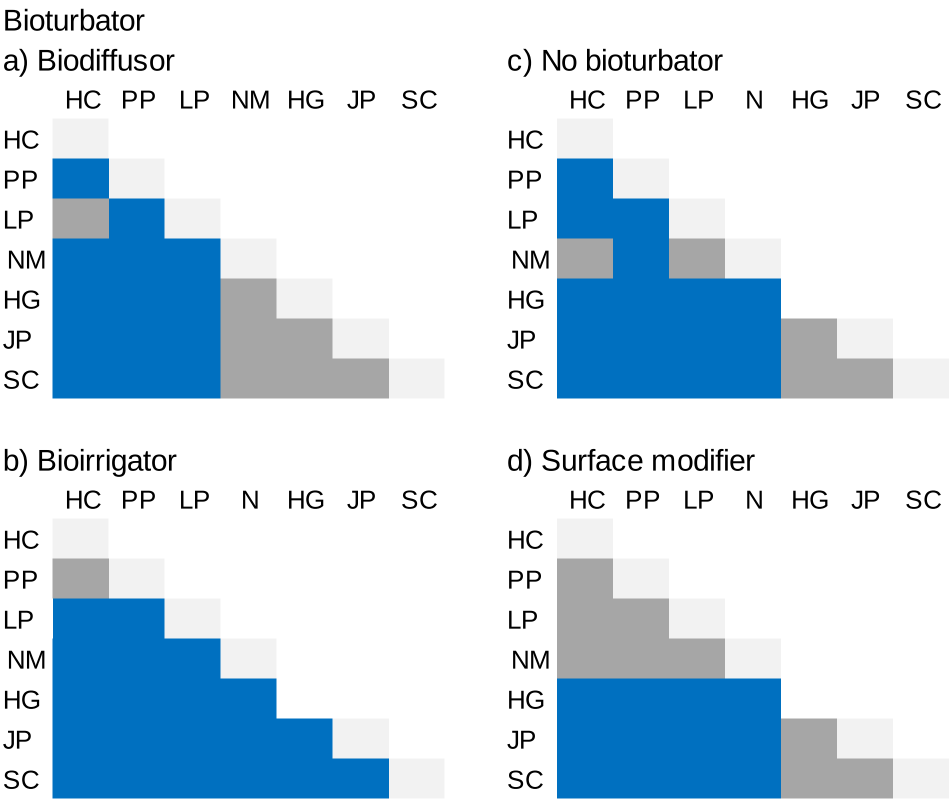
	HC	PP	LP	NM	HG	JP	SC
HC	⬜						
PP	▨	⬜					
LP	▨	▨	⬜				
NM	▨	▨	▨	⬜			
HG	🟦	🟦	🟦	🟦	⬜		
JP	🟦	🟦	🟦	🟦	▨	⬜	
SC	🟦	🟦	🟦	🟦	🟦	▨	⬜

b) Abundance (ind.m^2)



	HC	PP	LP	NM	HG	JP	SC
HC	⬜						
PP	▨	⬜					
LP	▨	▨	⬜				
NM	🟦	🟦	🟦	⬜			
HG	🟦	🟦	🟦	🟦	⬜		
JP	🟦	🟦	🟦	🟦	🟦	⬜	
SC	🟦	🟦	🟦	🟦	▨	🟦	⬜

Figure S1. Visual summary of PERMANOVA Pairwise test outcomes for benthic macrofauna between sampling sites: a) Richness, and b) Abundance (ind.m^2). Blue= significant difference $p<0.01$; Grey= not significant difference $p>0.01$. HC: Hunters Creek; PP: Pelican Point; LB: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.



Bioturbator

a) Biodiffusor

	HC	PP	LP	NM	HG	JP	SC
HC							
PP	🟦						
LP	▨	🟦					
NM	🟦	🟦	🟦				
HG	🟦	🟦	🟦	▨			
JP	🟦	🟦	🟦	▨	▨		
SC	🟦	🟦	🟦	▨	▨	▨	

c) No bioturbator

	HC	PP	LP	N	HG	JP	SC
HC							
PP	🟦						
LP	🟦	🟦					
NM	▨	🟦	▨				
HG	🟦	🟦	🟦	🟦			
JP	🟦	🟦	🟦	🟦	▨		
SC	🟦	🟦	🟦	🟦	▨	▨	

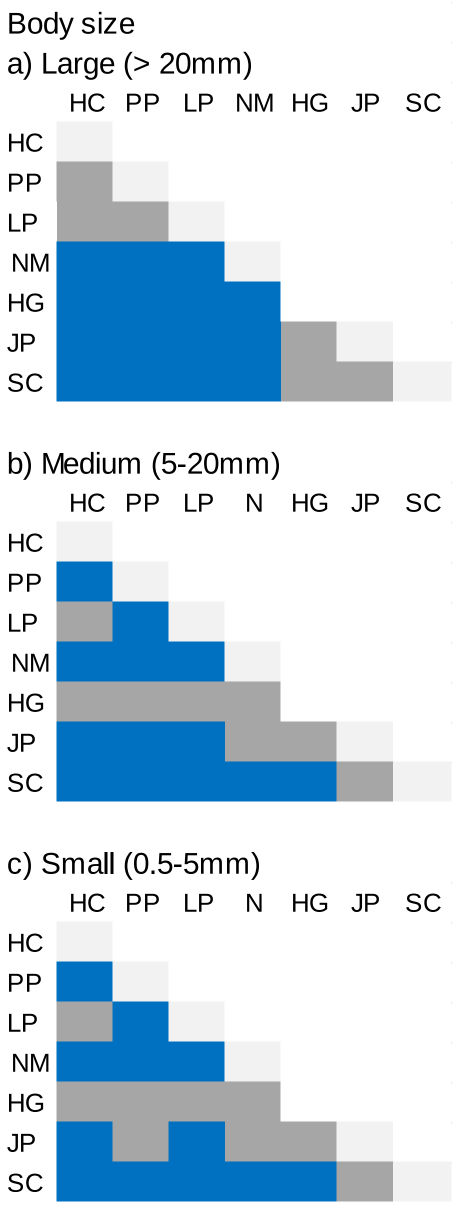
b) Bioirrigator

	HC	PP	LP	N	HG	JP	SC
HC							
PP	▨						
LP	🟦	🟦					
NM	🟦	🟦	🟦				
HG	🟦	🟦	🟦	🟦			
JP	🟦	🟦	🟦	🟦	🟦		
SC	🟦	🟦	🟦	🟦	🟦	🟦	

d) Surface modifier

	HC	PP	LP	N	HG	JP	SC
HC							
PP	▨						
LP	▨	▨					
NM	▨	▨	▨				
HG	🟦	🟦	🟦	🟦			
JP	🟦	🟦	🟦	🟦	▨		
SC	🟦	🟦	🟦	🟦	▨	▨	

Figure S2. Visual summary of PERMANOVA Pairwise test outcomes for macrobenthic functional trait Bioturbator between sites.. Blue= significant difference $p<0.01$ based on macrobenthic abundance; Grey= not significant difference $p>0.01$. Monte Carlo test 'P(MC)' was performed due to the number of unique permutations being <100. HC: Hunters Creek; PP: Pelican Point; LB: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.



Body size

a) Large (> 20mm)

	HC	PP	LP	NM	HG	JP	SC
HC							
PP	▨						
LP	▨	▨					
NM	🟦	🟦	🟦				
HG	🟦	🟦	🟦	🟦			
JP	🟦	🟦	🟦	🟦	▨		
SC	🟦	🟦	🟦	🟦	▨	▨	

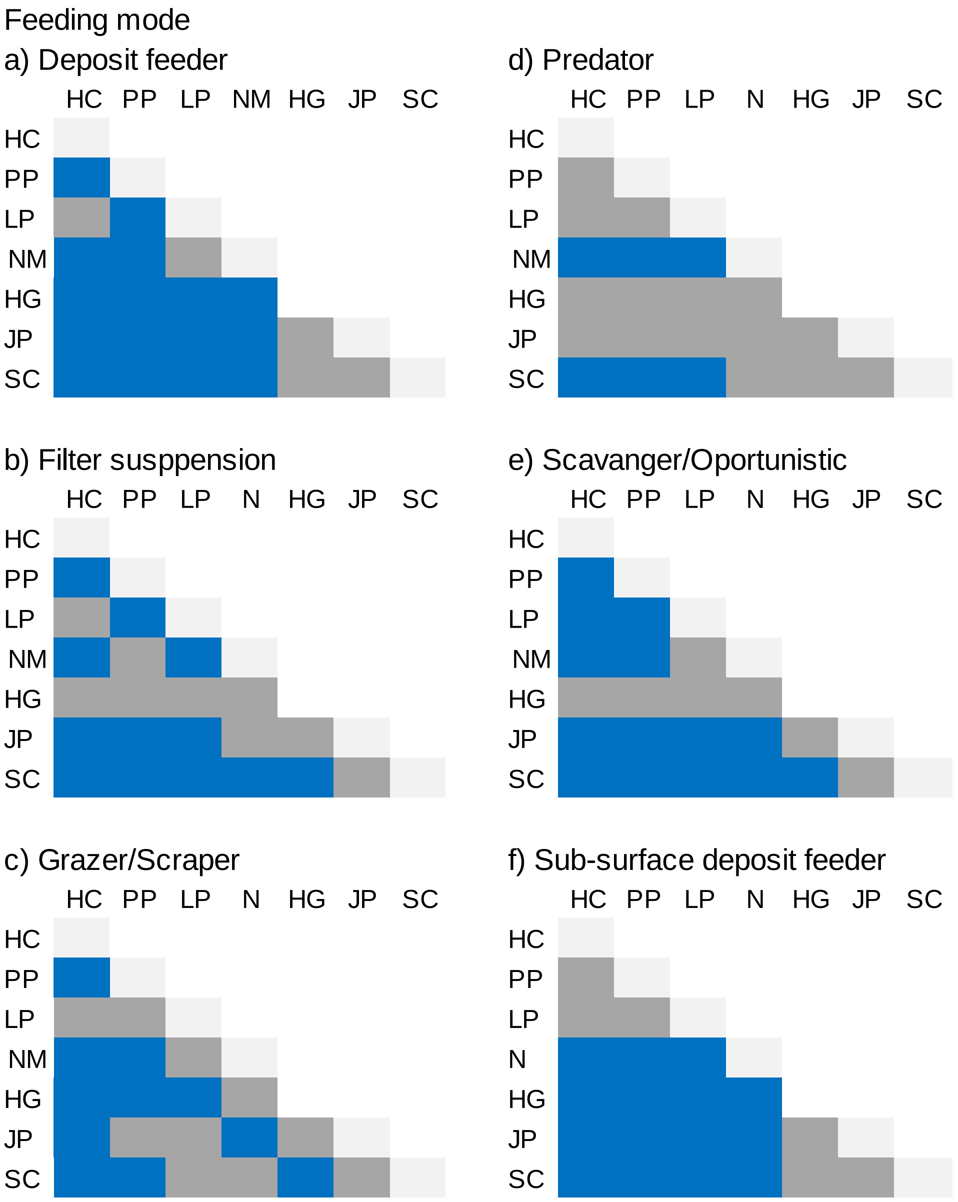
b) Medium (5-20mm)

	HC	PP	LP	N	HG	JP	SC
HC							
PP	🟦						
LP	▨	🟦					
NM	🟦	🟦	🟦				
HG	▨	▨	▨	▨			
JP	🟦	🟦	🟦	▨	▨		
SC	🟦	🟦	🟦	🟦	🟦	▨	

c) Small (0.5-5mm)

	HC	PP	LP	N	HG	JP	SC
HC							
PP	🟦						
LP	▨	🟦					
NM	🟦	🟦	🟦				
HG	▨	▨	▨	▨			
JP	🟦	▨	🟦	▨	▨		
SC	🟦	🟦	🟦	🟦	🟦	▨	

Figure S3. Visual summary of PERMANOVA Pairwise test outcomes for macrobenthic functional trait Body size between sites. Blue= significant difference p<0.01 based on macrobenthic abundance; Grey= not significant difference p>0.01. Monte Carlo test 'P(MC)' was performed due to the number of unique permutations being <100. HC: Hunters Creek; PP: Pelican Point; LB: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.



Feeding mode

a) Deposit feeder

	HC	PP	LP	NM	HG	JP	SC
HC							
PP	🟦						
LP	▒	🟦					
NM	🟦	🟦	▒				
HG	🟦	🟦	🟦	🟦			
JP	🟦	🟦	🟦	🟦	▒		
SC	🟦	🟦	🟦	🟦	▒	▒	

b) Filter susppension

	HC	PP	LP	N	HG	JP	SC
HC							
PP	🟦						
LP	▒	🟦					
NM	🟦	▒	🟦				
HG	▒	▒	▒	▒			
JP	🟦	🟦	🟦	▒	▒		
SC	🟦	🟦	🟦	🟦	🟦	▒	

c) Grazer/Scraper

	HC	PP	LP	N	HG	JP	SC
HC							
PP	🟦						
LP	▒	▒					
NM	🟦	🟦	▒				
HG	🟦	🟦	🟦	▒			
JP	🟦	▒	▒	🟦	▒		
SC	🟦	🟦	▒	▒	🟦	▒	

d) Predator

	HC	PP	LP	N	HG	JP	SC
HC							
PP	▒						
LP	▒	▒					
NM	🟦	🟦	🟦				
HG	▒	▒	▒	▒			
JP	▒	▒	▒	▒	▒		
SC	🟦	🟦	🟦	▒	▒	▒	

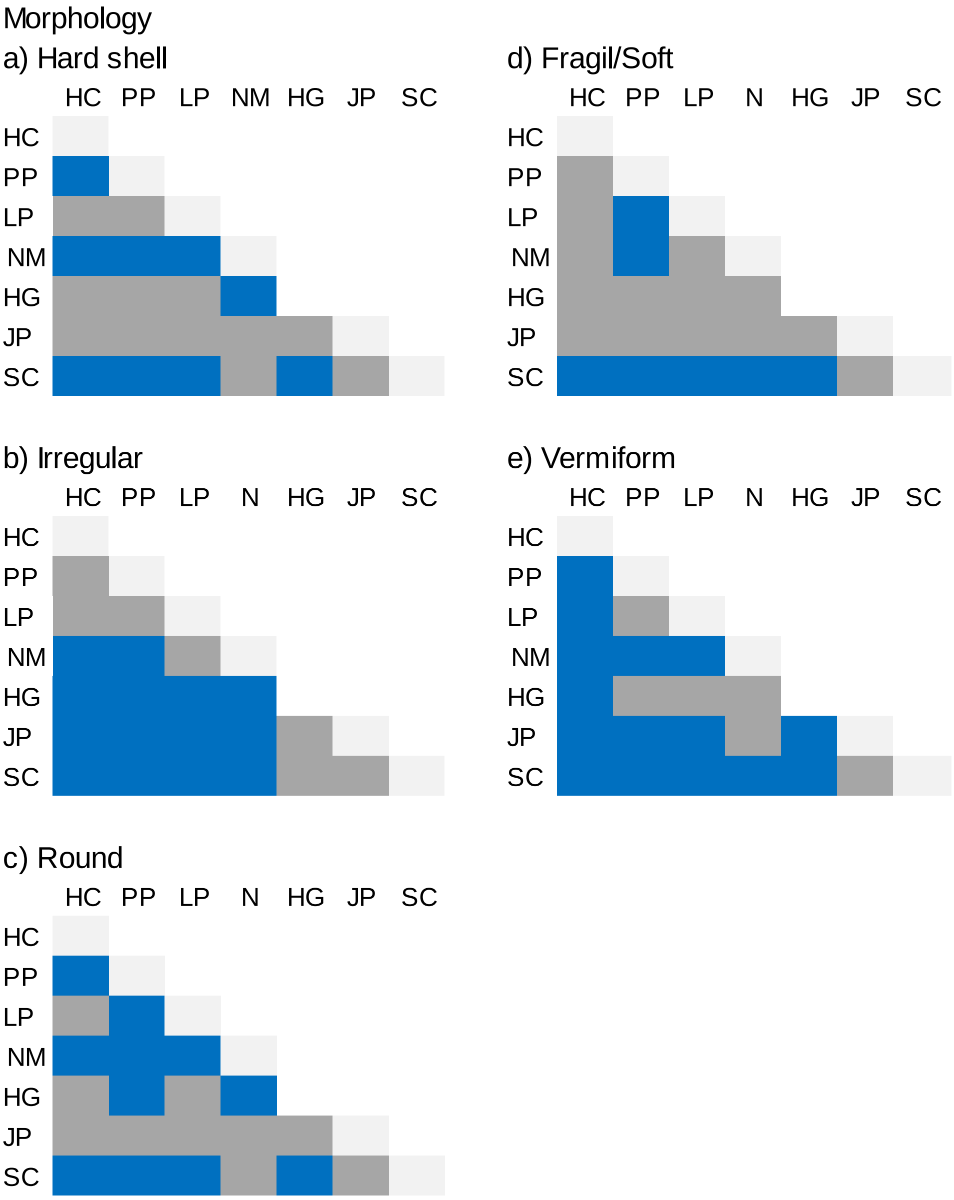
e) Scavanger/Oportunistic

	HC	PP	LP	N	HG	JP	SC
HC							
PP	🟦						
LP	🟦	🟦					
NM	🟦	🟦	▒				
HG	▒	▒	▒	▒			
JP	🟦	🟦	🟦	🟦	▒		
SC	🟦	🟦	🟦	🟦	🟦	▒	

f) Sub-surface deposit feeder

	HC	PP	LP	N	HG	JP	SC
HC							
PP	▒						
LP	▒	▒					
N	🟦	🟦	🟦				
HG	🟦	🟦	🟦	🟦			
JP	🟦	🟦	🟦	🟦	▒		
SC	🟦	🟦	🟦	🟦	▒	▒	

Figure S4. Visual summary of PERMANOVA Pairwise test outcomes for macrobenthic functional trait Feeding mode between sites. Blue= significant difference $p<0.01$ based on macrobenthic abundance; Grey= not significant difference $p>0.01$. Monte Carlo test 'P(MC)' was performed due to the number of unique permutations being <100. HC: Hunters Creek; PP: Pelican Point; LB: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.



Morphology

a) Hard shell

	HC	PP	LP	NM	HG	JP	SC
HC							
PP	🟦						
LP	▨	▨					
NM	🟦	🟦	🟦				
HG	▨	▨	▨	🟦			
JP	▨	▨	▨	▨	▨		
SC	🟦	🟦	🟦	▨	🟦	▨	

d) Fragil/Soft

	HC	PP	LP	N	HG	JP	SC
HC							
PP	▨						
LP	▨	🟦					
NM	▨	🟦	▨				
HG	▨	▨	▨	▨			
JP	▨	▨	▨	▨	▨		
SC	🟦	🟦	🟦	🟦	🟦	▨	

b) Irregular

	HC	PP	LP	N	HG	JP	SC
HC							
PP	▨						
LP	▨	▨					
NM	🟦	🟦	▨				
HG	🟦	🟦	🟦	🟦			
JP	🟦	🟦	🟦	🟦	▨		
SC	🟦	🟦	🟦	🟦	▨	▨	

e) Vermiform

	HC	PP	LP	N	HG	JP	SC
HC							
PP	🟦						
LP	🟦	▨					
NM	🟦	🟦	🟦				
HG	🟦	▨	▨	▨			
JP	🟦	🟦	🟦	▨	🟦		
SC	🟦	🟦	🟦	🟦	🟦	▨	

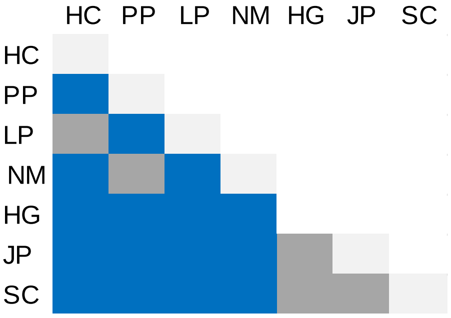
c) Round

	HC	PP	LP	N	HG	JP	SC
HC							
PP	🟦						
LP	▨	🟦					
NM	🟦	🟦	🟦				
HG	▨	🟦	▨	🟦			
JP	▨	▨	▨	▨	▨		
SC	🟦	🟦	🟦	▨	🟦	▨	

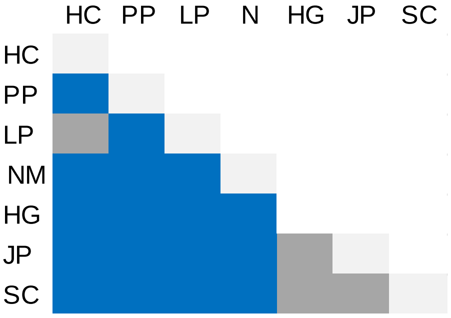
Figure S5. Visual summary of PERMANOVA Pairwise test outcomes for macrobenthic functional trait Morphology between sites. Blue= significant difference $p<0.01$ based on macrobenthic abundance; Grey= not significant difference $p>0.01$. Monte Carlo test ‘P(MC)’ was performed due to the number of unique permutations being <100. HC: Hunters Creek; PP: Pelican Point; LB: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

Living habit

a) Burrower



b) Free living/Surface crawler



c) Tube dwelling

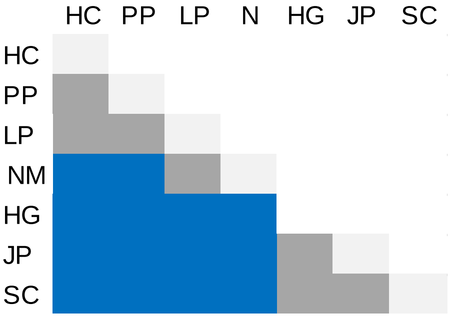
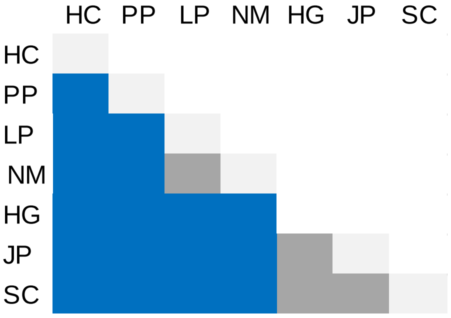


Figure S6. Visual summary of PERMANOVA Pairwise test outcomes for macrobenthic functional trait Living habit between sites. Blue= significant difference p<0.01 based on macrobenthic abundance; Grey= not significant difference p>0.01. Monte Carlo test 'P(MC)' was performed due to the number of unique permutations being <100. HC: Hunters Creek; PP: Pelican Point; LB: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

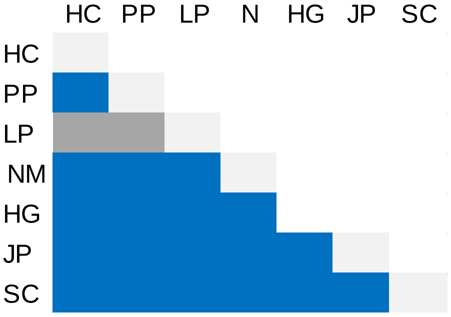
Sediment Position

a) Bentho-pelagic



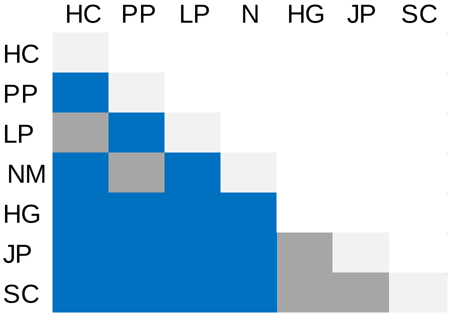
	HC	PP	LP	NM	HG	JP	SC
HC	⬜						
PP	🟦	⬜					
LP	🟦	🟦	⬜				
NM	🟦	🟦	▨	⬜			
HG	🟦	🟦	🟦	🟦			
JP	🟦	🟦	🟦	🟦	▨	⬜	
SC	🟦	🟦	🟦	🟦	▨	▨	⬜

b) Depper than 3cm



	HC	PP	LP	N	HG	JP	SC
HC	⬜						
PP	🟦	⬜					
LP	▨	▨	⬜				
NM	🟦	🟦	🟦	⬜			
HG	🟦	🟦	🟦	🟦			
JP	🟦	🟦	🟦	🟦	🟦	⬜	
SC	🟦	🟦	🟦	🟦	🟦	🟦	⬜

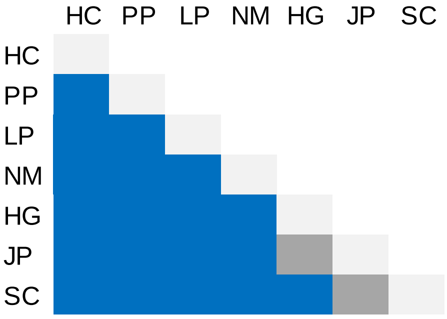
c) Surface shallow < 3cm



	HC	PP	LP	N	HG	JP	SC
HC	⬜						
PP	🟦	⬜					
LP	▨	🟦	⬜				
NM	🟦	▨	🟦	⬜			
HG	🟦	🟦	🟦	🟦			
JP	🟦	🟦	🟦	🟦	▨	⬜	
SC	🟦	🟦	🟦	🟦	▨	▨	⬜

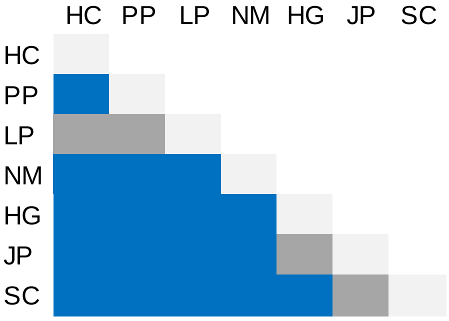
Figure S7. Visual summary of PERMANOVA Pairwise test outcomes for macrobenthic functional trait Sediment position between sites. Blue= significant difference p<0.01 based on macrobenthic abundance; Grey= not significant difference p>0.01. Monte Carlo test 'P(MC)' was performed due to the number of unique permutations being <100. HC: Hunters Creek; PP: Pelican Point; LB: Long Point; Nm: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

a) Taxa



	HC	PP	LP	NM	HG	JP	SC
HC	⬜						
PP	🟦	⬜					
LP	🟦	🟦	⬜				
NM	🟦	🟦	🟦	⬜			
HG	🟦	🟦	🟦	🟦	⬜		
JP	🟦	🟦	🟦	🟦	▨	⬜	
SC	🟦	🟦	🟦	🟦	🟦	▨	⬜

b) Traits



	HC	PP	LP	NM	HG	JP	SC
HC	⬜						
PP	🟦	⬜					
LP	▨	▨	⬜				
NM	🟦	🟦	🟦	⬜			
HG	🟦	🟦	🟦	🟦	⬜		
JP	🟦	🟦	🟦	🟦	▨	⬜	
SC	🟦	🟦	🟦	🟦	🟦	▨	⬜

Figure S8. Visual summary of PERMANOVA Pairwise test outcomes for macrobenthic structure based on a) taxa, and b) functional traits. Blue= significant difference p<0.01; Grey= not significant difference p>0.01. HC: Hunters Creek; PP: Pelican Point; LB: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

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Loss of benthic macrofauna functional traits correlates with changes in sediment biogeochemistry along an extreme salinity gradient in the Coorong lagoon, Australia

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ABSTRACT

Estuarine ecosystems are considered hotspots for productivity, biogeochemical cycling and biodiversity, however, their functions and services are threatened by several anthropogenic pressures. We investigated how abundance and diversity of benthic macrofauna, and their functional traits, correlate to sediment biogeochemistry and nutrient concentrations throughout an estuarine-to-hypersaline lagoon. Benthic communities and functional traits were significantly different across the sites analysed, with higher abundance and more traits expressed in the estuarine region. The results revealed that the benthic trait differences correlated with sediment biogeochemistry and nutrient concentrations in the system. The estuarine regions were dominated by high abundance of large burrowing and bioturbating macrofauna, promoting nutrient cycling and organic matter mineralisation, while these organisms were absent in the hypersaline lagoon, favouring accumulation of organic matter and nutrients in the sediment. The results highlight the importance of preserving healthy benthic communities to maintain ecosystem functioning and mitigate the potential impacts of eutrophication in estuarine ecosystems.

1. Introduction

Coastal soft sediment habitats are some of the most productive ecosystems worldwide, with multiple contributions to ecosystem services such as food production, protection, recreation, carbon sequestration, and nutrient cycling (Cai, 2011; Snelgrove et al., 2014; Douglas et al., 2019; Hillman et al., 2020). These ecosystems, especially estuaries, are considered hotspots for biogeochemical cycling, biodiversity, and productivity (Thrush et al., 2006; Douglas et al., 2019; Rodil et al., 2020). Benthic invertebrates play a key role in modifying sediment biogeochemistry and nutrient fluxes by actively dispersing, recycling and changing the sediments (Welsh, 2003; Thrush et al., 2006; Belley and Snelgrove, 2016), thus driving the functioning of coastal and estuarine sediments (Kauppi et al., 2018; Wrede et al., 2019; Mestdagh et al., 2020). However, estuarine ecosystems around the world are subjected to anthropogenic pressures such as coastal development, eutrophication, increased sediment loads, pollution, and climate change (Lotze et al., 2006; Chariton et al., 2010; Dittmann et al., 2015; Passeri et al., 2015), that may influence environmental conditions, and which can threaten benthic communities and consequently the ecosystem functioning and services they provide (Wetz and Yoskowitz, 2013; Caswell et al., 2018; Potter et al., 2021).

The functioning of estuarine sediments encompasses complex relationships of biological, chemical, and physical processes at different spatial and temporal scales (Waldbusser and Marinelli, 2006; Villnäs et al., 2019) that are often difficult to depict. The contribution of benthic invertebrates to sediment ecosystem services is influenced by abiotic and biotic factors which strongly interact. Abiotic factors include water and sediment conditions (e.g. water temperature, salinity, dissolved oxygen, sediment particle size, organic matter, nutrient concentrations), that in turn structure the biotic factors, i.e. microbial to macrofauna communities (Reise, 1985; Honkoop et al., 2006; Chariton et al., 2010).

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Benthic communities influence estuarine sediment properties, subject to their abundance and composition, but mainly according to the behavioural, morphological, and physiological characteristics, here defined as functional traits, of each species (Bremner, 2008; Beauchard et al., 2017). Benthic macrofauna functional traits are directly and indirectly related to several ecosystem functions, including carbon sequestration, nutrient cycling, oxygen consumption and sediment transport (Snelgrove et al., 2014; Lam-Gordillo et al., 2020a). For example, macrofauna can increase organic matter (OM) inputs to sediments through biodeposition (Graf and Rosenberg, 1997) and mix this OM into deeper strata via bioturbation (Kristensen, 2000; Welsh, 2003). Burrow construction and the irrigation of these burrows by their occupants, increases the surface area of contact between the sediment and water column, promoting solute exchange which creates mosaics of oxidised (redox) zones within the sediments (Nielsen et al., 2004; Robertson et al., 2009; Stief, 2013). These redox change zones, and in some cases the fauna themselves, can then act as substrates for colonisation by specific functional groups of bacteria such as nitrifying and denitrifying bacteria (Welsh and Castadelli, 2004; Stief, 2013; Welsh et al., 2015), which are ultimately responsible of organic matter decomposition and nutrient cycling (Welsh, 2003; Wyness et al., 2021). Sediment nutrient cycling is critical to maintain functioning of estuarine ecosystems, mitigating nutrient over-enrichment, i.e. eutrophication.

Benthic macrofauna are also considered powerful bio-indicators of environmental change, as their functional traits (e.g. long-life spans, limited mobility) can be affected by environmental conditions (Tweedley et al., 2012; Verissimo et al., 2012). Changes in abundance, diversity and functional traits are commonly reported as responses to changes in the environmental conditions, particularly disturbances that affect sediment biogeochemistry and structure (Verissimo et al., 2012; Borja et al., 2015). For example, when an estuary becomes eutrophic, the abundance of macrobenthic fauna increases but diversity decreases (Tweedley et al., 2012). Macrobenthic fauna also respond to salinity changes, with the abundance and diversity of macrobenthic fauna decreasing from estuarine to hypersaline conditions (Dittmann et al., 2015).

While changes in macrobenthic communities and their functional traits across estuarine gradients have been extensively studied in the northern temperate regions and tropical estuaries (e.g. Cloern, 2001; Villnäs et al., 2019; Medeiros et al., 2021), there is a little understanding on how these changes influence sediment biogeochemistry and nutrient cycling in systems with extreme salinity gradients (from estuarine to hypersaline conditions). The lack of understanding is even more evident in estuarine lagoons in arid or semi-arid climates, which are threatened by hydrological and climatic shifts, due to their generally higher evaporation rates and lower freshwater inflow, water extraction for irrigation, and climate change (Cloern et al., 2016; Tweedley et al., 2019; Mosley et al., 2020). The Coorong is an estuarine lagoon system and listed Ramsar site (Coorong and Lakes Alexandrina and Albert Ramsar Wetland), located at the terminus of the largest river system of Australia, the Murray-Darling Basin. It provides an ideal case study site as it is characterised by an extreme salinity gradient (Mosley et al., 2020) that strongly influences the abundance and distribution of benthic fauna (Dittmann et al., 2015; Dittmann et al., 2018). The Coorong has been experiencing increased frequency and severity of pressures, such as eutrophication, hypersalinity, drought (due to water abstraction for agriculture in the catchment and climate change), leading to a decline in its ecological health over recent decades (Dittmann et al., 2015; Mosley et al., 2020).

The ongoing pressures in the Coorong challenge the benthic communities' role in mitigating eutrophication, by limiting their survival, abundance and distribution. This estuarine lagoon system thus presents an important example for understanding the interactions between salinisation, benthic macrofauna and sediment biogeochemical processes. The aim of this study was to investigate how benthic macrofaunal communities and their functional traits change across an extreme salinity (freshwater to several times seawater concentrations) gradient, and whether there are corresponding patterns in sediment biogeochemistry and nutrient concentrations. We hypothesised that (1) benthic macrofauna, sediment biogeochemistry and nutrient concentrations will be different across the system, due to the strong salinity gradient, and that (2) pore water nutrient concentrations and sediment biogeochemistry will be correlated with benthic macrofauna, especially those with functional traits that enhance nutrient cycling and sediment redox status. It is hoped the results can be used to help identify management interventions required to improve the health of the Coorong and other estuarine-lagoon systems experiencing increased salinisation and eutrophication.

2. Methods

2.1. Study area

The Coorong is located in South Australia, at the end of Murray-Darlin Basin, the largest river catchment in Australia (Fig. 1). The Coorong covers three regions: the Murray Estuary, North Lagoon, and South Lagoon, which are connected via a narrow channel (<100 m). The Murray Estuary consists of several channels on either side of the river mouth opening to the Southern Ocean (Mosley et al., 2018). The region is microtidal, and water level in the lagoons are determined mainly by evaporation, wind, and water release over the river Murray barrages rather than by tides (Mosley et al., 2018). A strong salinity gradient characterises the Coorong with a corresponding eutrophication gradient increasing towards the hypersaline South Lagoon (Mosley et al., 2020). Seven sites across this system were selected and surveyed in spring 2020: Sites were ordered from North to South, which also reflected the increasing salinity gradient: Murray Estuary: Hunters Creek (HC) and Pelican Point (PP); North Lagoon: Long Point (LP) and Noonameena (NM); South Lagoon: Hells Gate (HG) Jack Point (JP) and Salt Creek (SC) (Fig. 1). All sites were surveyed when the mudflats were exposed and accessible from shore (Table S1).

2.2. Data collection

2.2.1. Biological data

Sediment samples for benthic macrofauna were taken using a handheld PVC cylindrical corer (83.3 cm^2 surface area) with five replicates randomly taken within an area of 5 m^2 per site. (Table S1). Samples were sieved through a 500 μm mesh size in the field and preserved in ethanol (70%) until further processing. In the laboratory, samples were sorted, and all organisms identified to the lowest possible taxonomic level and counted (Table S2).

2.2.2. Environmental variables

At each sampling site, environmental variables known to influence benthic communities in the Coorong were measured (Dittmann et al., 2015; Dittmann et al., 2018). Five replicate samples for each environmental variable were taken at each site within the same area (5 m^2) where the sediment samples for benthic macro fauna were collected. Water temperature (°C), salinity, and pH were measured in the overlying water during the macrofauna sampling using a Hannah HI98194 multiparameter meter and a refractometer (for salinities above 80). Sediment samples were taken using a cut off 10 mL syringe (surface area 1.8 cm^2 and 10 cm depth) to analyse OM content, sediment grain size, and chlorophyll-*a*, and using a cut-off 60 mL syringe (surface area 6.6 cm^2 and 10 cm depth) to analyse sediment nutrients. In addition, sediment pore water was collected using Rhizon samplers with a 0.2 um pore size (Seeberg-Elverfeldt et al., 2005) for analysing nutrients. Porewater nutrient and sediment samples were immediately stored in portable freezers and frozen to −20 °C until further analysis.

Sediment OM content (OM%) was determined by a partial combustion method; firstly by drying the sediment samples to constant weight

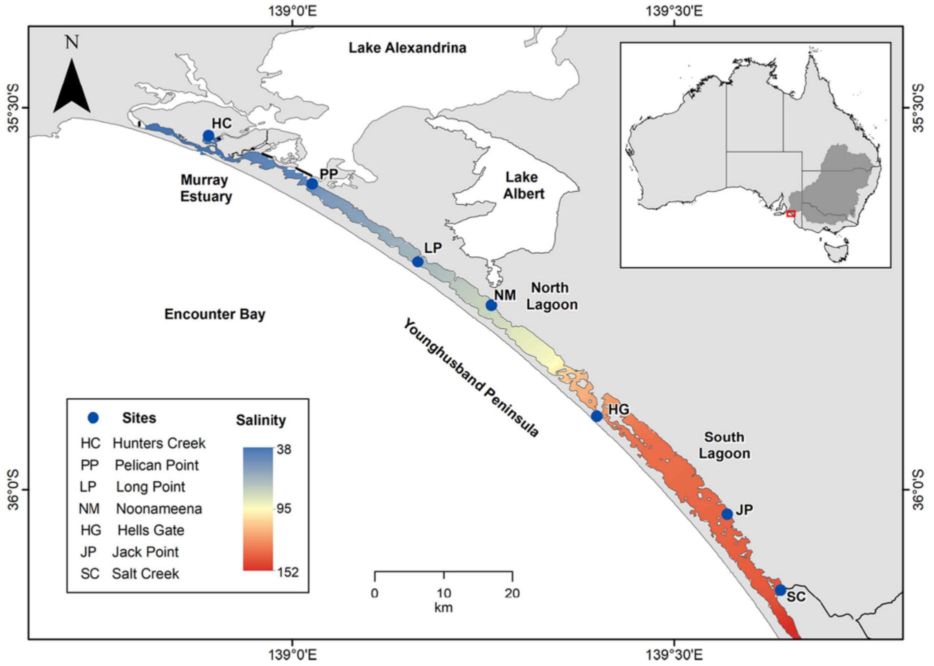

Fig. 1. Location of the sampling sites and salinity gradient across the Coorong. The inset indicates the catchment of the Murray-Darling River system in Australia and the red square the area shown in the main figure. Murray Estuary: HC and PP; North Lagoon: LP and NM; South Lagoon: HG, JP, and SC. Salinity data were generated using the 1-dimensional Coorong Hydrodynamic Model (Jöhnk and Webster, 2014), using historical data for boundary conditions and validated against recorded salinity at sensors (available from water.data.sa.gov.au). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

using an Ohaus MB45 Moisture Balance (controlling the temperature profile at 80 °C), then when constant weight was achieved, sediment samples were combusted in a furnace at 450 °C for 5 h, and OM content determined by gravimetry. Grain size was determined by laser diffraction using a particle size analyser (Malvern Mastersizer 2000). Average values for grain size fractions for each site were entered into the GRADISTAT program v8.0 (Blott and Pye, 2001) to obtain the median (D50 μm) and sorting coefficient (σG). Chlorophyll-a (g m^{-3}), as a proxy of microphytobenthos, was determined after extraction in 99% ethanol using a spectrophotometer (Thermo Scientific, Spectronic 200) and following protocols from Ritchie (2008). Sediment pH, conductivity, total phosphorus as well as total carbon and total nitrogen concentrations by LECO analysis were determined by the NATA accredited Environmental Analysis Laboratory at Southern Cross University, following strict quality control and assurance procedures. Porewater nutrient concentrations (mg L^{-1}) of nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+) and phosphate (PO_4^{3-}) were determined using a Skalar SAN++ SFA segmented flow analyser. Replicates were within 10% and recoveries for spiked samples were within 75–100% of expected values.

2.2.3. *Organic matter degradation*

Five Rapid Organic Matter Assessment (ROMA) plates were deployed at four sampling sites in the estuary and North Lagoon region (HC, PP, LP, NM) 11 days prior to the sampling, following a design by O'Meara et al. (2017). The ROMA plates have vertically-aligned columns of substrate-filled holes, and during the deployment period the consumption of the substrate within the holes has been found to be influenced by differences in redox conditions in marine sediments and vertical distributions of fauna (Hewitt et al., 1996; Thrush et al., 1996; Lohrer et al., 2010). The holes in the ROMA plates were initially filled with a substrate comprising a 0.029 g C/ml mixture of food grade agar, microcrystalline cellulose (CAS 9004-34-6; Thermofisher), and powdered bran. Ratios of these substrates were adapted from bait lamina recipes and optimized for estuarine ecosystems (O'Meara et al., 2017). After 11 days, ROMA plates were retrieved from the sediment and carbon consumption was measured by the change in agar volume in each hole on the ROMA plate following O'Meara et al. (2017). ROMA plates could not be used in the South Lagoon as the mixed substrate was not stable in salinities >80.

2.3. *Selection of functional traits and trait information*

To assess the relationship between benthic macrofauna functional traits and sediment biogeochemistry and nutrient concentrations, a set of six functional traits and 29 trait-modalities were selected (Table 1). The functional traits selected describe behavioural, morphological, and physiological attributes of the organisms, and are closely related to ecosystem functioning, such as nutrient cycling and sediment transport (Lam-Gordillo et al., 2020a). Trait information was obtained from the South Australia Macrobenthic Trait (SAMT) database (Lam-Gordillo et al., 2020b). The SAMT database applied a fuzzy coding procedure assigning scores from 0 to 1, with 0 being no affinity and 1 being high affinity to a trait (for details see Lam-Gordillo et al., 2020b).

Table 1
List of the functional traits and traits-modalities selected based on their effect on nutrient cycling and sediment transport (Lam-Gordillo et al., 2020a). Acronyms are used in Fig. 6.

Trait	Trait modalities	Acronym
Bioturbator	Biodiffusor	Bdiff
	Bioirrigator	Birri
	No bioturbation	Nbio
	Surface modifier	Sumo
Body size	Large (>20 mm)	Lar
	Medium (5–20 mm)	Med
	Small (0.5–5 mm)	Sma
Feeding mode	Deposit feeder	Defe
	Filter/suspension	Fisus
	Grazer/scraper	Graz
	Omnivore	On
	Predator	Pred
	Scavenger/opportunist	Scav
	Sub-surface deposit feeder	Ssdf
Morphology	Hard	Hard
	Hard exoskeleton	Hexos
	Hard shell	Hshell
	Irregular	Irre
	Round	Rou
	Soft/fragile	Fraso
	Vermiform	Verm
Living habit	Attached/sessile	Att/S
	Burrower	Burr
	Free living/surface crawler	Free
	Tube dwelling	Tudw
Sediment position	Attached	Att
	Bentho-pelagic	Bepel
	Deeper than 3 cm	Deep
	Surface shallow <3 cm	Sursh

2.4. *Data analysis*

2.4.1. *Environmental data analysis*

To test for differences in environmental variables between sites, univariate PERMutational ANalysis Of VAriance (PERMANOVA) and multiple pair-wise tests were conducted, using Euclidean distance and 9999 permutations for the single variables in PRIMER v7 with PERMANOVA− add on software (Anderson et al., 2008). Environmental data were normalised prior to multivariate analysis (Clarke et al., 2014) and tested for collinearity. As no redundant environmental variables were identified, all variables were included in the analyses. Principal Component Analyses (PCA) were performed to explore spatial patterns in environmental conditions using the package "vegan" (Oksanen et al., 2019) in R software (R Development Core Team, 2018).

2.4.2. *Biological data analysis*

Benthic macrofauna data were analysed for diversity (as species richness) and abundance (individuals per m^{-2}). Functional traits were analysed as community-level weighted means of trait values (CWM). CWM trait values were calculated using the package "FD" (Laliberté et al., 2014). Taxa abundance and CWM data were fourth root transformed prior to analyses. To assess community structure differences between sites, Principal Component Analysis (PCA) were performed for the benthic macrofauna and functional trait data with the package "vegan" (Oksanen et al., 2019). CWM and PCA were performed in R software (R Development Core Team, 2018). Differences across sites in species richness, abundance, community structure, and OM degradation (also testing for differences across depths) were analysed using PERMANOVA. For univariate tests for the single variables, the tests were based on Euclidean distance similarity and 9999 permutations. In addition, multiple pair-wise tests were conducted if the fixed factor (sites) was significant to identify which groupings contributed to differences from PERMANOVA main tests (Anderson et al., 2008). To evaluate the relationship between benthic macrofauna and environmental conditions (porewater nitrate, nitrite, ammonium, phosphate and sediment OM, total carbon, total nitrogen, and total phosphorus), non-parametric multiple regressions were performed with the DISTLM routine, using Euclidean distances, 9999 permutations, and the macrobenthic fauna as predictor variables (McArdle and Anderson, 2001). PERMANOVAs, pair-wise tests, and DISTLM analyses were carried out using PRIMER v7 with PERMANOVA+ add on.

To assess relationships between benthic macrofauna, their functional traits, and sediment biogeochemistry and porewater nutrient concentrations (fourth corner analysis), several generalized linear latent variable models (GLLVMs) were performed with the R package "gllvm" (Niku et al., 2020). GLLVMs were constructed using the six most abundant taxa across sites, and a negative binomial distribution as the best fit model (lowest Akaike information criterion – AIC; Table S3) (Niku et al., 2019). Level plots were performed for visualizing the interactions between taxa-traits and environmental conditions obtained with the GLLVMs using the R package "lattice" (Sarkar, 2008).

3. Results

3.1. *Environmental variables*

The environmental variables were characterised by a strong spatial differentiation between sites in the Murray Estuary, North Lagoon and South Lagoon. Significant differences in environmental variables were found across sites (PERMANOVA $p < 0.01$; Tables 2; S4; Fig. 2). Extreme hypersaline conditions (salinity >80) were recorded at sites in the South Lagoon compared to the other sites (Fig. 2a), while pH was more alkaline at PP, LP and NM compared to the other sites ($p < 0.01$; Table S4; Fig. 2b). Sediment chlorophyll *a* content, as a proxy for microphytobenthic biomass, showed higher concentrations at two sites (HC and LP), while the other five sites were more homogeneous (Fig. 2c). Sediment OM content was higher at sites in the South Lagoon (HG, JP, and SC) and lower in the North Lagoon (LP and NM) (Fig. 2d). Sediment grain size was coarser and poorly sorted in the South Lagoon sites compared to the other sites (Fig. 2e–f).

Porewater nitrate concentrations were greater at the Murray Estuary sites, decreasing towards the South Lagoon (Fig. 2g). Although concentrations of nitrite followed a similar pattern as nitrate, nitrite concentrations were lower (Fig. 2h). Porewater ammonium concentrations were higher at JP, SC in the South Lagoon and LP in the North Lagoon, with PP and LP significantly different compared to the other sites ($p < 0.01$; Table S4; Fig. 2i). In contrast, porewater phosphate concentrations were similar across all sites (Fig. 2j). Sediment total nutrient concentrations also varied significantly across sites ($p < 0.01$; Table 2; Fig. 2k–n). Total nitrogen, total carbon and carbon/nitrogen ratio followed the same pattern, with the highest concentrations recorded at sites in the South Lagoon (HG, JP, and SC), and decreasing concentrations from sites in the Murray Estuary towards the sites at the North Lagoon (Fig. 2k–m). Concentrations of total phosphorus were highest at HC, decreasing towards NM, but increasing again at the South Lagoon sites (Fig. 2n).

The PCA analyses revealed distinct spatial variation of the Coorong porewater nutrient concentrations and water column variables, as well as sediment variables with 58.4% and 82.8% of variability explained by the first two axes respectively (Fig. 3). Based on porewater nutrient concentrations, and sediment and water column variables, sites in the South Lagoon were separated from the other sites by salinity, organic matter content, sediment grain size and ammonium. Although less evident, sites in the Murray Estuary and North Lagoon were also differentiated, mainly by high concentrations of chlorophyll *a* at HC, and the more alkaline pH recorded at NM. Yet, large amount of variation was unexplained (Fig. 3a). Based on sediment variables, sites were separated according to their region: Murray Estuary (HC and PP), North Lagoon (LP and NM), and South Lagoon (HG, JP, and SC), with conductivity and total carbon as the main drivers (Fig. 3b).

Table 2
Test results from univariate one-way fixed factor PERMANOVA to compare the environmental conditions and nutrient concentrations across sites. Significant *p* values are highlighted in bold.

Source	df	SS	MS	Pseudo-*F*	*P*(perm)
Chlorophyll *a* (mg·m^{-3})					
Site	6	30.027	5.004	11.132	**0.0001**
Residual	28	12.588	0.449		
Total	34	42.615			
Organic matter (%)					
Site	6	20.250	3.375	37.402	**0.0001**
Residual	28	2.530	0.090		
Total	34	22.800			
Median grain size (D50)					
Site	6	218,000.000	36,340.000	63.495	**0.0001**
Residual	28	16,025.000	572.330		
Total	34	234,000.000			
Sorting (σG)					
Site	6	5.219	0.869	1.484	0.1651
Residual	28	16.403	0.585		
Total	34	21.622			
pH					
Site	6	1.630	0.271	4.161	**0.0002**
Residual	28	1.820	0.065		
Total	34	3.450			
Salinity					
Site	6	43,544.000	7257.300	2691.400	**0.0001**
Residual	28	75.500	2.696		
Total	34	43,619.000			
Nitrate (mg·L^{-1})					
Site	6	0.655	0.109	6.734	**0.0001**
Residual	28	0.454	0.016		
Total	34	1.110			
Nitrite (mg·L^{1})					
Site	6	0.085	0.014	1.503	**0.007**
Residual	28	0.266	0.009		
Total	34	0.352			
Ammonium (mg·L^{-1})					
Site	6	5.537	0.922	2.075	0.0439
Residual	28	12.454	0.444		
Total	34	17.991			
Phosphate (mg·L^{-1})					
Site	6	0.229	0.038	2.282	0.0182
Residual	28	0.468	0.016		
Total	34	0.697			
Total nitrogen (% TN)					
Site	6	0.018	0.003	21.839	**0.0001**
Residual	14	0.002	0.001		
Total	20	0.020			
Total carbon (% TC)					
Site	6	10,860.000	181.000	285.180	**0.0001**
Residual	14	8.880	0.634		
Total	20	1094.900			
Carbon/nitrogen (TC/NT)					
Site	6	734,000.000	122,000.000	102.520	**0.0001**
Residual	14	16,706.000	1193.300		
Total	20	751,000.000			
Total phosphorus (mg/kg)					
Site	6	276,000.000	45,965.000	48.728	**0.0001**
Residual	14	13,206.000	943.300		
Total	20	289,000.000			

3.2. *Macrobenthic fauna composition*

In total, 17 taxa were recorded across seven sites in the Coorong. The taxa richness recorded between sites was significantly different (PERMANOVA $p < 0.01$; Table 3), with significantly higher taxa richness at HC, PP, LP and NM compared to the three sites in the South Lagoon which contained almost no benthic macrofauna ($p < 0.01$; Fig. S1a). In terms of overall lagoonal benthic macrofauna abundance, Crustacea was the taxon with the greatest abundance (62.5%), followed by Bivalvia (21.1%) and Annelida (9.3%) (Fig. 4a). The total abundance of macrofauna individuals was significantly different across sites (PERMANOVA $p < 0.01$; Table 3). Individual densities at HC PP, and LP were > 100,000 ind·m^2, and significantly higher compared to the other four sites, NM with less than 30,000 ind·m^2, and HG, LP, and SC with less than 3000 ind·m^2 ($p < 0.01$; Figs. 4b; S1b).

3.3. *Functional traits composition*

The functional traits and their modalities (as CWM) varied significantly across all sites in the Coorong (Table 4). In general, sites in the Murray Estuary (HC and PP) and North Lagoon (LP and NM) were more similar to each other compared to the sites in the South Lagoon (HG, JP, and SC) (Fig. 5). In pairwise comparisons, significant differences in CWM trait modalities across sites were also identified (PERMANOVA $p < 0.01$; Figs. S2–S7). The expression of several functional trait modalities was similar across sites in the Murray Estuary and North Lagoon. In contrast, some trait modalities were absent at sites in the South Lagoon. For example, 'biodiffussor', 'bioirrigator' and 'surface modifier' were significantly higher at sites in the Murray Estuary and North Lagoon, but almost non-existent at sites in the South Lagoon, where 'no bioturbator' was the main trait expressed ($p < 0.01$; Figs. 5a; S2). 'Large' body size was only recorded in Murray estuary and North Lagoon sites, while 'medium' body size was significantly higher at JP and SC sites in the South Lagoon compared to the other sites ($p < 0.01$; Figs. 5b; S3). In terms of feeding mode, sites in the South Lagoon were mainly dominated by 'scavengers/opportunistic', however HG, JP, and SC were not significantly different to the other sites ($p < 0.01$; Figs. 5c; S4). 'Irregular' and 'vermiform' modalities were significantly different across the majority of the sites, while the other morphological trait modalities were more similar across sites. ($p < 0.01$; Figs. 5d; S5). The functional trait modalities 'burrower' and 'tube dwelling' were significantly higher at sites in the Murray Estuary and North Lagoon compared to the sites at the South Lagoon, while 'free living/surface crawler' was the only trait modality recorded at sites in the South Lagoon ($p < 0.01$; Figs. 5e; S6). Sediment position showed a similar pattern to living habit, with the modalities 'deeper than 3 cm' and 'surface shallow (<3 cm)' significantly higher at sites in the Murray Mouth and North Lagoon compared to the sites in the South Lagoon, while 'bentho-pelagic' was the unique modality recorded at the South Lagoon sites ($p < 0.01$; Figs. 5f; S7).

Across the entire Coorong, the macrobenthic functional trait modalities which were most expressed, in terms of community-level weighted means (CWM), were scavenger-opportunistic (Feeding Mode; contribution: 51.8%), medium size (5–20 mm) (Body Size; contribution: 48.9%), free living (Living Habit; contribution: 66.5%), no bioturbator (Bioturbation; contribution: 44.9%), bentho-pelagic (Sediment Position; contribution: 63.1%), and 'fragile-soft' Morphology with a contribution of 37.0% (Table 5).

3.4. *Macrobenthic and functional traits structure*

Significant community differences were identified across sites for both taxa and functional traits (PERMANOVA $p < 0.01$, Table 6). The PCA analysis revealed different structures across sites with 49.4% of the variability explained by the first two axes in taxa composition, and 83.3% of the variability explained by the first two axes in trait composition (Fig. 6). Based on taxa, sites were separated according to region Murray Estuary (HC and PP), North Lagoon (LP and NM), and South Lagoon (HG, JP, and SC). Sites in the South Lagoon were grouped together by a dominance of benthic insect larvae, North Lagoon sites LP and NM grouped mainly by Capitellidae, and Murray Estuary sites HC and PP by the snails *S. fragilis* and Hydrobiidae (Fig. 6a). The majority of the sites were significantly different to each other, except HG to JP, and

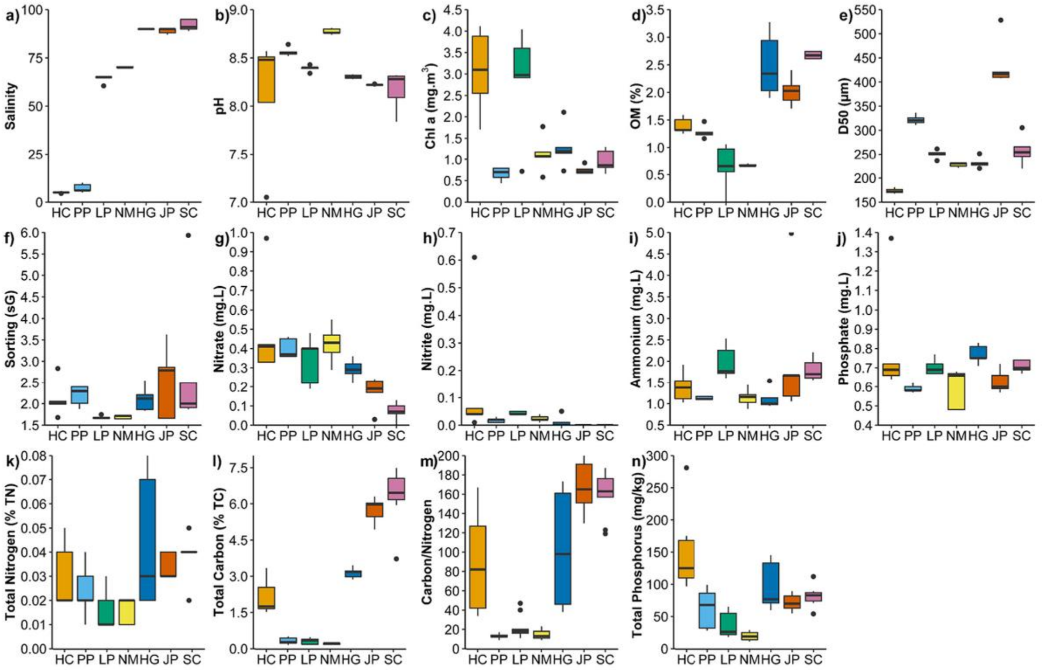

Fig. 2. Boxplots of the environmental variables recorded in the Coorong across sampling sites. Water column ($n = 5$) (a) salinity and (b) pH. Sediment ($n = 5$) (c) chlorophyll *a*, (d) organic matter content (OM), (e) mean grain size (D50), and (f) sorting coefficient. Pore water ($n = 5$) concentrations of (g) nitrate, (h) nitrite, (i) ammonium, and (j) phosphate. Sediment ($n = 3$) total concentrations of (k) nitrogen, (l) carbon, (m) carbon/nitrogen, and (n) phosphorus. HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

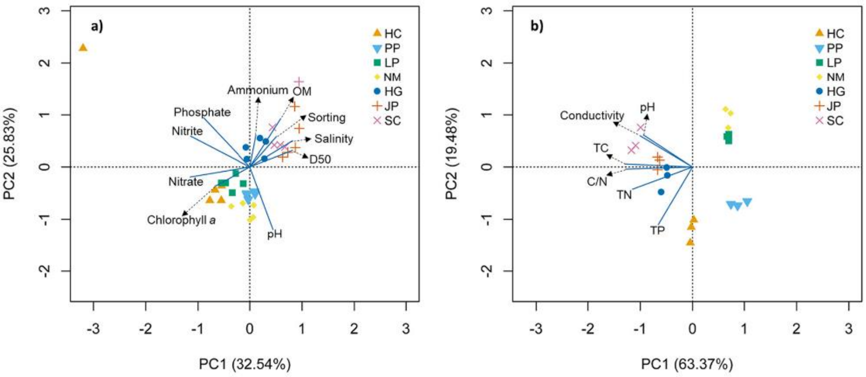

Fig. 3. Principal Component Analysis (PCA) plots for the environmental conditions measured across the seven sampling sites in the Coorong. a) Porewater nutrients and water quality variables; $n = 5$, b) sediment variables; $n = 3$. Black arrows point out origins of the labels to avoid overlaps. HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

JP to SC ($p < 0.01$; Fig. S8a). Although less evident, a separation between sites was also identified based on functional traits, HC, PP and LP were significantly more similar to each other, while sites in the South Lagoon were differentiated from the other sites by the trait modalities 'no bioturbation', 'free living', 'bentho-pelagic', 'scavenger' and 'grazer' (Figs. 6b; S8b).

Table 3
Test results from univariate one-way fixed factor PERMANOVA to compare number of taxa (richness) and abundance of macrobenthic fauna across sampling sites. Significant *p* values are highlighted in bold.

Source	df	SS	MS	Pseudo-*F*	*P*(perm)
Number of taxa (richness)					
Site	6	197.09	32.848	52.258	**0.0001**
Residual	28	17.60	0.628		
Total	34	214.69			
Abundance (ind·m^2)					
Site	6	2.19E+11	3.65E+10	42.178	**0.0001**
Residual	28	2.42E+10	8.66E+08		
Total	34	2.43E+11			

3.5. Relationships between macrobenthic fauna functional traits and porewater nutrient concentrations, sediment biogeochemistry and organic matter degradation

DISTLM analyses revealed relationships between benthic macrofauna, mainly Capitellidae, *S. aequisetis*, *A. semen*, *H. alba*, and Amphipoda, and the concentrations of porewater nutrients and sediment variables (Table 7; Fig. 7). Porewater concentration of nitrate was correlated with the abundance of *S. aequisetis*, *A. semen*, and Amphipoda (Table 7), showing low concentrations of nitrate when low abundance of macrobenthic fauna was recorded (Fig. 7a). Concentrations of nitrite in porewater followed a similar pattern to nitrate, being greater when high abundance of macrobenthic fauna was recorded (Fig. 7b), suggesting that the concentrations of nitrite were also influenced by *S. aequisetis*, *A. semen*, *H. alba*, and Amphipoda (Table 7). Porewater ammonium and phosphate concentrations were not significantly correlated to the benthic macrofauna ($p > 0.01$). However, for ammonium an opposite pattern compared to nitrate and nitrite was identified with concentrations increasing from sites in the Murray Estuary towards sites in the South Lagoon (Fig. 7c), while phosphate concentrations were very similar across all sites (Fig. 7d).

Sediment OM content showed an inverse relationship with the abundance of the benthic macrofauna (Table 7). OM was lower when the abundance of benthic macrofauna increased (Fig. 7e). Total carbon was significantly correlated with Capitellidae, *S. aequisetis*, *A. semen*, and Amphipoda (Table 7), with sediment total carbon decreasing with increasing abundance of benthic macrofauna (Fig. 7f). Sediment total nitrogen also showed a significant correlation of lower concentration at higher abundances of macrobenthic fauna (Capitellidae, *E. variabilis*, Corophiidae and Amphipoda) (Fig. 7g). Sediment total phosphorus content was also correlated to the abundance of benthic macrofauna (Table 7), being highest at both high and low macrobenthic fauna abundances and lowest at intermediate abundances (Fig. 7h).

Significant relationships were identified between the benthic macrofauna, their functional traits, and porewater nutrient and sediment variables (Fig. 8). Across all seven sites surveyed, we identified stronger relationships between functional traits and porewater nutrients than with sediment variables and functional traits relationships. Sites at the Murray Estuary (HC and PP) showed strong correlation of various functional traits to nitrate, nitrite, sediment OM, and total phosphorus contents. For example, the trait modalities 'bioirrigator', 'deposit feeder', 'scavenger', 'sub-surface deposit feeder', and 'surface shallow <3 cm' were correlated to porewater nitrite concentration and sediment OM content (Fig. 8a–b). At sites in the North Lagoon (LP and NM), trait modalities of bioturbator, body size and sediment position were the most correlated to porewater nitrite concentration, and sediment OM, chlorophyll-*a*, total carbon and total nitrogen contents (Fig. 8c–d). Sites in the South Lagoon (HG, JP, and SC) showed fewer and lower correlations between functional traits, porewater nutrient concentrations and sediment conditions. The trait modalities 'no bioturbation', 'medium' body size, 'free living' and 'bentho-pelagic' were the most correlated to porewater phosphate, and sediment OM and chlorophyll-*a* content (Fig. 8e–g).

Sediment OM degradation rates at the Murray Estuary and North Lagoon sites, determined using ROMA plates, differed significantly across sites and depths within sites (Table 8). Sites at the Murray Estuary (HC and PP) showed higher OM degradation rates compared to sites in the North Lagoon (LP and NM) (Fig. 9). Degradation rates in HC were significantly higher in the 1–3 cm depth horizon compared to other depths ($p < 0.01$; Table S5). At PP, degradation rates followed a similar pattern to those at HC, but the 4–7 cm depth horizon was also significantly different to the 16–19 cm horizon ($p < 0.01$; Table S5). LP and NM showed similar OM degradation rates across depths ($p > 0.01$; Table S5). Similar degradation rates were found at HC compared to PP, and LP compared to NM ($p > 0.01$; Table S6). The OM degradation rates at sites in the Murray Estuary were significantly different compared to sites in

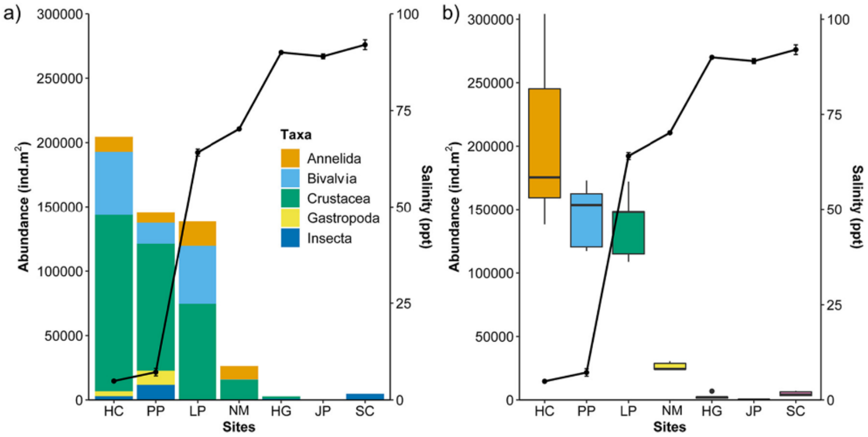

Fig. 4. Mean ($n = 5$) total abundance of benthic macrofauna (a) stacked bar graph by taxa and (b) box plot of all taxa pooled across each of the seven sampling sites in the Coorong. Black line shows the salinity at each sampling site. Error bars for salinity show the standard error (SE). HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

Table 4
Summary of the test results from univariate one-way fixed factor PERMANOVA to compare functional trait modalities across sampling sites. NC: no computed. Significant *p* values are highlighted in bold.

Trait	Trait modality	Pseudo-F	*p* value	Permutations
Bioturbator	Biodiffusor	42.568	**0.0001**	9946
	Bioirrigator	195.570	**0.0001**	9955
	No bioturbation	3375.40	**0.0001**	9913
	Surface modifier	282.060	**0.0001**	9945
Body size	Large (>20 mm)	105.030	**0.0001**	9946
	Medium (5–20 mm)	15.744	**0.0001**	9952
	Small (0.5–5 mm)	12.620	**0.0001**	9943
Feeding mode	Deposit feeder	95.299	**0.0001**	9960
	Filter/suspension	17.619	**0.0001**	9946
	Grazer/scraper	11.973	**0.0001**	9941
	Omnivore	NC	NC	NC
	Predator	1.088	0.3735	9945
	Scavenger/ opportunist	26.874	**0.0001**	9939
	Sub-surface deposit feeder	319.350	**0.0001**	9949
Living habit	Attached/sessile	NC	NC	NC
	Burrower	614.040	**0.0001**	9948
	Free living/surface crawler	724.460	**0.0001**	9952
	Tube dwelling	38.939	**0.0001**	9943
Morphology	Hard	NC	NC	NC
	Hard exoskeleton	NC	NC	NC
	Hard shell	9.853	**0.0001**	9933
	Irregular	299.160	**0.0001**	9947
	Round	10.034	**0.0001**	9951
	Fragile/soft	9.196	**0.0001**	9945
	Vermiform	47.164	**0.0001**	9948
Sediment position	Attached	NC	NC	NC
	Bentho-pelagic	1116.200	**0.0001**	9951
	Deeper than 3 cm	52.144	**0.0001**	9949
	Surface shallow <3 cm	1447.000	**0.0001**	9947

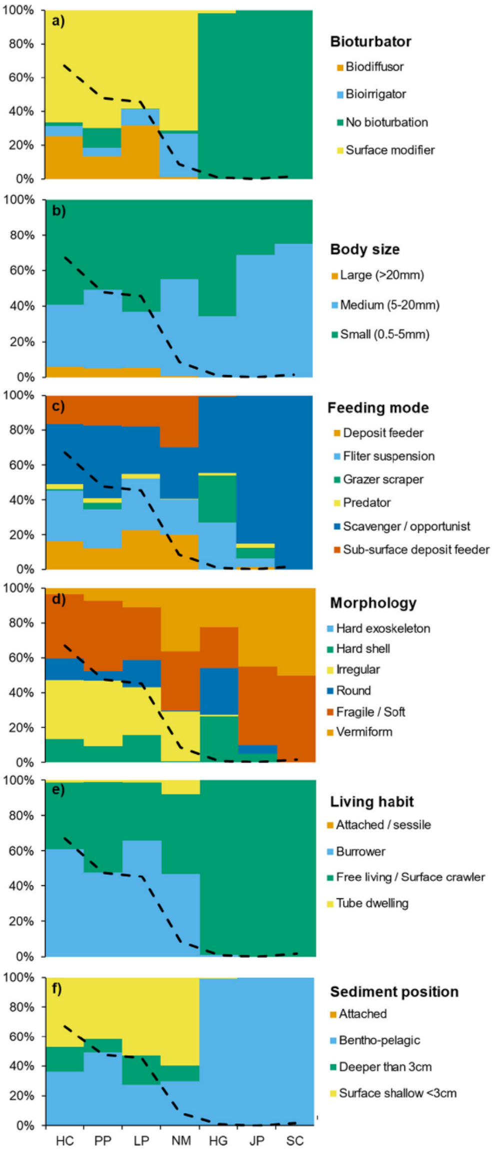

Fig. 5. Community-weighted means (CWM) of functional trait-modalities expression. Scale represents the percentage contribution to CWM recorded in the Coorong across sampling sites. Black dotted line shows the relative abundance to the maximum abundance recorded. HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

the North Lagoon in the 1–3 cm depth horizon ($p < 0.01$; Table S6). Significant differences were also found at HC and PP compared to LP in the 4–7 cm depth horizon, and at PP compared to LP and NM in the 16–19 cm depth horizon ($p < 0.01$; Table S6).

4. Discussion

In this study, we analysed benthic macrofauna communities, their functional traits, and the relationships between these biotic components, porewater dissolved and sediment total nutrients in the Coorong lagoon system along a salinity gradient from estuarine-to-hypersaline conditions. Our results revealed significantly different benthic communities and functional traits across the sampling sites mainly mediated by the extreme salinity gradient. Macrobenthic functional trait relationships with dissolved and solid phase nutrients suggested variation in sediment biogeochemistry and nutrient concentrations correlated with these biotic components, that in turn could enhance different ecosystem functioning across this system.

In accordance with our first hypothesis, we found that the extreme salinity gradient in the system strongly influenced the benthic macrofauna, delimitating their presence/absence, community structure, and therefore expression of functional traits, consistent with previous studies in the system (Dittmann et al., 2015, 2018). Despite the differences in macrobenthic communities and functional traits found across the entire system and between regions, communities and traits were similar within each of the regions. Benthic macrofauna community richness and abundance were higher within the Murray Estuary region (sites HC and PP), where salinity was typically brackish to marine due to freshwater inputs from the River Murray-Lower Lakes. Abundance decreased in the North Lagoon (sites LP and NM; salinity 50–70), and the lowest benthic macrofauna richness and abundances were found at the South Lagoon sites (HG, JP, and SC), where hypersaline (89–92) conditions were recorded. This pattern of decreasing benthic macrofauna, in terms of both abundance and richness, was attributed to the salinity tolerance of the organisms that inhabit the system, with bivalves, crustaceans,

Table 5
Total CWM contribution of functional traits and their modalities across sampling sites. Highest contribution shown in bold.

Trait	Trait modality	CWM trait contribution
Bioturbator	Biodiffusor	10.19
	Bioirrigator	6.63
	No bioturbation	**44.86**
	Surface modifier	38.31
Body size	Large (>20 mm)	2.51
	Medium (5–20 mm)	**48.95**
	Small (0.5–5 mm)	48.55
Feeding mode	Deposit feeder	10.36
	Filter/suspension	19.03
	Grazer/scraper	5.39
	Omnivore	0.00
	Predator	1.78
	Scavenger/opportunist	**51.77**
	Sub-surface deposit feeder	11.68
Living habit	Attached/sessile	0.00
	Burrower	31.76
	Free living/surface crawler	**66.55**
	Tube dwelling	1.69
Morphology	Hard	0.00
	Hard exoskeleton	0.00
	Hard shell	10.11
	Irregular	18.36
	Round	9.43
	Fragile/soft	**37.01**
	Vermiform	25.10
Sediment position	Attached	0.00
	Bentho-pelagic	**63.08**
	Deeper than 3 cm	8.07
	Surface shallow <3 cm	28.84

Table 6
Test results from univariate one-way fixed factor PERMANOVA to compare macrobenthic community structure based on taxa and functional traits across sampling sites. Significant *p* values are highlighted in bold.

Source	df	SS	MS	Pseudo-*F*	*P*(perm)
Community					
Taxa					
Site	6	69,634.000	11,606.000	29.589	**0.0001**
Residual	28	10,982.000	392.230		
Total	34	80,617.000			
Traits					
Site	6	42,000.000	6990.000	19.502	**0.0001**
Residual	28	10,000.000	358.610		
Total	34	52,000.000			

gastropods, and polychaetes occurring at salinities <60 ppt, while only insect larvae were found in hypersaline conditions in the South lagoon (Dittmann et al., 2015; Remaili et al., 2018).

Functional traits were site-dependent, and attributed to changes in both benthic macrofauna and habitat conditions; a finding commonly reported in other systems (e.g. Douglas et al., 2019; Gammal et al., 2019; Henseler et al., 2019; Villnäs et al., 2019). The differences identified in functional traits followed a similar pattern as the taxonomic composition, with higher expression of trait modalities at the Murray Estuary sites, and the lowest recorded in the South Lagoon sites. However, the multivariate structure of the functional trait composition showed similarities in trait expression at HC, PP and LP, NM distinct from trait compositions in from other sites, and the South Lagoon sites grouping together, indicating that the functional traits at the study sites were more homogenous than the taxonomic composition, similar to findings reported in other studies (e.g. Wong and Dowd, 2015; Henseler et al., 2019; Lam-Gordillo et al., 2021).

Sediment biogeochemistry and porewater nutrients changed across the system, showing significant differences between sites and regions, which concurred with the extreme salinity gradient. We found indications that these differences were correlated with the benthic macrofauna (abundance, community structure) and their functional traits, as frequently described in other studies (e.g. Braeckman et al., 2014; Villnäs et al., 2019; Bon et al., 2021). For example, sites in the Murray Estuary and North Lagoon regions showed the highest porewater concentrations of nitrate and nitrite, which coincided with the highest abundance of benthic macrofauna dominated by burrowing and bioturbating taxa, particularly the polychaete *Simplisetia aequisetis*. This implies that these macrobenthic organisms could influence sediment nutrient cycling, which aligned with our second prediction. Benthic macrofauna have been shown to increase rates of total dissolved inorganic nitrogen export from the sediment to the overlying water (see review by Stief, 2013), which would decrease porewater ammonium concentrations due to increased ammonium loss. Macrofauna can also stimulate rates of bacterial nitrification, a biological sink for ammonium and source of nitrite and nitrate, and rates of denitrification, which is a sink for nitrate and a source or sink for nitrite, favouring benthic nitrogen loss as gaseous end-products via coupled nitrification-denitrification (Welsh, 2003; Stief, 2013; Norkko et al., 2019; Wyness et al., 2021). This is proposed to occur by promoting sediment oxygenation, which is correlated to the trait 'bioturbation', i.e. as the burrow wall sediments increase the volume of oxic sediments, where nitrification can occur, the total surface area of oxic-anoxic interfaces increases and denitrification is enhanced by up to several fold (Kristensen, 2000; Welsh, 2003; Stief, 2013). Thus, the presence of active nitrification within the sediments lining macrofaunal burrows would tend to increase average porewater nitrite and nitrate concentrations, as these solutes would accumulate within the oxic sediment layer and this effect would increase with increasing macrofauna abundance, as the relative volume of burrow wall sediments increased (Welsh, 2003, Stief, 2013). In the Coorong, the presence of macrofauna burrows in the Murray Estuary and North Lagoon sediments favoured lower porewater ammonium concentrations due to increased rates of conversion of ammonium to nitrite and nitrate via nitrification, and the diffusion of porewater ammonium in and outside the burrow by bioirrigation (Welsh, 2003, Stief, 2013). These results align with a long-term mesocosm experiment using the Thalassinidean shrimp (*Trypaea australiensis*), which reported a decrease in sediment ammonium content compared to the sediment control, as well as stimulated nitrification rates and ammonium effluxes to the water column (Jordan et al., 2009).

At sites in the South Lagoon, the absence of burrowing and bioturbating macrofauna, and thereby oxic burrow wall sediments where nitrification could occur, resulted in lower average pore water nitrate and nitrate concentrations, and is likely to have contributed to the higher porewater concentrations of ammonium recorded at these sites. The absence of faunal burrows would favour accumulation of ammonium in the sediment porewater due to decreased conversion of ammonium to nitrite and nitrate, and decreased ammonium efflux to the water column, as diffusive exchange between the sediment and overlying water would be limited to the sediment surface (Welsh, 2003, Stief, 2013). However, no significant correlation between ammonium, phosphate and the macrobenthic abundance was found, which could be explained by other processes occurring in the lagoon, such as aquatic plants uptake (*Ruppia* sp.), eutrophication, and high sulfate reduction (Mosley et al., 2020).

In the Coorong sediments, the modern OM deposited and degraded was consistent with an algal (phytoplankton-derived) source based on C and N isotope and ^{13}C NMR techniques (Krull et al., 2009). Differences in sediment OM content and total carbon (% TC) also corresponded with differences in the benthic macrofauna, with a general increase in sediment OM and total carbon with decreasing benthic macrofauna abundance. Lower sediment OM contents were found in the Murray Estuary and North Lagoon, correlated with benthic macrofauna performing bioturbating and burrowing activities (e.g. *A. semen*, *Capitella* sp., *S. aequisetis*), but were also in concordance with the high expression of the functional trait modalities 'deposit feeder', 'filter suspension' and

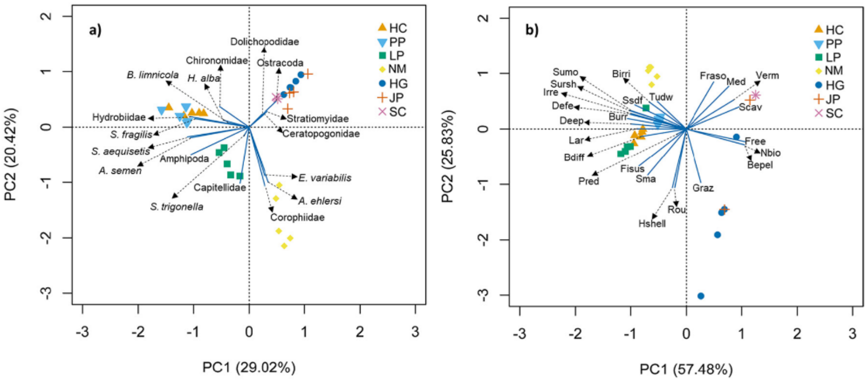

Fig. 6. Principal Component Analysis (PCA) plots for benthic communities based on the taxonomic (a) and trait (b) composition across sampling sites. Black arrows point out origins of the labels to avoid overlap. HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek. Labels (acronyms) in panel b) are defined in Table 1.

Table 7
Result of DISTLM forward analysis. Only significant ($p < 0.01$) results are shown.

Variable	R^2	SS (trace)	Pseudo-F	p-Value	Proportion
All	0.63				
Capitellidae		43.306	4.817	0.0004	0.127
Simplisetia aequisetis		64.435	7.716	0.0001	0.190
Arthritica semen		64.258	7.690	0.0001	0.189
Hiatula alba		45.445	5.091	0.0046	0.134
Amphipoda		81.150	10.346	0.0001	0.239
Nitrate	0.68				
Simplisetia aequisetis		0.312	12.929	0.0008	0.282
Arthritica semen		0.294	11.896	0.0009	0.265
Amphipoda		0.428	20.748	0.0001	0.386
Nitrate	0.44				
Simplisetia aequisetis		0.036	3.772	0.0004	0.103
Arthritica semen		0.038	3.963	0.0004	0.107
Hiatula alba		0.124	17.911	0.0093	0.352
Amphipoda		0.030	3.042	0.0031	0.084
Organic matter	0.92				
Capitellidae		14.473	57.516	0.0001	0.635
Euchone variabilis		4.969	9.209	0.0035	0.218
Simplisetia aequisetis		7.522	16.273	0.0006	0.330
Arthritica semen		7.916	17.577	0.0003	0.348
Amphipoda		13.367	46.875	0.0001	0.587
Corophiidae		7.775	17.102	0.0003	0.341
Ostracoda		4.813	8.842	0.0039	0.211
Total carbon	0.97				
Capitellidae		657.270	28.535	0.0002	0.600
Simplisetia aequisetis		434.750	12.512	0.0021	0.397
Arthritica semen		418.660	11.763	0.0041	0.382
Amphipoda		741.680	39.895	0.0001	0.677
Total nitrogen	0.97				
Capitellidae		0.015	64.905	0.0001	0.774
Euchone variabilis		0.006	8.027	0.0086	0.297
Amphipoda		0.009	14.935	0.0014	0.440
Corophiidae		0.008	11.736	0.0015	0.382
Total phosphorus	0.98				
Capitellidae		183,400.000	33.001	0.0001	0.635
Euchone variabilis		89,584.000	8.535	0.0096	0.310
Hiatula alba		127,250.000	14.948	0.0052	0.440
Corophiidae		109,220.000	11.543	0.0043	0.378

'sub-surface deposit feeder'. It has been suggested that high abundance of biodiffuser and biorrigator fauna traits in combination with other feeding modes enhance microbial activities which are ultimately responsible for OM remineralisation, therefore promoting nutrient cycling (Welsh, 2003; Braeckman et al., 2014; Villnäs et al., 2019; Bon et al., 2021). For example, organisms which inhabit burrows are proposed to influence OM degradation rates by increasing oxygen transfer to the sediment and the overall volume of oxic sediment by irrigating their burrows with the overlying water (Kristensen, 2000; Welsh, 2003). Bioturbation by organisms can influence OM degradation rates by physically transporting organic particles between sediment redox zones, resulting in decomposition occurring under alternating oxic-anoxic conditions (Aller, 1994). However, this could be also correlated to a eutrophication gradient, with lower OM content in water and consequently lower OM loads to the sediment, as previously suggested in another system (Grebmeier et al., 1988).

In contrast, higher sediment OM and total carbon contents were recorded at sites in the South Lagoon, which is consistent with the low abundance and low taxonomic and functional trait diversity present in this region. The macrobenthic communities at sites in the South Lagoon consisted of low abundances of primarily of small sized insect larvae with free living/surface crawler living habit. Thus, these communities would only have limited interaction with the sediment and little, if any, influence on oxygen availability in the deeper sediments. Thus, aerobic sediment zones were largely limited to the sediment surface and dependent upon diffusion of oxygen from the overlying water. Consequently, the bulk of the sediment OM would be permanently buried in anoxic sediment layers, where OM mineralisation rates are low (Kristensen, 2000) favouring OM accumulation. The findings suggesting that sediment OM content correlated with macrofauna communities by stimulating OM mineralisation rates was also supported by our in situ determinations of OM degradation rates using the ROMA plates technique at the Murray Estuary and North Lagoon sites, indicating that higher organic matter degradation rates in surface sediments occurred when bioturbating and burrowing macrobenthic abundance is greater. Laboratory and/or field transplantation experiments would be beneficial to better establish causal links between macrobenthic fauna, organic matter and nutrient cycling processes in the Coorong.

5. Conclusion

Changes in benthic macrofauna abundance and functional trait composition across sites and regions were mainly determined by the

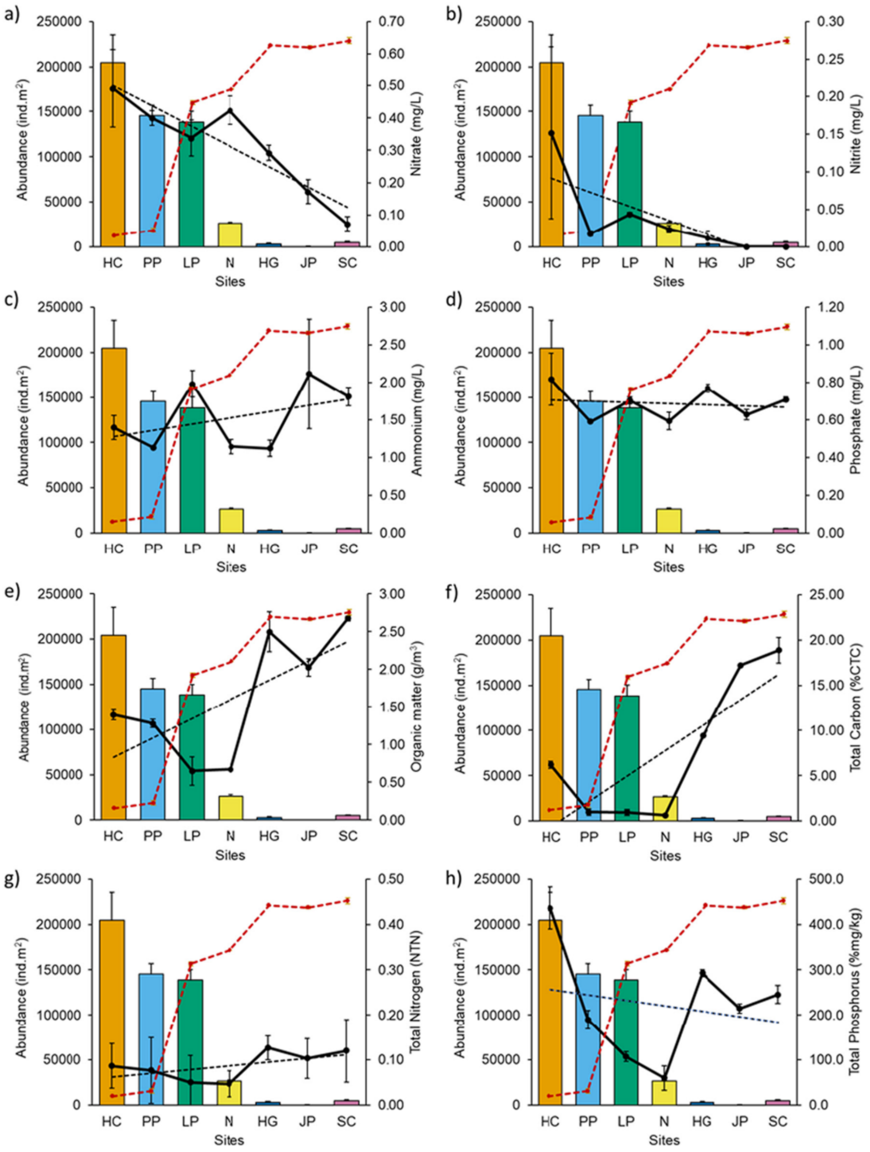

Fig. 7. Bar graphs showing the mean total abundance of benthic macrofauna in relation to (a–d) pore water nutrient concentrations, and (e-h) sediment variables ~~in the~~ across sampling sites. Error bars show the standard error (SE). Dotted lines show the trend line of each variable. For reference the red dotted lines show the relative salinity pattern, but the scale is not shown (refer Figs. 1 and 2). HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

extreme salinity gradient in the Coorong, and corresponded with changes in the sediment biogeochemistry. Differences in nutrient and organic matter patterns across the system were highly correlated with changes in macroinvertebrate diversity, abundance and functional traits. The high abundance and diversity of benthic macrofauna in the Murray Estuary and North Lagoon regions correlated with lower sediment concentrations of total nitrogen and total carbon, higher concentrations of oxidised nitrogen species (nitrate and nitrite) in porewater, and higher carbon mineralisation rates. In contrast, in the hypersaline South Lagoon larger bioturbating macrobenthic organisms were absent, and the loss of these organisms appeared to result in reduced nutrient and organic matter processing, which could favour

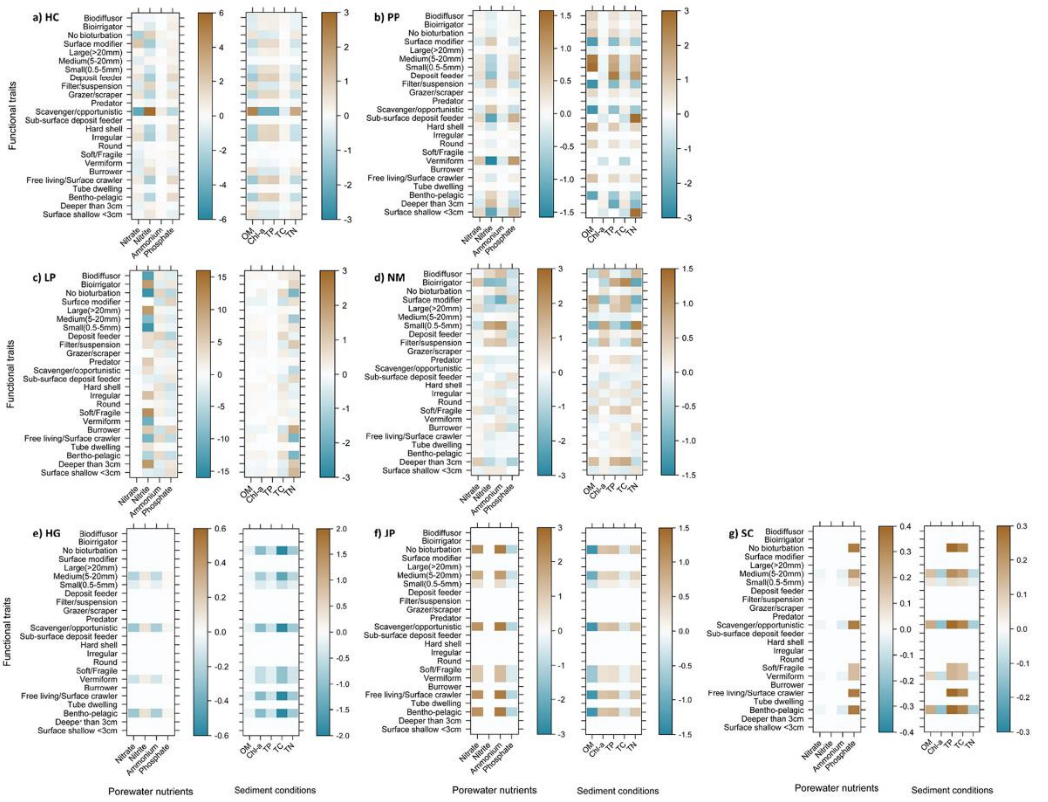

Fig. 8. Level plot for the fourth corner interaction (benthic macrofauna abundance, functional traits, and sediment conditions) using NB-GLLVM showing the interactions by site. The colour scale indicates significant interactions and magnitudes of the point estimates. HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena; HG: Hells Gate; JP: Jack Point; SC: Salt Creek.

Table 8
Test results of univariate one-way fixed factor PERMANOVA comparing organic matter degradation rates determined using ROMA plates across the four sampling sites in the Murray Estuary (Hunters Creek, Pelican Point) and North Lagoon (Long Point, Noonameena). Significant *p* values are highlighted in bold.

Source	df	SS	MS	Pseudo-*F*	P(perm)
Site	3	0.033	0.011	14.878	**0.0001**
Depth	4	0.055	0.014	18.832	**0.0001**
Site × depth	12	0.043	0.003	4.847	**0.0001**
Residual	80	0.059	0.001		
Total	99	0.190			

eutrophication conditions. This limited ecosystem functioning has likely had serious implications for management and conservation as the Coorong is now experiencing major issues with persistent and large-scale algal blooms. Further process-based research (e.g. using mesocosms and/or in situ experiments) would be beneficial to confirm the links between benthic ecosystem function and sediment quality along the Coorong. The research highlights the importance of preserving benthic communities for improving resilience to eutrophication issues, and to ensure healthy functioning of estuarine benthic ecosystems.

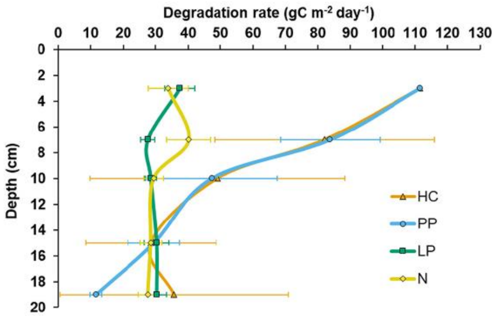

Fig. 9. Organic matter degradation rate across depths and sites in the Coorong, based on Rapid Organic Matter Assessment (ROMA) plates. Data points indicate mean values ($n = 5$) and error bars show the standard error (SE) HC: Hunters Creek; PP: Pelican Point; LP: Long Point; NM: Noonameena.

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CRediT authorship contribution statement

OL-G and SD conceived the original ideas for the manuscript with input and assistance from LM, SS and DW. OL-G developed the outline, collected, and analysed the data, prepared the figures and tables. OL-G wrote the manuscript with critical review and contributions from LM, SS, DW, and SD.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2021.113202.

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Appendix E. Supplementary information for Chapter 6.

Table S1. Summary of the variables measured during the *in-situ* experiment to investigate the effects of benthic macrofauna on biogeochemical conditions in Coorong sediments.

Measurement parameter/technique	Variable	Before experiment (at each site)	Week 0	Week 1	Week 2	Week 3	Week 4
Abundance	Macrofauna	x		x	x	x	x
Sediment	Grain size	x		x	x	x	x
	Sorting	x		x	x	x	x
	Fine sand content	x		x	x	x	x
	Total nitrogen	x		x			x
	Total organic carbon	x		x			x
Porewater	Salinity	x		x	x	x	x
	Nitrate	x		x	x	x	x
	Nitrite	x		x	x	x	x
	Ammonium	x		x	x	x	x
	Phosphate	x		x	x	x	x
DET-DGT	Sulfide		x	x			x
	Iron		x	x			x
DET	Ammonium		x	x			x
	Phosphate		x	x			x
	Nitrate		x	x			x

Table S2. Mean values of the sediment conditions recorded at Long Point and Policeman Point sites pre-experiment. D50= median grain size, FS = fine sand content, SE= Standard error (n = 3).

	D50 (um)	SE	Sorting	SE	FS (%)	SE	Total Organic Carbon	SE	Total Nitrogen	SE	Macrofauna (ind.m2)	SE
Long Point	229.39	20.72	1.75	0.03	0.45	0.04	0.21	0.04	0.02	0.01	6666.93	4525.72
0-2 cm	218.19	23.63	1.70	0.00	0.49	0.04	0.30	0.01	0.03	0.00	16520.66	2321.13
2-10 cm	208.42	11.54	1.75	0.03	0.48	0.03	0.17	0.01	0.02	0.00	3360.13	1046.18
10-20 cm	261.55	15.05	1.79	0.03	0.38	0.02	0.15	0.01	0.02	0.00	120.00	0.00
Policeman Point	173.63	3.83	1.64	0.05	0.61	0.04	0.19	0.05	0.02	0.00	0.00	0.00
0-2 cm	175.07	6.09	1.62	0.06	0.64	0.05	0.29	0.01	0.03	0.00	0.00	0.00
2-10 cm	170.81	1.96	1.58	0.02	0.66	0.02	0.15	0.01	0.01	0.00	0.00	0.00
10-20 cm	175.02	3.45	1.73	0.02	0.54	0.01	0.12	0.01	0.02	0.00	0.00	0.00

Table S3. Mean values of salinity and nutrient concentrations in porewater recorded at Long Point and Policeman Point sites pre-experiment. SE= Standard error (n = 3).

	Salinity	**SE**	**Nitrate (μmol/L)**	**SE**	**Nitrite (μmol/L)**	**SE**	**Ammonium (μmol/L)**	**SE**	**Phosphate (μmol/L)**	**SE**
Long Point	22.11	1.24	0.32	0.16	2.17	0.22	60.98	7.21	2.42	0.32
0-2 cm	21.00	1.00	0.32	0.00	2.17	0.00	49.34	2.77	2.53	0.42
2-10 cm	21.00	1.00	0.00	0.16	2.17	0.22	57.10	4.99	2.32	0.32
10-20 cm	24.33	0.67	0.65	0.16	2.17	0.22	75.95	0.55	2.32	0.21
Policeman Point	160	0.00	1.94	1.29	3.04	0.22	154.11	39.91	6.53	1.47
0-2 cm	160	0.00	3.06	0.65	3.26	0.22	115.31	29.38	4.32	0.74
2-10 cm	160	0.00	2.74	0.16	3.04	0.22	145.80	27.72	6.21	0.74
10-20 cm	160	0.00	0.16	2.10	2.83	0.22	201.23	53.22	9.06	1.37

Table S4. Test results from univariate one-way fixed factor PERMANOVA to compare *S. aequisetis* abundance between densities, weeks, depths, and sediment sources. Significant results are shown in bold. Den = density, We = weeks, Dep = depth, Si = sediment source.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Den	3	4216.6	1405.50	2.480	**0.0284**	9939
We	3	19573.0	6524.30	11.513	**0.0001**	9943
Dep	2	171390.0	85697.00	151.220	**0.0001**	9947
Si	1	3277.3	3277.30	5.783	**0.0043**	9954
DenxWe	9	9966.9	1107.40	1.954	**0.0169**	9918
DenxDep	6	6305.2	1050.90	1.854	**0.0430**	9936
DenxSi	3	1477.2	492.42	0.869	0.5062	9947
WexDep	6	55946.0	9324.30	16.454	**0.0001**	9943
WexSi	3	585.1	195.02	0.344	0.9234	9943
DepxSi	2	757.5	378.74	0.668	0.6002	9939
DenxWexDep	18	21211.0	1178.40	2.079	**0.0008**	9867
DenxWexSi	9	6543.8	727.09	1.283	0.1989	9910
DenxDepxSi	6	7248.5	1208.10	2.132	**0.0180**	9927
WexDepxSi	6	4396.8	732.80	1.293	0.2152	9928
DenxWexDepxSi	18	18226.0	1012.50	1.787	**0.0061**	9868
Res	216	122410.0	566.69			
Total	323	487260.0				

Table S5. Test results from univariate one-way fixed factor PERMANOVA to compare macrobenthic fauna abundance between density treatments, weeks, depths, and sediment sources. Significant results are shown in bold. Den = density, We = weeks, Dep = depth, Si = sediment source.

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Den	3	2883.4	961.15	1.356	0.1964	9913
We	3	10916.0	3638.60	5.135	**0.0001**	9935
Dep	2	242350.0	121170.00	171.000	**0.0001**	9939
Si	1	1428.8	1428.80	2.016	0.0965	9953
DenxWe	9	6755.8	750.65	1.059	0.3901	9865
DenxDep	6	7966.8	1327.80	1.874	**0.0069**	9891
DenxSi	3	1529.5	509.82	0.719	0.7298	9935
WexDep	6	19738.0	3289.60	4.642	**0.0001**	9902
WexSi	3	3112.7	1037.60	1.464	0.1420	9926
DepxSi	2	2281.3	1140.60	1.610	0.1200	9948
DenxWexDep	18	15436.0	857.57	1.210	0.1329	9861
DenxWexSi	9	6244.2	693.80	0.979	0.5107	9888
DenxDepxSi	6	7193.1	1198.80	1.692	**0.0216**	9914
WexDepxSi	6	7023.3	1170.50	1.652	**0.0281**	9929
DenxWexDepxSi	18	15630.0	868.35	1.225	0.1104	9864
Res	216	153060.0	708.61			
Total	323	533780.0				

Table S6. Test results from univariate one-way fixed factor PERMANOVA to compare salinity, median grain size, sorting coefficient, and find sand content between treatment densities, weeks, depths, and sediment sources. Only significant results are shown. Den = density, We = weeks, Dep = depth, Si = sediment source.

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Salinity						
Den	3	137.54	45.85	3.137	**0.0156**	9960
We	3	1568.00	522.65	35.760	**0.0001**	9958
Dep	2	1191.30	595.63	40.752	**0.0001**	9958
DenxWe	9	245.31	27.26	1.865	**0.0461**	9943
WexDep	6	490.03	81.67	5.588	**0.0001**	9943
WexSi	3	332.70	110.90	7.588	**0.0001**	9947
DenxWexSi	9	272.59	30.29	2.072	**0.0239**	9941
Median grain size (D50)						
We	3	11641.00	3880.50	11.134	**0.0001**	9954
Dep	2	46911.00	23455.00	67.297	**0.0001**	9939
Si	1	1510.10	1510.10	4.333	**0.0415**	9816
WexSi	3	6529.50	2176.50	6.245	**0.0003**	9953
DepxSi	2	19916.00	9957.80	28.571	**0.0001**	9948
Sorting (σG)						
Si	1	0.83	0.83	170.270	**0.0001**	9852
WexSi	3	0.06	0.02	4.449	**0.0044**	9957
DepxSi	2	0.04	0.02	3.633	**0.0281**	9954
DenxWexSi	9	0.09	0.01	2.000	**0.0397**	9940
DenxDepxSi	6	0.09	0.02	3.174	**0.0040**	9935
WexDepxSi	6	0.09	0.01	2.967	**0.0082**	9943
Find Sand (%)						
We	3	0.07	0.02	9.708	**0.0001**	9950
Dep	2	0.37	0.19	73.275	**0.0001**	9953
Si	1	0.11	0.11	43.857	**0.0001**	9838
DepxSi	2	0.16	0.08	30.988	**0.0001**	9949

Table S7. Test results from univariate one-way fixed factor PERMANOVA to compare sediment total carbon and total nitrogen content between treatment densities, weeks, depths, and sediment sources. Only significant results are shown. Den = density, We = weeks, Dep = depth, Si = sediment source.

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Total Organic Carbon (%TOC)						
We	1	0.07	0.07	63.043	**0.0001**	9849
Dep	2	0.23	0.11	96.500	**0.0001**	9957
Si	1	0.02	0.02	13.103	**0.0002**	9845
DenxSi	3	0.01	0.00	2.884	**0.0346**	9944
WexSi	1	0.01	0.01	9.106	**0.0038**	9858
DepxSi	2	0.01	0.01	6.087	**0.0031**	9953
Total Nitrogen (%TN)						
We	1	0.01	0.01	25.490	**0.0001**	9846
Dep	2	0.00	0.00	10.829	**0.0001**	9952

Table S8. Test results from univariate one-way fixed factor PERMANOVA to compare porewater ammonium, phosphate, nitrate, and nitrite concentrations between treatment densities, weeks, depths, and sediment sources. Only significant results are shown. Den = density, We = weeks, Dep = depth, Si = sediment source.

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Ammonium (mg/L)						
We	3	865.62	288.540	9.232	**0.0001**	9951
Dep	2	1660.70	830.360	26.567	**0.0001**	9950
Si	1	462.93	462.930	14.811	**0.0001**	9852
DenxWe	9	780.78	86.754	2.776	**0.0035**	9917
WexDep	6	416.43	69.406	2.221	**0.0290**	9936
WexSi	3	302.77	100.920	3.229	**0.0132**	9948
Phosphate (mg/L)						
We	3	1.71	0.571	2.905	**0.0330**	9936
Dep	2	5.79	2.893	14.705	**0.0001**	9954
Si	1	32.98	32.977	167.650	**0.0001**	9823
WexSi	3	3.38	1.128	5.734	**0.0009**	9945
DepxSi	2	5.60	2.798	14.225	**0.0001**	9950
Nitrate (mg/L)						
Den	3	0.19	0.065	4.803	**0.0016**	9957
We	3	0.69	0.231	17.213	**0.0001**	9947
Si	1	0.08	0.076	5.670	**0.0174**	9830
DenxWe	9	1.03	0.115	8.550	**0.0001**	9940
DenxSi	3	0.26	0.087	6.509	**0.0003**	9955
WexSi	3	1.18	0.394	29.320	**0.0001**	9958
DenxWexSi	9	0.89	0.099	7.337	**0.0001**	9933
Nitrite (mg/L)						
No significantly differences were found						

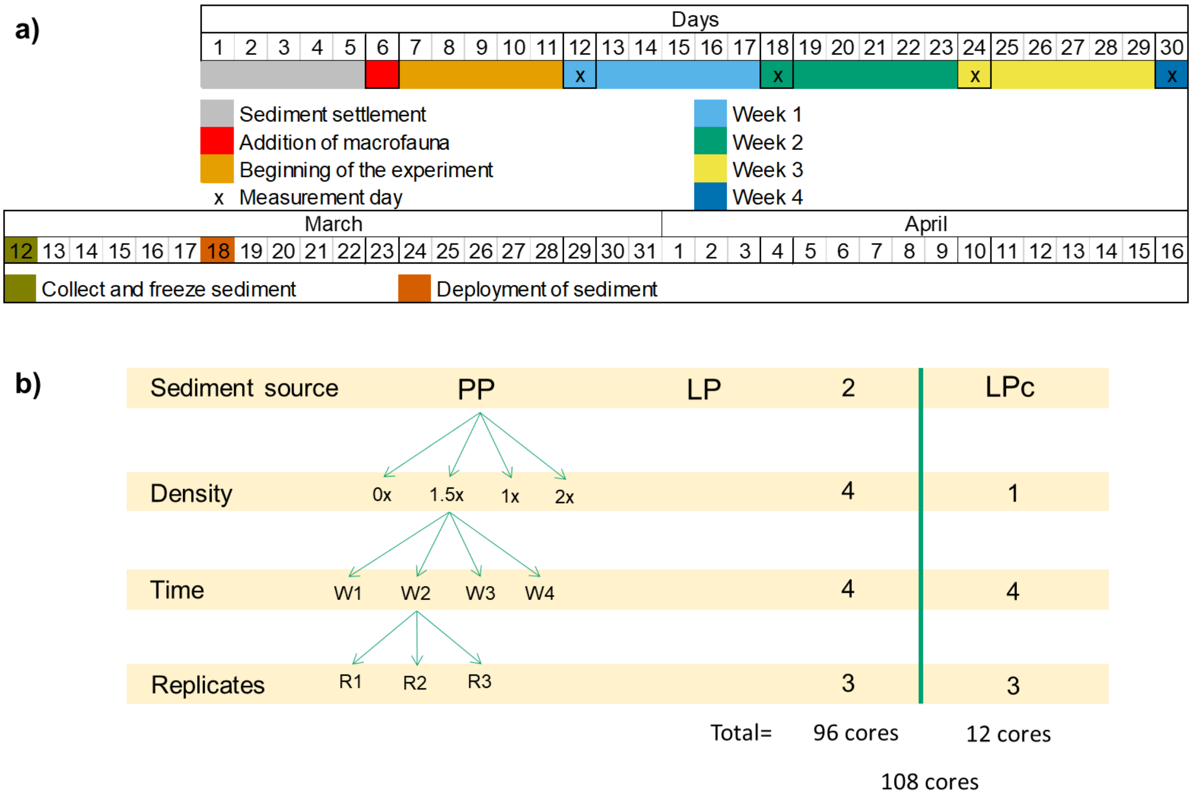

Figure S1. a) Timeframe and design for the *in situ* experiment to investigate the effects of bioturbation by benthic macrofauna on biogeochemical conditions in Coorong sediments. b) Experimental design. Levels are illustrated just once for each factor for clarity. PP: Policeman Point, LP: Long Point, LPc: Control.

Figure S2. Experimental design setting and measurement process carried out. a) Collection, transportation and b) freezing of sediment. c) Addition of mesh lids and tags to each of the experimental units. d) Deployment of experimental units. e) Illustration of experimental unit in the sediment under water. f-g) Aerial views of the complete grid of experimental units deployed at Long Point. h-i) Deployment of DGT/DET probes. j-k) *In situ* field laboratory set-up for sample processing and analysing the DGT/DET probes. l) Extraction of porewater using Rhizon samplers for analysing porewater salinity and nutrients at different depths. m) Sectioning of sediment into different depth horizons. n) Multi-tasking process of sediment collection for nutrient and sediment grain size and organic matter. o-p) Sediment sieving and sorting for macrobenthic fauna, and storage of samples in containers for further analyses.

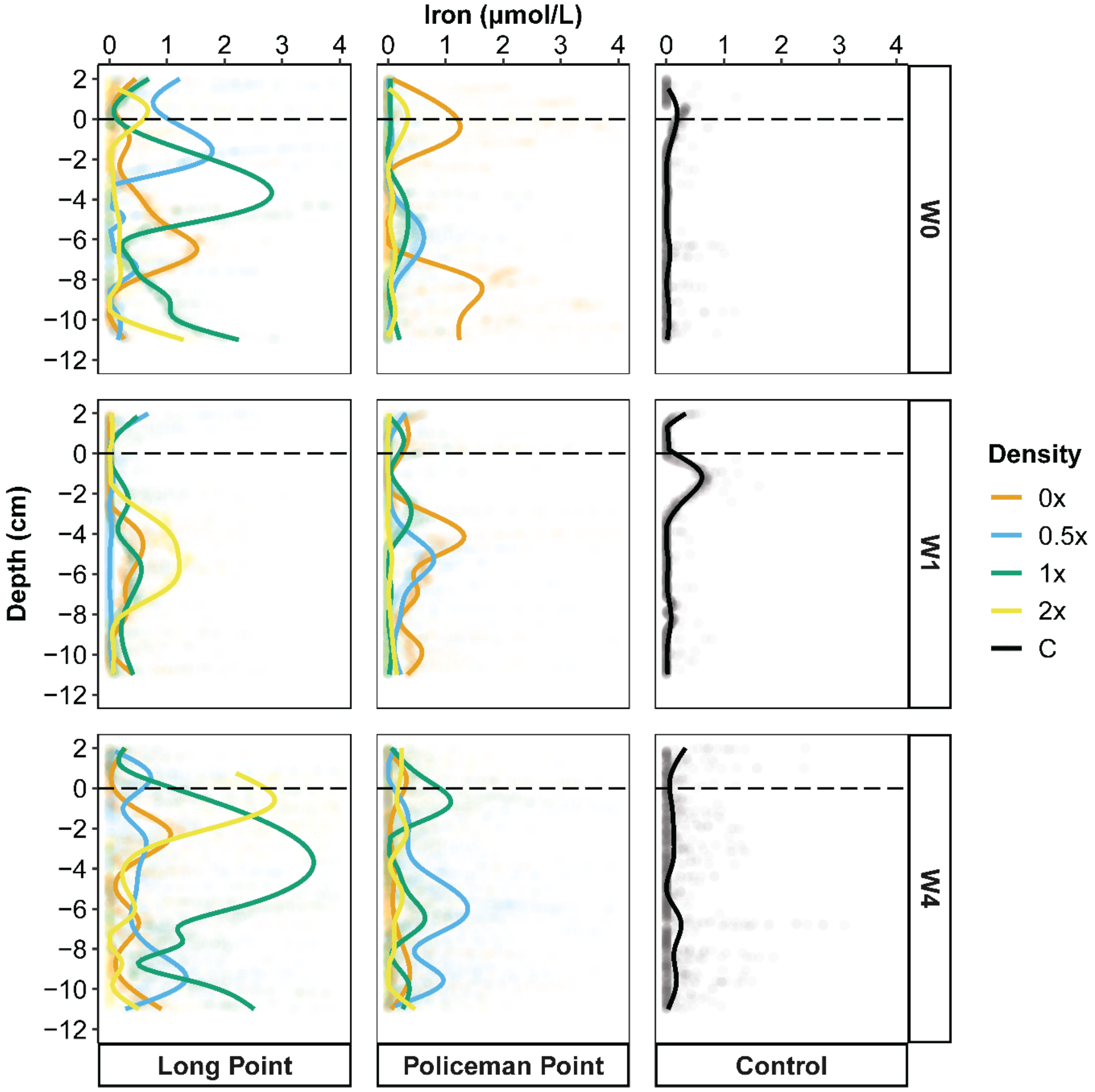

Figure S3. Generalized Additive Model (GAM) plots for porewater iron (II) concentrations. For better representation, extreme values are not shown, refer to Figure 7b for those values. Plots show significant differences of iron concentrations, and the influence of *S. aequisetis* and other macrofauna densities across weeks and depths. Colour shading represents the data values. W0 = Week 0, W1 = Week 1, W4 = Week 4. 0× = no *S. aequisetis* added, 0.5× = 3 *S. aequisetis*, 1× = 5 *S. aequisetis*, and 2× = 10 *S. aequisetis* added, C= Control. n=3.

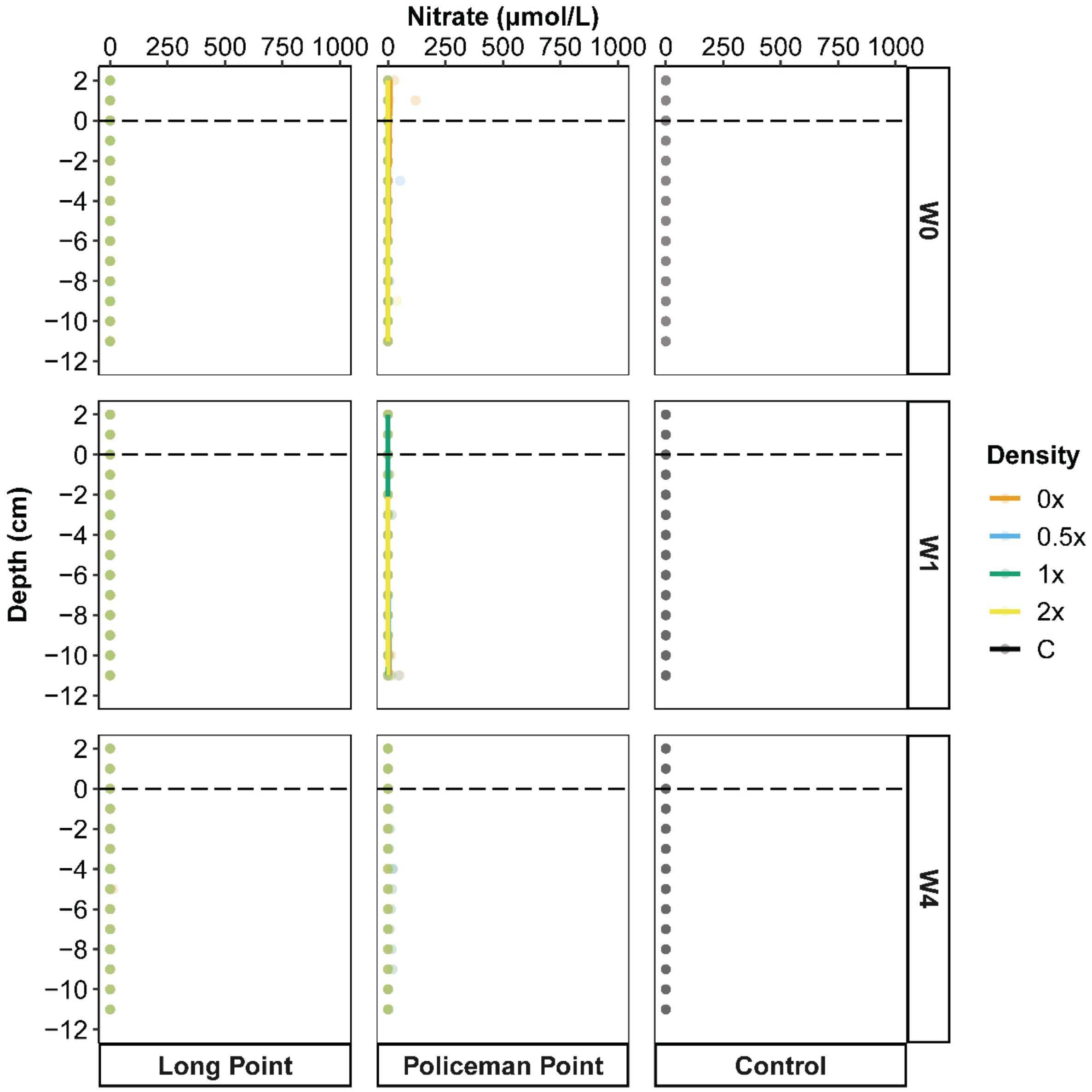

Figure S4. Generalized Additive Model (GAM) plots for porewater nitrate concentrations. Plots show values close to zero and no significant differences across weeks and depths. Colour shading represents the data values. W0 = Week 0, W1 = Week 1, W4 = Week 4. 0× = no *S. aequisetis* added, 0.5× = 3 *S. aequisetis*, 1× = 5 *S. aequisetis*, and 2× = 10 *S. aequisetis* added, C= Control. n=3.