Ecosystem functioning of polychaete reefs (*Ficopomatus enigmaticus*) in the Coorong, South Australia

By

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Preface

Pelicans in the vicinity of a polychaete reef (*Ficopomatus enigmaticus*) in the Coorong, South Australia. Photo credit: Laura Schroder.

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Thesis Summary

Biogenic reefs are created by calcifying invertebrates, which are important ecosystem engineers of shallow water environments. The provision of a living three-dimensional hard structure supports biodiversity by increasing the habitat heterogeneity in coastal ecosystems. Biogenic reefs are not only created by coral or shellfish, but also by polychaete worms such as those from the family Serpulidae. The ecosystem engineering role of reef-building polychaetes has received less scientific attention than typical biogenic reef builders. Ecosystem functions from biogenic reefs can include improvements to water quality through filtration, stabilisation of sediment, and provision of habitat for fish and invertebrates. For temperate estuaries in the Southern Hemisphere, polychaete reefs can be the only provider of biogenic reefs, yet the ecological interactions and ecosystem functions of polychaete reefs are not well known. There is limited insight into the value of polychaete reefs in the absence of other biogenic reefs (e.g. coral or shellfish) as primary habitat for both invertebrates and fish. This project filled knowledge gaps on the ecological interactions of polychaete reefs, focusing on their positive effects for associated fauna in an otherwise soft-sediment environment lacking physical structure and other biogenic reefs.

The cosmopolitan polychaete species *Ficopomatus enigmaticus* (Fauvel 1923) is one of the most prominent providers of serpulid reefs across brackish to hypersaline conditions in sheltered coastal lagoons and estuaries. It was proposed to have an Australian origin yet, molecular evidence for a true origin remains unclear. Biogenic reefs created by *F. enigmaticus* vary with the environment, and growth can be prolific under eutrophic conditions. Chapter 2 presents a classification of polychaete reef morphologies, and a spatial analysis on the density and distribution of reefs in a large temperate estuary in southern Australia; The Coorong. A remote sensing and ground truth approach identified irregular, halo and platform reefs in the estuary which reached high densities, compared to circular, irregular and platform types in the lagoon which reached lower densities. Average reef size increased from the estuary to lagoon, correlating with a gradient from low to high eutrophic conditions (i.e., reduced flushing). Chapter 3 used a radiocarbon dating approach to determine the history of *F. enigmaticus* reefs in the Coorong. Reef cores collected were modern in radiocarbon age, providing some evidence that the establishment of *F. enigmaticus* in the estuary and lagoon likely coincided with major ecological changes in the Coorong over the last two to three decades.

The effect of ecosystem engineers on associated fauna can vary with reef size and spatial extent. The different habitats of polychaete reefs in the Coorong provided a unique opportunity to test the effect of reef habitats on macroinvertebrate and fish diversity and abundance in the estuary and lagoon (Chapters 4 and 5).Chapter 4 describes the native fish diversity, abundance and community associated with polychaete reefs in the estuary and lagoon of the Coorong and compares these to non-reef habitats in similar and shallow depths. Fish surveys included a total of 192 fyke net deployments in spring, summer and autumn over two years. Small bodied and estuarine species are associated with polychaete reefs in the Coorong, particularly for Gobiidae. Spatial and temporal patterns of reef communities indicate fish at different life stages from juvenile to adult are associated with reefs for sheltering, feeding or breeding behaviours. To further elucidate interactions and foraging habitat value of polychaete reefs for fish, in Chapter 5 the macroinvertebrates associated with reef, reef sediments and non-reef sediments, were compared. This project provides novel insight into the ecosystem functions of temperate polychaete reefs, and their habitat value for associated fish and macroinvertebrates.

Declaration

I, Laura Schroder certify that this thesis:

1. does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university

2. and the research within will not be submitted for any other future degree or diploma without the permission of Flinders University; and

3. 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.

4. has been completed without the use of generative artificial intelligence tools

Signed: Laura Schroder

Date: 28/9/25

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Fish sampling was carried in accordance with the Australian Code for the Care and Use of Animals for Scientific Purposes, 8th Edition 2013, and the South Australian Animal Welfare Act 1985. Approval from the Flinders University and Southern Adelaide Local Health Network Animal Welfare Committee was granted for this project from October 2021 to December 2024 (AEC BIOL4446-3).

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Chapter 1. General Introduction

Biogenic reefs are complex, three-dimensional structures that increase habitat heterogeneity, which can be important for the provision of ecosystem services (Rullens et al., 2019; Sheehan et al., 2015; Stewart-Sinclair et al., 2020; Rullens et al., 2019). A typical biogenic reef is carbonate in nature, created from the accumulation of living and dead structure of a hard bodied animal like coral and shellfish (e.g., oyster and mussel species) (Boström et al., 2011; Commito et al., 2008; zu Ermgassen et al., 2020). Less common biogenic reefs are built by bryozoans, razor clam, rhodoliths and polychaete worms (Bruschetti, 2019; Dutka et al., 2022; Roos et al., 2024). Biogenic reefs provide a hard substrate for sessile organisms to settle on (e.g., sponges, bryozoans, barnacles, macroalgae) and shelter or foraging habitat for invertebrates, fish and birds (Bracken et al., 2007; Bruschetti, 2019). The ecosystem functions of biogenic reefs support key ecosystem services in estuarine and marine environments such as habitat provision for biodiversity, nursery grounds for supporting fisheries stocks, coastal protection, improvements to water quality, and carbon capture (Barbier, 2019; Lefcheck et al., 2019; McLeod et al., 2019). In this chapter, an overview of biogenic reefs is given followed by a summary of current literature on their role in the coastal environment, their ecosystem functions, and knowledge gaps of biogenic reefs built by polychaete worms. At the end of this chapter, after discussion on the topical theme of polychaete reefs and emerging knowledge gaps, the thesis, aims, objectives and structure are outlined.

1.1 Overview of biogenic reefs

1.1.1 Structural complexity of biogenic reefs

Biogenic reefs vary in their structural complexity such as vertical relief, surface area, patchiness and connectivity (Bateman and Bishop, 2017; Howie and Bishop, 2021). Coral is a globally dominant biogenic reef type and can cover expansive areas of the seafloor (~350,000 km^2 globally) (Lyons et al., 2024). The calcified green algae, *Halimeda,* grows on existing coralline deposits and forms large bioherms hundreds of metres wide and several tens of metres tall (McNeil et al., 2021; Reolid et al., 2024). Oyster and mussel reefs form low relief reefs in both intertidal or subtidal zones of estuaries and bays (Howie and Bishop, 2021). For instance, a small natural oyster reef could be 1.5 hectares and consist of 50 oysters m^2 (Gillies et al., 2017). Rhodoliths form beds that can be up to 75 km^2 and secondary engineering can rearrange rhodoliths into smaller mounds reaching densities of 5 mounds per 25 m^2 (Roos et al., 2024).

Bryozoan reefs are rare in shallow marine waters but can form continuous rows of reefs up to 1.5 m in height and ~2 km^2 in total area (Dutka et al., 2022). Polychaete worms through their gregarious nature can also form biogenic reefs (Giangrande et al., 2020). In comparison to typical biogenic reefs included in the seascape (e.g., coral and shellfish), polychaete reefs have been understudied (Boström et al., 2011; Montefalcone et al., 2022).

Polychaetes from the families Sabellariidae, Terebellidae and Serpulidae, construct habitation tubes by different processes, which builds the framework for their biogenic reefs (Giangrande et al., 2020). Sabellarid reefs are formed by polychaetes which cement sand and shell fragments together with mucus, into tubes (Rabuat et al., 2009). Sabellarid reefs are delicate structures on the seafloor, often in hummocks up to 15 m^2 and ~10 cm in height, which together can cover several km^2 (Degraer et al., 2008; Noernberg et al., 2010). The largest sabellarid reefs recorded covered an area of ~100 hectares (Dubois et al., 2006). Cyclical changes in sabellarid reefs can occur in one year, which includes different phases of settlement, growth, and degeneration in response to seasonal changes (e.g., storm events) (Eeo et al., 2017; Gravina et al., 2018).

Serpulid polychaetes differ in their reef-building ability, as individuals construct their habitation tube from calcium carbonate (argonite and calcite) (Montefalcone et al., 2022). Juveniles settle upon adult tubes, and reefs form from intertwined tubes of multiple generations of worms (Schwindt 2004b). Stability in serpulid reefs is achieved through population crashes and bursts which consolidate the reef framework (Aliani et al., 1995). Serpulid reefs can persist over many decades, with individual reefs reaching several metres in diameter and height, and high densities up to 370 reefs ha^{-1} (Schwindt et al., 2004b). While polychaete reefs have been identified as important biogenic habitats to be conserved and protected (Palmer et al., 2021; Van der Reijden et al., 2021), some reefs are constructed by non-native serpulids (Alvarez-Aguilar et al., 2022).

1.1.2 Distribution of biogenic reefs

Biogenic reefs, including reef-building polychaetes are globally distributed (Montefalcone et al., 2022). Coral reefs are most extensive in tropic and subtropical regions of the world (Lyons et al., 2024). In comparison, shellfish, rhodolith and polychaete reefs are more typically found in temperate environments, especially in estuaries and coastal bays where coral reefs are excluded (Beck et al., 2009; Montefalcone et al., 2020; Roos et al., 2024).

Biogenic reefs can exist in cold-water environments, including unique species of corals, bryozoans and polychaetes (Fortunato, 2015; Henry and Roberts, 2017; Montes-Herrera et al., 2024).

Biogenic reef distributions are influenced by environmental conditions. Abiotic factors like salinity, nutrients, water temperature, depth and currents influence the physiology, reproduction and growth of reef-builders (Bishop and Peterson, 2006; Esquivel-Muelbert et al., 2022; Ponti et al., 2021). For example, tropical oyster reefs are generally faster growing than temperate oyster reefs due to warmer water temperatures (Richardson et al., 2022). In serpulid reefs, growth is fastest in low flow speed, brackish salinity, nutrient rich and shallow water environments (Bruschetti, 2019). Biotic factors which influence biogenic reefs can include predation, competition (e.g., with other reef-building species), parasitism and disease (Gribben et al., 2019; Esquivel-Muelbert et al., 2022; Bateman and Bishop, 2017). Environmental changes including disturbance events can also impact biogenic reefs and their spatial distribution through time (Beck et al., 2009; Gravina et al., 2018).

1.1.3 Anthropogenic impacts on biogenic reefs

Global declines in biogenic reefs are a major threat to biodiversity and associated losses in ecosystem functioning (Gladstone-Gallagher et al., 2019; Ponti et al., 2021). Anthropogenic disturbances such as coastal development, pollution, over-harvesting, dredging and trawling have already caused and are continuing to cause declines in biogenic reef habitats (Thrush et al., 2001; Ponti et al., 2021). In coastal ecosystems, dredging of the seafloor has resulted in significant environmental degradation and the loss or local extinction of biogenic reef habitats (Alleway and Connell, 2015; Thurstan et al., 2024). Oyster reefs have been highly impacted with an estimated loss of 90% of reefs from coastal bays and estuaries worldwide (Beck et al., 2011). In the Foeaux Strait, New Zealand, the historical oyster reefs serve as an illustration of the impacts of dredging and over-harvesting, where 600 km^2 of the seafloor were completely exploited in a period of 130 years (Cranfield et al., 1999). The disturbance caused by dredging homogenised the seafloor, removed epifauna (Cranfield et al., 1999), decreased macrobenthic diversity (Thrush et al., 2001), and had a reciprocating impact upon demersal fish species (Carbines et al., 2004). Similarly in other parts of the world, historically large-scale oyster reefs are now collapsed or remain as small, fragmented reefs due to similar disturbances such as in Europe (zu Ermagassen et al., 2023), Australia (Alleway and Connell, 2015; Crawford et al., 2020) and North America (Kirby, 2004). Globally, oyster reef exploitation first occurred in estuaries closest to urban centres but spread to more distant estuaries, and along entire coastlines (Kirby, 2004).

In comparison to the exploitation of shellfish reefs, human impacts upon polychaete reefs are often small-scale disturbances. Polychaete reefs can be vulnerable due to their occurrence which overlaps with human activities (Plicanti et al., 2016). Persistent small-scale disturbances such as human trampling on the intertidal flats of North-west Portugal can still cause significant reductions (up to 40 % on average) in the percentage coverage of polychaete reefs of *Sabellaria alveolata* (Plicanti et al., 2016). Furthermore, boating activities may damage reefs such as from propellor impacts or anchoring (Smith et al., 2005).

Biogenic reefs are facing growing anthropogenic pressures, not only due to current human disturbances, but also because of future climate change (Hoegh-Guldberg et al., 2017; Ponti et al., 2021; Wernberg et al., 2024). Warming temperatures threaten coral reefs in particular, as prolonged heat stress events induce bleaching that expels the zooxanthellae which have a symbiotic relationship with the coral (Magel et al., 2019). For polychaete reefs, warming temperatures could threaten populations which are important reservoirs of genetic diversity, as predicted for the polychaete species *Sabellaria alveolata* in its northern range of the Irish Sea and English Channel (Nunes et al., 2021). Ocean acidification also threatens biogenic reefs including bryozoans and polychaetes which have carbonate structures (Cornwall et al., 2021; Fortunato, 2015; Schonberg et al., 2017). Australian estuaries are already under pressure from climate change with rapidly acidifying waters at a rate of 0.09 pH units per year (Scanes et al., 2020), which could threaten distributions of carbonate polychaete reefs.

1.2 The role of biogenic reefs in the coastal environment

1.2.1 *Ecosystem engineering effect*

Many biogenic reef building species are ecosystem engineers of coastal environments (Bruschetti, 2019; Buschbaum et al., 2009). Their ecosystem engineering effect regulates both biotic and abiotic resources (Jones et al., 1994), which can further structure the associated ecological communities (Bruschetti, 2019; Stone et al., 2019). Species which create biogenic reefs and thus physically change the environment by adding structures, are classified as autogenic engineers (Jones et al., 1994). Furthermore, the ecosystem engineering capacity of biogenic reef builders includes abiotic changes caused by their activities. For example, reef building can contribute to sediment accumulation and stabilisation (Salvador de Paiva et al.,

2018) and alter water flow near the seabed (Kitsikoudis et al., 2020; Monismith, 2007). For polychaete reefs, water flow velocities can be altered beyond the spatial scale of their immediate structures, as faster flows occur on the windward side of reefs, and slower flows occur on the leeward direction (Borsje et al., 2014; Schwindt et al., 2004b). Oyster reefs may also alter hydrodynamics, although this may vary with reef condition (Kitsikoudis et al., 2020). Living reefs were found to have a drag coefficient of nearly two times higher compared to degraded reefs with no living oysters, indicating that their rougher surface may attenuate flows better, increasing sedimentation and thereby sheltering nearby shorelines (Kitsikoudis et al., 2020). While effects of coral and shellfish reefs are well studied, scientific attention has only recently turned to polychaete reefs as ecosystem engineers in coastal environments (Bruschetti, 2019).

1.2.2 *Foundation species*

Foundation species encompass species, or a group of functionally close taxa, that create complex habitats (Angelini et al., 2011). As defined by Ellison (2019) a foundation species dominates numerically in the ecosystem and determines the associated taxa diversity as they are the 'foundation' for and often occur near the base of interaction networks. For example, the presence of marine foundation species, which included coral and oyster reefs, increased the abundance and diversity of invertebrates and fish (Bracken et al., 2007). In marine ecosystems, foundation species may be separated spatially or can co-occur. A unique example in an intertidal, soft sediment environment with limited opportunities for anchorage, is provided by the polychaete, *Eudistylia vancouveri*, which builds worm tubes embedded in the sand and offers a substrate for kelp, another foundation species, to attach and grow (Bracken, 2018). Other examples of reef building polychaete species that are referred to as foundation species include *Sabellaria alveolata,* with constructions forming, large reefs in bays along the European coast (Dubois et al., 2006). In comparison, other biogenic reefs (e.g. oysters) have been identified as critical foundation species contributing to the resilience of coastal ecosystems and have recently received attention due to the benefits from their conservation and restoration (Ridlon et al., 2021).

1.2.3 Ecosystem functioning

The combined effect of all natural processes (i.e., biological and physical) that sustain an ecosystem provides the framework needed to support ecosystem functioning (Lam-Gordillo et al., 2020; Wallace, 2007). Ecosystem functioning is fundamental for attaining ecosystem services such as provisioning, supporting, regulating and cultural services from the environment (Barbier, 2019; Newton et al., 2018; Wallace, 2007). Key ecosystem functions of biogenic reefs include habitat, sediment stability, benthic-pelagic coupling, water filtration and carbon capture (De Smet et al., 2015; Fodrie et al., 2017; Kent et al., 2017a; Kent et al., 2017b; La Peyre et al., 2019; Rullens et al., 2019).

Habitat complexity provided by biogenic reefs is a key component of functioning coastal environments (Barbier et al., 2011; Lefcheck et al., 2019). Resilience of biodiversity and preservation of ecosystems functions is an integral part to avoid the further loss of ecosystem services into the future (Gladstone-Gallagher et al., 2019; Rullens et al., 2019;Stewart-Sinclair, 2020).

1.3 Ecosystem functions of biogenic reefs

1.3.1 *Shelter provision*

Biogenic reefs can provide shelter for a variety of biota such as meiofauna (Ape et al., 2018; Ataide et al., 2014), macrofauna (Crawford et al., 2020), fish (Rabaut et al., 2010; Van der Reijden et al., 2019) and, for intertidal reefs, birds (Bruschettii et al., 2009). Common macroinvertebrates that seek refuge in reefs, in the case of mussel beds, include polychaetes, which are found in high abundance amongst trapped sediments in the reef (Borthagaray and Carranza, 2007). Crustaceans are also commonly found sheltering in the vicinity of biogenic reefs, constructed by mussels and oysters, which offer a predator refuge (Borthagaray and Carranza, 2007; McLeod et al., 2020). Across temperate biogenic reefs, increased densities of crustaceans in reef compared to soft sediment habitats have been observed, suggesting reefs have an important shelter function (McLeod et al., 2020; Schwindt et al., 2001). Resident crabs seek refuge (Table 1.1) or construct their burrows directly under polychaete reef edges (Schwindt et al., 2001). An individual polychaete reef, several metres in diameter, supports on average 42 adult *Cyrtograpsus angulatus* crabs, and with an average reef density of 99 reefs ha^{-1} in the Mar Chiquita lagoon, this equates to 3,600 adult crabs ha^{-1} (Schwindt et al., 2001).

It is well known that biogenic reefs such as coral and shellfish, provide refuge for fish fauna (Brandl et al., 2018; Gilby et al., 2018; Pratchett et al., 2008; Pratchett et al., 2011; Reeves et al., 2020; Stella et al., 2011). In comparison, there is a limited insight on the shelter provision of polychaete reefs for fish, which is mainly based on anecdotal observations (Table 1.1). Few quantitative studies have investigated the non-trophic interactions between fish and polychaete reefs (Table 1.1). These include the juvenile flatfish, *Pleuronectes platessa,* that seek shelter amongst *Lanice conchilega* reefs (Rabaut et al., 2010), and the catshark *Scyliorhinus canicular,* which rests exclusively amongst *Sabellaria spinulosa* reefs (Van der Reijden et al., 2019). For serpulid polychaetes such as *F. enimgaticus* that form prolific and large reef structures, no studies have quantified non-trophic interactions between fish and reef such as the provision of shelter (Table 1.1). There is emerging evidence that sabellarid reefs influence multiple components of the biotic community, including both fish and macroinvertebrates from the epibenthos and hyperbenthos (De Smet et al., 2015), yet this remains a knowledge gap for serpulid reefs.

Table 1.1. Examples of trophic and non-trophic interactions between species of crab, fish and birds with polychaete reefs.

Polychaete reef species	Location	Organism category/ Associated species	Reliance on reef	Process (Trophic/ Non-trophic)	Biotic interaction	Reference
Ficopmatus enigmaticus (Serpulidae)	Argentina (Mar Chiquita lagoon)	**Crab** *Cyrtograpsus angulatus* (Varuninae)	Resident	Non-trophic & trophic	Promotive (habitat refuge), construct burrows under reef. Predation on invertebrates in soft sediments next to reef	Schwindt et al., 2001
	Argentina (Mar Chiquita lagoon)	**Fish** *Austrogobius parri* (Gobiidae)	n/a	Trophic	Predation on *F. enigmaticus*	Olivier et al., 1972, in Obenat & Pezzani, 1994
	Italy (Pro River Delta)	*Liza saliens* (Mugilidae)	n/a	Trophic	Grazing on reef, biting tube edges	Bianchi & Morri, 1996
		Gobius niger (Gobiidae)*, Anguilla anguilla* (Anguillidae)	n/a	Trophic	Predation on *F. enigmaticus*	
	Argentina (Mar Chiquita lagoon)	**Bird** *Tringa melanoluca* (Scolopacidae)*, Tringa Flavipes* (Scolopacidae)*, Calidris fuscicollis* (Scolopacidae)	Visitor	Trophic	Predation, on reef associated epifauna	Bruschetti et al., 2009
		Phalacrocorax olivaceus (Phalacrocoracidae)*, Larus dominicanus* (Laridae)*, Larus maculipennis* (Laridae)*, Anas* spp. (Anatidae)*, Vanellus chilensis* (Charadriidae)*, Milvago chimango* (Falconidae)	Resident	Non-trophic	Resting on reefs	
Serpula vermicularis (Serpulidae)	Scotland (Loch Creran)	**Crab** *Necora puber* (Polybiidae)	Visitor	Trophic	Attempted predation of *S. vermicularis*	Poloczanska et al., 2004
		Fish			Predation, on reef associated epifauna	
		Crenilabrus melops (Labridae)*, Labrus bergylta* (Labridae)	Visitor	Trophic	Sub-lethal predation of *S. vermicularis* branchial crowns	
		Pomatoschistus sp. (Gobiidae)	Visitor	Trophic	Foraging for fish in vicinity of reefs	
		Bird *Phalacrocorax aristotelis* (Phalacrocoracidae)	Visitor	Trophic		

Table 1.1. cont.

Polychaete reef species	Location	Organism category/ Associated species	Reliance on reef	Process (Trophic/ Non-trophic)	Biotic interaction	Reference
Lanice conchilega (Terebellidae)	Belgium (Bay of Heist)	**Fish** *Pleuronectes platessa* (Pleuronectidae)	Resident	Non-trophic	Promotive (habitat refuge) for juveniles	Rabaut et al., 2010
Sabellaria spinulosa (Sabellariidae)	Netherlands (Dutch Brown Bank area)	**Crab** *Cancer pagurus* (Cancridae)	Resident	Non-trophic	Refuge amongst hard substrate in reef	Van der Reijden et al., 2019
		Necora puber (Polybiidae)	Resident	Non-trophic	Refuge amongst hard substrate in reef	
		Fish *Scyliorhinus canicular* (Scyliorhinidae)	Resident	Non-trophic	Resting amongst reefs	
Diopatra leuckarti (Onuphidae)	Hawaii (Oahu)	**Crab** *Calcinus laeuimanus* (Diogenidae), *Calappa hepatic* (Calappidae)	n/a n/a	Trophic & Non-trophic	Predation on *D. leuckarti* or other taxa in reef community and burrows in reef.	Bailey-Brock, 1984
		Fish *Bathygobius* sp. (Gobiidae),*Mulloidichtys* spp (Mullidae), *Kuhlia sandvicensis* (Kuhliidae) and *Asterropteryx semipunctatus* (Gobiidae)		Trophic	Predation on *D. leuckarti* or other taxa in reef community	
		Bird *Pluvialis dominica* (Charadriidae)			Feeding at low tide on *D. leuckarti* mounds, preying on other taxa in reef community (e.g. crustaceans, melanid snails, plant material	

1.3.2 *Feeding sites*

Biogenic reef structures are often colonised by a variety of sessile organisms including algae and invertebrates like barnacles (McLeod et al., 2014). Consequently, not only the reef building animal itself but the other organisms they host, may be utilised as a food source by mobile fauna (e.g McLeod et al., 2014). For example, gastropods dominate macroinvertebrates in mussel bed communities, reflecting the availability of their main prey, turf algae, on the shells (McLeod et al., 2014; McLeod et al., 2020). High abundances of echinoderms on oyster reefs have been found to graze on filamentous algae as well as sessile organisms attached to reef shells (Crawford et al., 2020). The trophic interaction of grazing has been observed for omnivorous crabs and fish (e.g. mullet) in polychaete reefs (Table 1.1). Additional observations recorded from polychaete reefs include crabs, gobies and mullet preying directly on the tubeworms themselves, or infauna (Table 1.1). Birds can utilise polychaete reefs in intertidal habitat for foraging and feeding upon epifauna such as crustaceans (Bailey-Brock, 1984; Bruschetti et al., 2009). In some environments, bird foraging in the vicinity of polychaete reefs could have the potential to hinder fish activity due to a predation threat.

In estuarine and coastal environments, biogenic reefs serve as productive foraging grounds for fish fauna (Kent et al., 2017; La Peyre et al., 2019; Palmer et al., 2021). Yet, the importance of polychaete reefs as feeding sites is only beginning to emerge (Chong et al., 2021; Palmer et al., 2021). Furthermore, few studies have investigated day versus night movements of fish around polychaete reefs (Poloczanska et al., 2004). In Baffin Bay, a hypersaline estuary located in Texas, serpulid reefs constructed by *Hydroides dianthus,* offer a stable and highly productive foraging habitat for fish (Palmer et al., 2021). In contrast to surrounding soft sediments, reefs host up to a 100-fold greater biomass of benthic macroinvertebrate communities, which is thought to provide a consistent food source to higher-level consumers and thus supporting the local fisheries stocks (Palmer et al., 2021). The Jeram Reef, Malaysia, consisting of tubes built by *Sabellaria jeramae*, also supports local fisheries by functioning as a feeding and refuge area for over 50 different fish species (Chong et al., 2021). Further investigations on fish associations with serpulid reef are needed to understand trophic relationships in reef habitats (Montefalcone et al., 2022).

1.3.3 *Nursery sites*

Structured habitats including biogenic reefs have an important nursery role in marine and estuarine ecosystems, supporting greater juvenile survival and density of fauna, such as fish and invertebrates, than unstructured soft sediments (Lefcheck et al., 2019). In comparison to coral reefs, there are fewer investigations on the nursery effect of shellfish reefs (Lefcheck et al., 2019). Polychaete reefs may also function as nursery habitat for invertebrate and fish (Bruschetti, 2019). For example, in the Mar Chiquita lagoon, *F. enigmaticus* reefs enhance the recruitment of the native crab, *Cyrtograpsus angulatus*, by increasing the density of juveniles through providing refuge (Luppi and Bas, 2002). Similarly, *Sabellaria wilsoni* form biogenic reefs that support the recruitment of juveniles of the crab *Clibanarius symmetricus,* thus acting as a nursery habitat (Aviz et al., 2021).

Polychaete reefs of *L. conchilega*, in the North Sea, provide key structures that contribute to small scale variations in the distribution of the juvenile flatfish, *Pleuronectes platessa* (Rabaut et al., 2009). In the presence of reefs, the density of juvenile *P. platessa* significantly increased, up to three-fold, in comparison to nearby control soft sediments (Rabaut et al., 2009). Juvenile *P. platessa,* selected reef habitat of for feeding and refuge (Rabaut et al., 2013). Manipulative experiments showed juveniles of *Solea solea* also sought refuge in engineered habitat mimicking *L. conchilega* (Rabaut et al., 2013). These studies suggest polychaete reefs serve as a nursery habitat for juvenile fish such as flatfish, by providing both refuge and important feeding grounds. Further investigations are needed to determine whether other reef building polychaetes which construct larger and more prolific reefs such as serpulids, also provide a nursery habitat for not only invertebrate fauna, but also for juvenile fishes.

1.4 Polychaete reefs

1.4.1 *Natural history of Ficopomatus enigmaticus*

Ficopomatus enigmaticus (Fauvel, 1923) is a marine polychaete belonging to the family Serpulidae, and one of the most prolific reef-building polychaete species across brackish and sheltered coastal waters worldwide (Montefalcone et al., 2022). The true origin of the species remains unclear, but the presumed native range is in temperate regions of the Indian Ocean, including Australia (Dew, 1959; Ten Hove and Weerdenburg, 1978). Scientific records of marine invertebrates in Australia are limited and were also taken after European settlement (Ponder et al., 2002). In Australia, the first record of *F. enigmaticus* was noted from the Cook's River (New South Wales) in 1910 (Dew, 1959), and by the 1930s it was widely recorded across southern Australia (Allen, 1953). *Ficopomatus enigmaticus* was first introduced and described in France around the same period (Fauvel 1923). The uncertainty of an Australian origin is raised from the early records which coincide with the start of the global shipping trade that facilitated the spread of sedentary marine invertebrate species into Australian coastal waters from ship fouling and ballast water (Allen, 1953). Genetic diversity patterns across southern Australia suggest three putative species, which do not conform to an east to west phylogeographic spread which would be expected for a native marine species (Styan et al., 2017). To resolve whether the *F. enigmaticus sensu lato* group could be of Australian origin, further morphological analysis combined with genetic evidence is needed (Kupriyanova et al., 2023; Styan et al., 2017; Tovar Hernández et al., 2022).

Ficopomatus enigmaticus is mostly considered to be a marine invasive species with a cosmopolitan distribution (Alvarez-Aguilar et al., 2022). The introduction of *F. enigmaticus* to many parts of the world has been facilitated by the global shipping trade (Allen, 1953) but may have also spread with migratory shorebirds (Bruschetti et al., 2009). The establishment of *F. enigmaticus* into new waters correlates with anthropogenic changes in the environment, for instance, certain abiotic conditions that the species can tolerate or thrive in (Montefalcone et al., 2022). The proliferation of *F. enigmaticus* is common in eutrophic systems and includes the estuaries, lagoons, and marinas of the Mediterranean (Bianchi and Morri, 1996; Brundu and Magni, 2021; Forn´os et al., 1997; Ntzoumani et al., 2024), South America (Schwindt et al., 2004a, 2004b), South Africa (Bezuidenhout and Robinson, 2020; Davies et al., 1989; McQuaid and Griffiths, 2014), North-Western France (Charles et al., 2018), the Atlantic (Costa et al., 2019), and the Baltic Sea (Hille et al., 2021). The ability for *F. enigmaticus* to invade different waters worldwide may be an effect of its gregarious nature and reef-building success.

1.4.2 *Reef building in Ficopomatus enigmaticus*

Calcareous reef development by *F. enigmaticus* reefs can consist of large masses of intertwined tubes with up to 180,000 worms m^{-2} (Aliani et al., 1995). The requirements needed by *F. enigmaticus* for reproduction and growth are salinities between 10% and 30% (Bianchi and Morri, 1996; Hartmann-Schröder, 1967), water temperatures above 18 °C (Hartmann-Schröder, 1967) and low flowing, sheltered, shallow waters (Forn´os et al., 1997; Bianchi and Morri, 1996; Schwindt et al., 2004b;). An initial hard substrate is essential for the initiation of a reef, and juveniles will favour to settle upon adult tubes, thus over time the reef framework will consist of multiple generations of worms and their intertwined habitation tubes (Schwindt et al., 2004b). *Ficopomatus enigmaticus* lives in a tube secreted from its own collar gland by using seawater ions (Aliani et al., 1995; Smith et al., 2013), and as it grows, the worm constructs a bigger habitation tube which shows growth rings and inter-rings (Schwindt et al., 2004b). Tubes of *F. enigmaticus* are delicate (90 µm thin) and made up of calcite (98% Wt%) and magnesium carbonate (Aliani et al., 1995; Smith et al., 2013). To increase the reef stability, the reef building strategy in *F. enigmaticus* suggests that there are population crashes, and subsequent bursts of growth (Montefalcone et al., 2022). For instance, aperiodic floods can cause the near mass mortality of reefs (Alliani et al., 1995) which may be due to a range of changed conditions such as lowered salinities (e.g., <10 ppt), lowered temperatures and higher current speeds (Bianchi and Morri, 1996; Hartmann-Schröder, 1967). The near mass mortality of adult worms in the reef generates new space, and upon return of favourable conditions, the recruitment of juveniles on to existing adult tubes helps to consolidate the reef framework (Alliani et al., 1995). Over time, individual reefs can also be joined together to form large platform reefs (Schwindt et al., 2004b).

1.4.3 *Knowledge on Ficopomatus enigmaticus*

There is global knowledge on *F. enigmaticus*, and more literature in recent years from increasing listings on the species' distribution in new parts of the world (Alvarez-Aguilar et al., 2022). There are few studies on aspects like the life history, taxonomy and reef morphology and mapping, in comparison to the ecological effects of *F. enigmaticus* (Figure 1.1). Most knowledge on the ecological effects of *F. enigmaticus* has come from Argentina in South

America (Figure 1.1) (Schwindt et al., 2001; Méndez Casariego et al., 2004; Bruschetti et al., 2009; Bazterrica et al., 2014). There is far less known from the putative native range of *F. enigmaticus* in the Indo-Pacific region, including Australia where it could potentially show different responses and ecological interactions (Figure 1.1.).

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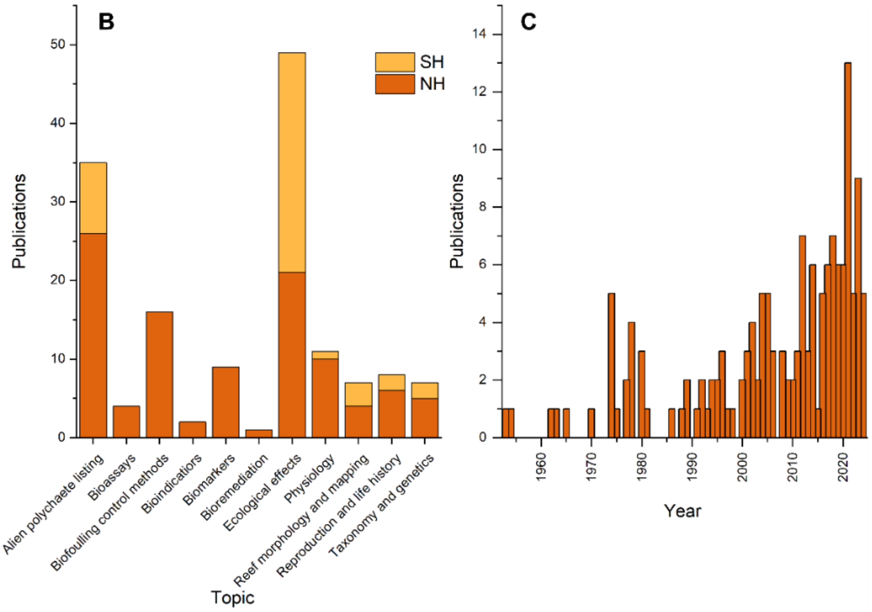

Figure 1.1. Global literature on *Ficopomatus enigmaticus* identified based on **A)** the geographical distribution of the origin of the publications, **B)** the spread of publications by research topic and by Southern and Northern Hemispheres (SH and NH, respectively), and **C)** the number of peer reviewed publications on *F. enigmaticus* across time. Data were retrieved from Scopus database (https://www.scopus.com/search/form.uri#basic on 25/11/2024), using the search categories "Title", "Abstract", "Keywords" with the terms "ficopomatus enigmaticus" OR "mercierella enigmatica".

1.4.4 The Coorong estuary and lagoons

The Coorong estuary and lagoons provide a case study for the ecological effects of polychaete reefs built by *Ficopomatus enigmaticus* in a region of southern Australia that occurs in the putative native range. The Coorong is a large temperate estuarine and lagoonal system, listed as a Ramsar wetland of international importance (Phillips and Muller 2006). Located at the terminus of Australia's largest river basin, the Murray-Darling Basin (MDB), the Coorong receives freshwater flows from the Murray River via the Lower Lakes (Lake Alexandrina and Lake Albert) (Figure 1.2). Barrages were constructed in the 1930s and regulate freshwater flow releases into the Coorong, before they discharge to the Southern Ocean through the opening of the Murray Mouth (Gibbs et al., 2018). The mixing zone of waters between the barrages and open ocean is known as the Murray Mouth estuary of the Coorong (herein 'Murray Estuary'), a narrow channel (~500 m width and 5-6 m maximum depth) that is subject to tidal influence (Webster, 2010). Adjacent, the Coorong stretches over 100 kilometres of the coast as two shallow (~1.5 m depth) connected lagoons, the North Lagoon and South Lagoon, which are protected from the Southern Ocean by the Younghusband Peninsula (Gibbs et al., 2018).

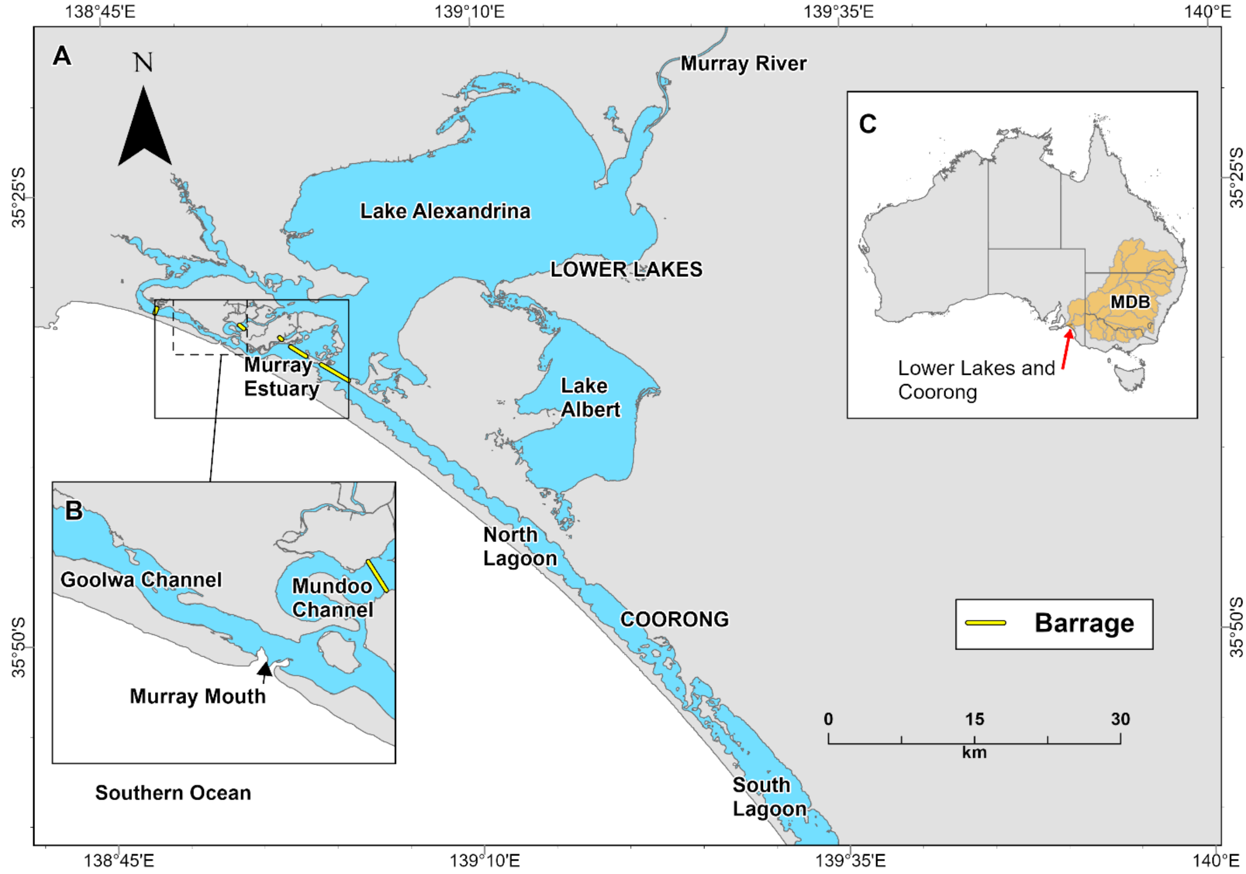

Figure 1.2. A) Location of the Coorong, in Southern Australia, and **B)** the Murray Mouth at the terminus of the Murray Darling Basin (MDB) in **C)**. Map **A)** and **B)** source: WaterConnect, Government of South Australia[2]. Map **C)** No source acknowledged[3].

The productive waters, and abundance of native fauna and flora of the Coorong is reflected by a long history of cultural heritage and occupancy by the local indigenous people (Hemming, 2018). The ecosystem in the Coorong is dynamic, providing important estuarine and nursery habitats for native species of invertebrates, fish and water birds (Noye, 1974). In addition, estuarine mudflats rich in macroinvertebrates are important in supporting the food web and foraging habitat for migratory shore birds in the summer (Dittmann et al., 2018). In recent times, water for the environment is regulated at specific times and frequencies to support key species, such as the provision of a salt-wedge for *Acanthopagrus butcheri* (black bream)

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[2] River Murray shapefile (CC BY 4.0) was downloaded from https://www.waterconnect.sa.gov.au/Systems/SitePages/Spatial%20Data.aspx (accessed 28/2/2025)

[3] Murray Darling Basin (no attribution required) web map downloaded at https://www.arcgis.com/home/item.html?id=152cd62c03c04302a1bd2def758c3e1b

during the spawning season (Rumbelow, 2018). Fishways at the barrages also facilitate natural fish migrations upstream or downstream to fulfill their life histories, such as for diadromous species like *Pseudaphritis urvillii* (congolli) and *Geotria australis* (pouch lamprey) that migrate between freshwater and marine environments (Bice et al., 2018). The Coorong supports economically important commercial fisheries for estuarine species *A. butcheri*, and marine estuarine-opportunist species including *Aldrichetta forsteri* (yellow-eye mullet), *Rhombosolea tapirina* (greenback flounder) and *Argyrosomus japonicus* (mulloway) (Ferguson et al., 2013).

Freshwater flows through a complex of barrages are critical in maintaining connectivity and estuarine habitats in the Coorong (Ye et al., 2020). Barrage flows have been highly variable between years, and high freshwater flows have been experienced since the commencement of the field work in 2022 for this PhD project. In summer of 2022/23, a large flood event occurred where the total barrage flow was 16,500 GL (Water Data SA, 2023) (Figure 1.3).

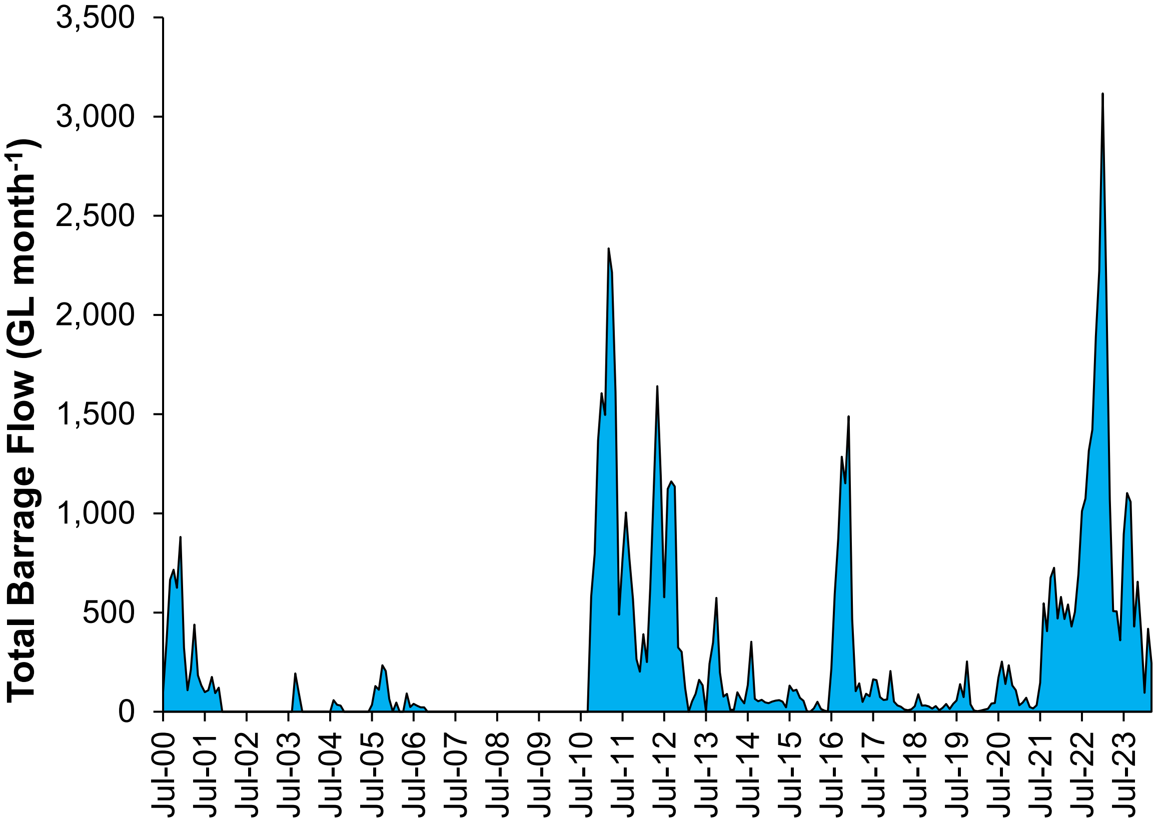


Figure 1.3. Total barrage flow per year (GL month^{-1}) into the Coorong from the flow years July 2000 to March 2024, showing the very high flow event in summer of 2022-23. Data were sourced from Water Data SA (DEW, 2025).

In the Coorong, the salinity gradient observed is typically estuarine conditions in the Murray Estuary to marine conditions in the North Lagoon (Figure 1.4A and B). High evaporation, low freshwater input and reduced flushing over the last two decades has caused extreme salinisation in the South Lagoon (Mosely et al., 2023) (Figure 1.4C). In flow years 2022 and 2023, the average salinities in the Murray Estuary were low and were representative of a freshwater environment in summer (Figure 1.4A). The North Lagoon salinities (flow years 2022 and 2023) were lower than the long-term average and resembled that of the typical estuarine conditions of the Murray Estuary (Figure 1.4B). The South Lagoon remained hypersaline (flow years 2022 and 2023), with average salinities slightly lower than the long-term averages (Figure 1.4C).

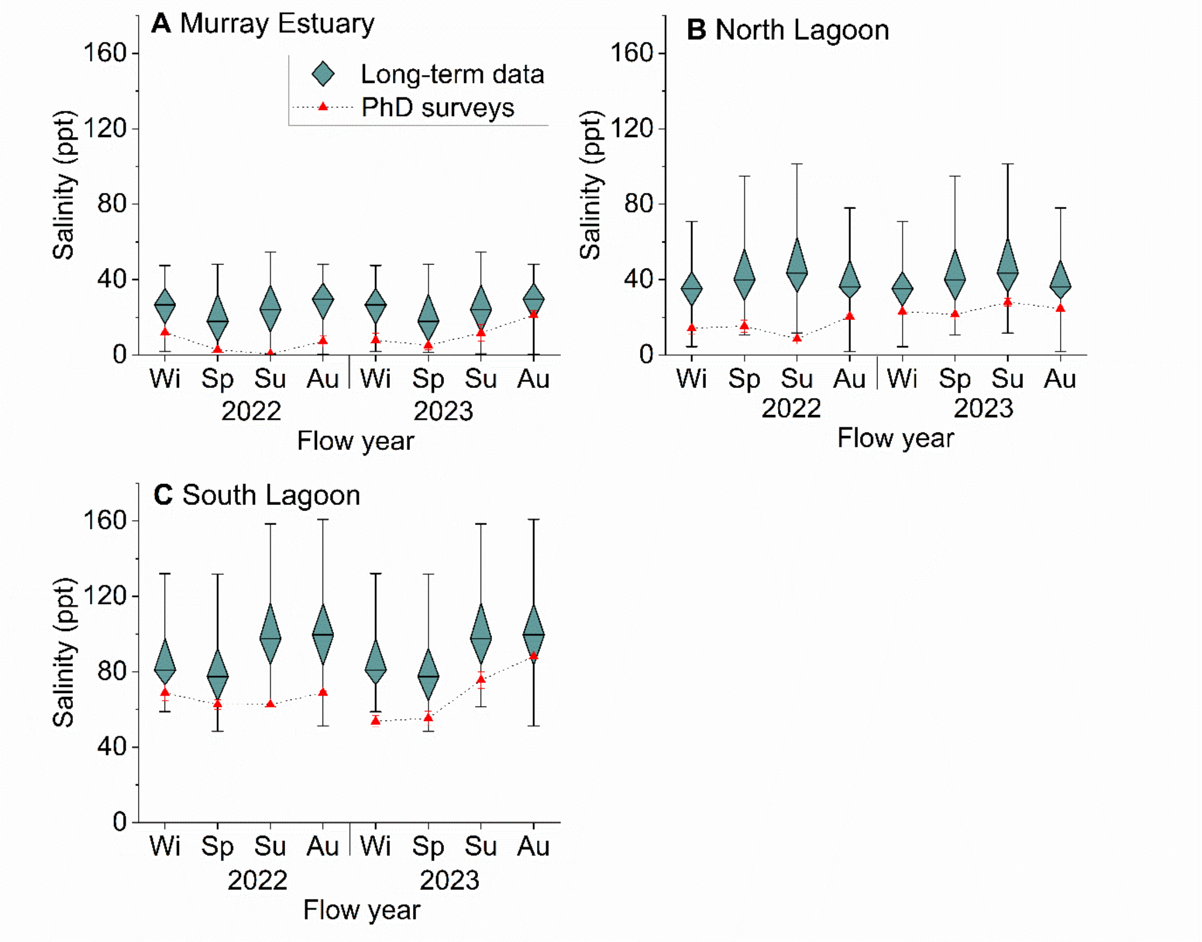


Figure 1.4. Salinity during the duration of surveys in this PhD study (flow years 2022 and 2023) compared to long term data (2000-2022) in **A)** the Murray Estuary, **B)** North Lagoon and **C**) South Lagoon of the Coorong over winter (Wi), spring (Sp), summer (Su) and autumn (Au) seasons. Data were sourced from Water Data SA (DEW, 2025).

1.5 Thesis aim and objectives

The overall aim of this PhD project was to investigate the ecosystem functioning of polychaete reefs. The focus of this project was on serpulid reefs, their structural complexity, different reef types, and their ecosystem function of habitat provisioning for multiple biota. The polychaete reefs studied, and field investigations of fauna associations with reefs were carried out in the Coorong, a large temperate estuary in southern Australia (Section 1.4).

Although some polychaete reefs are built by cryptogenic species, in environments lacking natural or biogenic reefs, this study contributes new knowledge on their provision of ecosystem functions which could have an important contribution to ecosystem services. Research on polychaete reefs built by *F. enigmaticus* in its putative native range is limited, and results will contribute new knowledge on the ecology of polychaete reefs in southern Australia. The findings from this PhD project were contrasted with *F. enigmaticus* studies across their introduced range to determine if there are similarities in positive or negative ecological roles of reefs in the environment. Furthermore, the ecosystem functions of polychaete reefs were compared and contrasted to other biogenic reefs in the marine and estuarine environment to identify whether they support similar or dissimilar ecosystem functions and services. The specific aims and hypothesis of each data chapter are:

Chapter 2: The aim of this chapter was to increase the understanding of the structural complexity provided by polychaete reefs of *F. enigmaticus*. Specific aims were to (1) classify polychaete reefs based on size and morphology, (2) quantify reef density, (3) asses their spatial distribution and (4) assess the correlation between reefs (e.g., density, size) with the environmental gradient in the Coorong in southern Australia.

Chapter 3: This chapter aimed to investigate the history of polychaete reefs in the Coorong in southern Australia, and whether a radiocarbon dating approach along multiple depths of polychaete cores could reveal a snapshot of the environmental history.

Chapter 4: This chapter aimed to address a knowledge gap on fish community associations with polychaete reefs of *F. enigmaticus* (Serpulidae) through field investigations and knowledge of reef distribution from Chapter 2. It was hypothesised that (1) the total abundance and diversity of native fish is higher in polychaete reef than non-reef habitat, and (2) the native fish community differs between polychaete reef and non-reef habitats. An extreme flood event during the study period also allowed a secondary aim, which was to investigate spatial and temporal variations in fish community structure in response to changed environmental conditions (e.g., lower salinities) and stressors (e.g., invasive species).

Chapter 5: The aim of this chapter was to increase knowledge on the demersal (mobile epifauna) and benthic macroinvertebrate communities in polychaete reef habitats. It was hypothesised that polychaete reefs have a (1) higher abundance and higher diversity of both demersal and benthic macroinvertebrates. Hypothesis (2) was that the community composition of demersal and benthic macroinvertebrates differs in reef compared to non-reef habitats and substrates. Hypothesis (3) was that a similar community composition of demersal and benthic macroinvertebrates occurs between the estuarine and lagoon regions. Hypothesis (4) was that the community composition of demersal and benthic macroinvertebrates varies across seasons. Hypothesis (5) was that the reef habitat has a greater magnitude of effect on the benthic macroinvertebrate community than the demersal macroinvertebrate community.

1.6 Thesis structure

My PhD project consists of a general introduction chapter (Chapter 1), four major data chapters (Chapters 2–5), and a general discussion (Chapter 6). Data Chapters 2 and 4, have been written as manuscripts for peer reviewed scientific journals, but have been formatted consistently as the other data chapters within this thesis. The last chapter of this thesis is a general discussion chapter (Chapter 6) that contributes to the topical research theme on biogenic reefs by adding an understanding of the role of polychaete reefs in the environment.

Chapter 2 presents a new classification on the different reef morphologies, to aid the consistency in terminology of reef morphologies globally found for *F. enigmaticus* polychaete reefs. My findings contributed to a new insight on the spatial distribution of *F. enigmaticus* reefs in the Coorong, southern Australia. I assessed the long-term environmental drivers which correlated with different reef types, and I advanced knowledge on the structural complexities of polychaete reefs. This chapter is published in Estuarine, Coastal and Shelf Sciences. Schroder, L., Lam-Gordillo, O., Dittmann, S., 2024. Classification, density, and spatial distribution of polychaete reefs in the Coorong, South Australia. Estuarine, Coastal and Shelf Science 306, 108905, https://doi.org/10.1016/j.ecss.2024.108905.

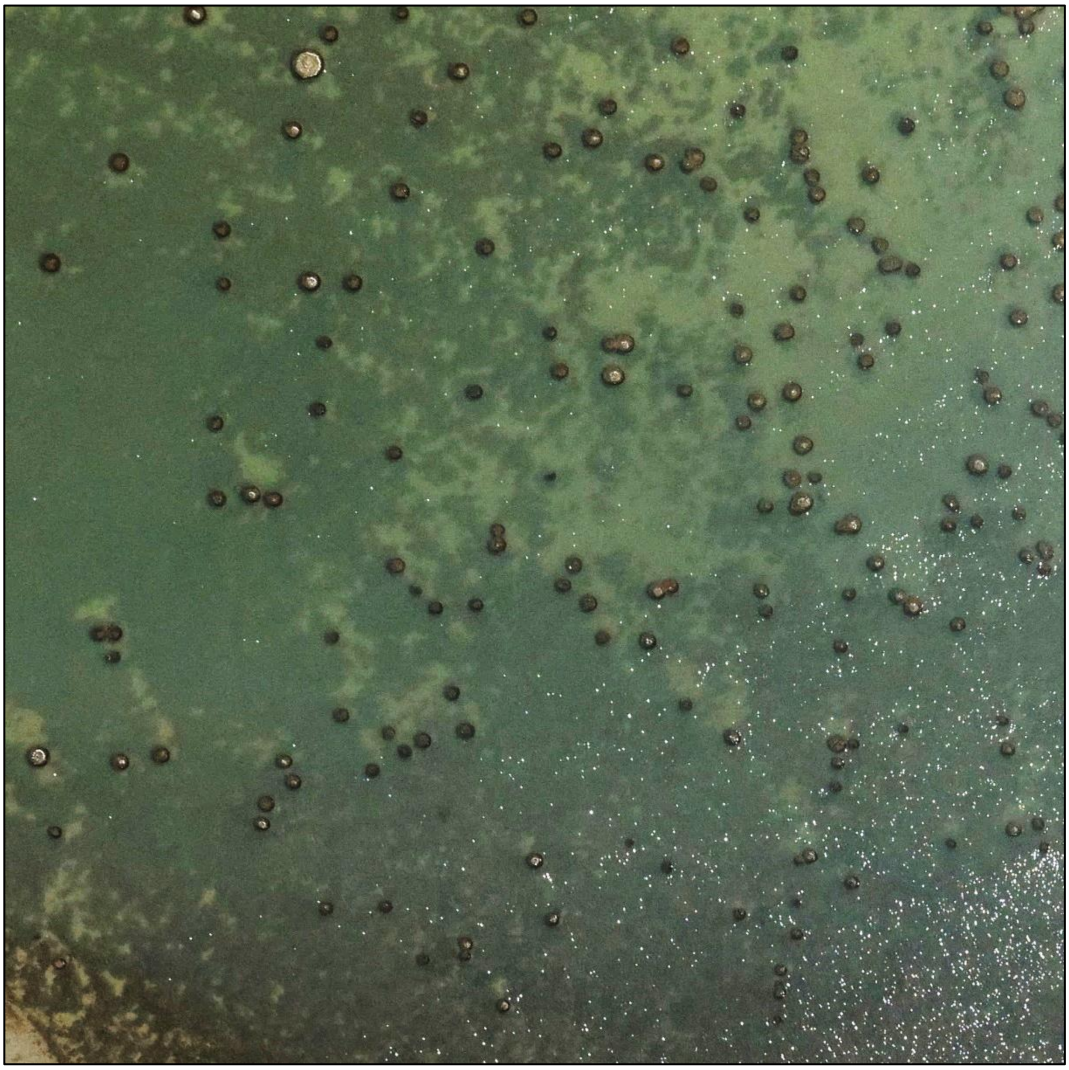
Chapter 3 addressed a key knowledge gap on the history of polychaete reefs in the Coorong, southern Australia. A novel approach of dating polychaete tubes from different depths along the core revealed a bomb-pulse signal in $F^{14}C$. This finding builds on the information found in Chapter 2, suggesting anthropogenic impacts in the Coorong have facilitated reef expansion.

Chapter 4 presents a field study on the fish community associated with polychaete reefs of *F. enigmaticus*, using knowledge on reefs from Chapter 2 to fill a key knowledge gap on the use of serpulid reef by fish fauna. Fish surveys were carried out over two consecutive years during spring, summer and autumn seasons to evaluate spatial and temporal changes in fish associations with reefs. This chapter is now published in Marine Environmental Research. Schroder, L., Lam-Gordillo, O., Ye, Q. and Dittmann, S., 2025. Estuarine fish dynamics associated with polychaete reefs and environmental stressors. Marine Environmental Research, p.107212, https://doi.org/10.1016/j.marenvres.2025.107212.

Chapter 5 examined the association of benthic and demersal macroinvertebrates with polychaete reefs, and increased the information known on how multiple biota respond to serpulid reefs. This chapter also built upon Chapter 2, to understand whether different reef habitats in the estuary and lagoon influenced patterns in macroinvertebrate communities.

Chapter 6 is the general discussion that summarized the main findings of the data chapters (Chapters 2–5) and evaluates the ecosystem functions of polychaete reefs compared to other biogenic reefs in the marine and estuarine environment. In Chapter 6, the conservation and management of polychaete reefs of *F. enigmaticus* in Southern Australia are discussed, and future directions for research are highlighted.

Chapter 2. Classification, density and spatial distribution of polychaete reefs in the Coorong, South Australia



Aerial view of polychaete reefs taken in 2020, near Seven Mile in the North Lagoon of the Coorong. Reproduced with permission from Airborne Research Australia.

2.1 Publication details

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2.2 Author contributions

Laura Schroder: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Orlando Lam-Gordillo:** Writing – review & editing, Methodology. **Sabine Dittmann:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

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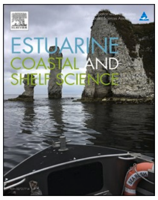

Classification, density, and spatial distribution of polychaete reefs in the Coorong, South Australia

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ABSTRACT

The cosmopolitan species *Ficopomatus enigmaticus* is one of the most prominent providers of polychaete reefs in shallow and brackish waters. The effects of polychaete reefs on the environment can be positive or negative subject to their structural complexity and vary with local environmental conditions and over time. The Coorong is a large temperate estuarine and lagoonal system with extensive polychaete reefs built by *F. enigmaticus*. The aims of this study were to (1) classify polychaete reefs based on size and morphology, (2) quantify reef density, (3) assess their spatial distribution and (4) assess the correlation between reefs (e.g., density, size) with the environmental gradient. Structural morphologies of *F. enigmaticus* were classified as either halo, circular, irregular, platform or fringing reef types. The largest densities of polychaete reefs were recorded in the vicinity of the mouth of the estuary with 224 reefs per ha compared to the lagoon (62 reefs per ha). The most common reef morphology was circular and largest sizes in the lagoon were positively correlated with salinity, chlorophyll *a*, TRIX (trophic index) and bicarbonate. The largest reef diameter recorded was 11.3 m, exceeding previously known *F. enigmaticus* circular reef formations globally. The growth of large circular reefs may have benefitted from low flows and eutrophic conditions in the Coorong during the last two decades. This study serves as an important baseline for future assessments of reef change in a Ramsar listed wetland. Furthermore, this study highlights reef characteristics of *F. enigmaticus* across an environmental gradient, which can be informative for the management of flow and eutrophication in estuaries and coastal lagoons.

1. Introduction

Biogenic reefs are created by calcifying animals, which are important ecosystem engineers in shallow water environments through their provision of unique three-dimensional hard structures (Bruschetti, 2019). Reef-building polychaetes, in particular the cosmopolitan polychaetes from the family Serpulidae, also have a profound role as ecosystem engineers (Giangrande et al., 2020; Montefalcone et al., 2022). Serpulid reefs can provide a wide range of functions such as a living space and refuge for other species, nursery habitat, sediment stabilisation (Schwindt et al., 2004a), and carbonate deposition and carbonate storage (Bruschetti, 2019; Montefalcone et al., 2022). Additional services include water quality improvements (e.g., Bruschetti et al., 2008; Bruschetti et al., 2018; Pan and Marcoval, 2014; Piccardo et al., 2024), and reef associated fisheries (e.g., Chong et al., 2021; Palmer et al., 2021). The effects of polychaete reefs can be positive (e.g., biogenic structure provision, sediment stabilisation etc.) or negative (e.g., biological fouling, inhibiting vessel navigation), which can vary amongst reef building species, locality, habitat (e.g., estuary), local environmental conditions, and potential changes through time (Montefalcone et al., 2022).

Globally, *Ficopomatus enigmaticus* (Fauvel 1923) is one of the most prominent providers of serpulid reefs across brackish and sheltered coastal lakes, lagoons, and estuaries (Montefalcone et al., 2022). The true origin of the species remains unclear, but some early historical records speculate a possible native range in Australia (Dew, 1959). Evidence from genetic diversity patterns across Southern Australia suggests the occurrence of three putative species (Styan et al., 2017), but more analysis on morphology and DNA sequences are needed to resolve if the *F. enigmaticus sensu lato* group could be of Australian origin (Kupriyanova et al., 2023; Styan et al., 2017; Tovar-Hernández et al., 2022).

Calcareous reef development by *F. enigmaticus* can be rapid due to the gregarious nature of the polychaete which can form large masses of interweaved tubes up to 180,000 worms m^{-2} (Aliani et al., 1995). The

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main environmental conditions that are required by *F. enigmaticus* for reproduction and growth include brackish salinities between 10 and 30% (Hartmann-Schröder, 1967; Bianchi and Morri, 1996), water temperatures above 18 °C (Hartmann-Schröder, 1967) and shallow waters with low current speeds (Bianchi and Morri, 1996; Schwindt et al., 2004b). *Ficopomatus enigmaticus* prefers both brackish and sheltered waters that are protected from wind, wave or tide activity (Schwindt et al., 2004a; Fornós et al., 1997).

Recent introductions of *F. enigmaticus* worldwide have been facilitated by anthropogenic induced changes in the environment that the species can tolerate and thrive in (Montefalcone et al., 2022). The proliferation of reefs is common in eutrophic systems and examples include the estuaries, lagoons, and marinas in the Mediterranean (Bianchi and Morri, 1996; Brundu and Magni, 2021; Fornós et al., 1997; Ntzoumani et al., 2024), South America (Schwindt et al., 2004a, 2004b), South Africa (Bezuidenhout and Robinson, 2020; Davies et al., 1989; McQuaid and Griffiths, 2014), North-Western France (Charles et al., 2018), Atlantic (Costa et al., 2019), and Baltic Sea (Hille et al., 2021). The Mar Chiquita is a large coastal lagoon in Argentina and has the highest densities of reefs recorded globally, with a maximum of 370 reefs per ha^{-1} and an average reef cover of 86% in the lagoon (Schwindt et al., 2004a). The physical structures of reefs can lead to significant abiotic changes (e.g., hydrodynamics and sediment transport) (Schwindt et al., 2004a) and biotic changes for epifauna, macrofauna (e.g., crustaceans, polychaetes) in surrounding soft sediments, and local and migratory shorebirds through trophic (e.g., predator-prey) and non-trophic (e.g., burrowing, sheltering, resting) interactions (Bruschetti et al., 2009; Martinez et al., 2020; Schwindt et al., 2001). The ecological effects of *F. enigmaticus* in smaller estuaries with lower reef densities (<20 % coverage of lagoon) can still be significant and cause long term changes (Brundu and Magni, 2021; McQuaid and Griffiths, 2014). For example, a positive and 190-fold increase in biomass of infauna living in *F. enigmaticus* reefs occurred in the Zandvlei estuary within 70 years of reef development (McQuaid and Griffiths, 2014). Recently, patterns in infauna and benthic assemblages relating to different reef characteristics such as volume, size and density emerged when comparing estuaries that have many small reefs versus those with fewer but larger reef structures (Brundu and Magni, 2021).

Individual reef characteristics of *F. enigmaticus* such as size and morphology vary across localities and are influenced by environmental conditions and substrate (Fornós et al., 1997; Schwindt and Iribarne, 1998; Schwindt et al., 2004b) (Supplementary Table S1). When water flows are uniform, circular type reefs form, whereas uni-directional flows can cause reef elongation (Schwindt and Iribarne, 1998). The largest individual reefs built by *F. enigmaticus* are circular formations reaching 7 m in diameter and 0.5 m in height from the shallow (<1 m) and protected parts of the Mar Chiquita (Schwindt et al., 2004a). In comparison in a Mediterranean lagoon, cauliflower-like patch reefs up to 4.5 m in diameter and 2.4 m height can develop in 3 m channel depths (Fornós et al., 1997). Horizontally protruding platforms built by *F. enigmaticus* are also known to form fringing reefs growing on rocky platforms in the littoral zone, reaching up to 20 m in length and 1 m in height (Fornós et al., 1997). Growth of closely situated reefs can cause them to merge and form large platforms (Schwindt and Iribarne, 1998). Disturbances cause reef change and can result in mortality of reef in the centre, causing an accumulation of sediments and micro-atoll (Fornós et al., 1997) or halo like structures (Keene, 1980; Ntzoumani et al., 2024; Schwindt and Iribarne, 1998).

Southern Australia is in the putative native distribution range of the species (Styan et al., 2017) yet the structural complexity including size and morphology of serpulid reefs build by F. enigmaticus have not yet been described in South Australia. The Coorong is a large temperate estuarine and lagoonal system in Southern Australia, with a salinity gradient from estuarine to hypersaline (Gibbs et al., 2018). Historically, serpulids were widespread in the southern sections of the Coorong, where fossil deposits exceeded 700 years b. p. (Bone and Wass, 1990). According to early anecdotal records, living reefs of *F. enigmaticus* were present in the southern sections, but have since become non-existent in this part of the Coorong due to extreme hyper-salinity (Geddes and Butler, 1984). Reefs of *F. enigmaticus* are now confined to the estuary and northern Coorong in brackish and marine salinities (Dittmann et al., 2009). Only one previous study mapped reef occurrence of *F. enigmaticus* in the Coorong but was limited to a single channel (i.e., Mundoo Channel) and occurred during the Millennium Drought (Benger, 2010). The main objective of this study was to describe, classify, and map the density of modern polychaete reefs in the Coorong using a combined approach of digital aerial imagery and a ground truth survey. It was hypothesised that reef density and size will vary along the environmental gradient of the Coorong, with lower densities and larger reef sizes at the most sheltered localities at the furthest distance away from the mouth of the River Murray and freshwater inflow.

2. Methods

2.1. Study area

The study focused on the Coorong system, a Ramsar listed wetland of international importance (Phillips and Muller, 2006), located at the terminus of the Murray-Darling Basin in Australia (Fig. 1). Freshwater flows from the Murray River via Lakes Alexandrina and Albert into the Coorong lagoons through constructed barrages, and then through the estuary to the open sea. The Murray Mouth estuary (Murray Estuary) is a narrow channel (~500 m width and 6 m maximum depth) which is subject to microtidal influence and high wave energy from the Southern Ocean (Webster, 2010). Adjacent, the Coorong stretches over 100 km as two shallow connected lagoons, the North and South Lagoon, which are protected from the open ocean by the Younghusband Peninsula. The North Lagoon constitutes 85 km^2 and apart from several constriction points, has a wide, shallow channel (average of 1.5 km width and 1.2 m depth) (Webster, 2010). The typical salinity gradient for the Coorong is 20 in the Murray Estuary and up to 90 in the South Lagoon (Mosley et al., 2023). The average North Lagoon salinities range between 30 and 80 (Mosley et al., 2023). Water levels in the Coorong depend on the frequency, volume, and timing of freshwater flows but also fluctuate with wind speed and direction (Gibbs et al., 2018). Water levels are also affected by climatic phenomena, with low water levels and droughts occurring during El Niño (dry) and higher water levels and potentially floods during La Niña (wet) (Ryan, 2018).

Ficopomatus enigmaticus reefs in the Coorong are found in both the Murray Estuary (ME) and North Lagoon (NL), yet no reefs are found in vicinity of the main barrages where higher flows are prevalent (Benger, 2010; Dittmann et al., 2009). For the investigation, study sites were chosen based on the quality of available imagery, the occurrence of reefs, the logistics for a ground truth survey and sites where supplementary water quality data could be obtained. Study sites across the salinity gradient of the Coorong included the Goolwa Channel (GC), Long Point (LP), Noonameena (NM), and Rob's Point (RP) (Fig. 1).

2.2. Environmental data

The environmental conditions of salinity, temperature (°C) and water depth (m AHD) were collected to infer later spatial differences in reef distribution that could be attributed to the natural environmental gradient of the Coorong. Salinity was calculated from the specific electrical conductivity (EC, mS cm^{-1} at 25 °C) using the equation for the Coorong from Mosley et al. (2023). Environmental data from the three water monitoring stations closest to the mapped study sites (GC, LP, RP) were obtained from WaterData SA (https://water.data.sa.gov.au) for flow years 2000–2022 and averaged across seasons. As a proxy for the influence of freshwater inflow and tides at each mapped study site (GC, LP, NM, and RP), the distance from the nearest main barrage (Goolwa barrage for GC and Tauwitchere barrage for LP, NM, and RP) and

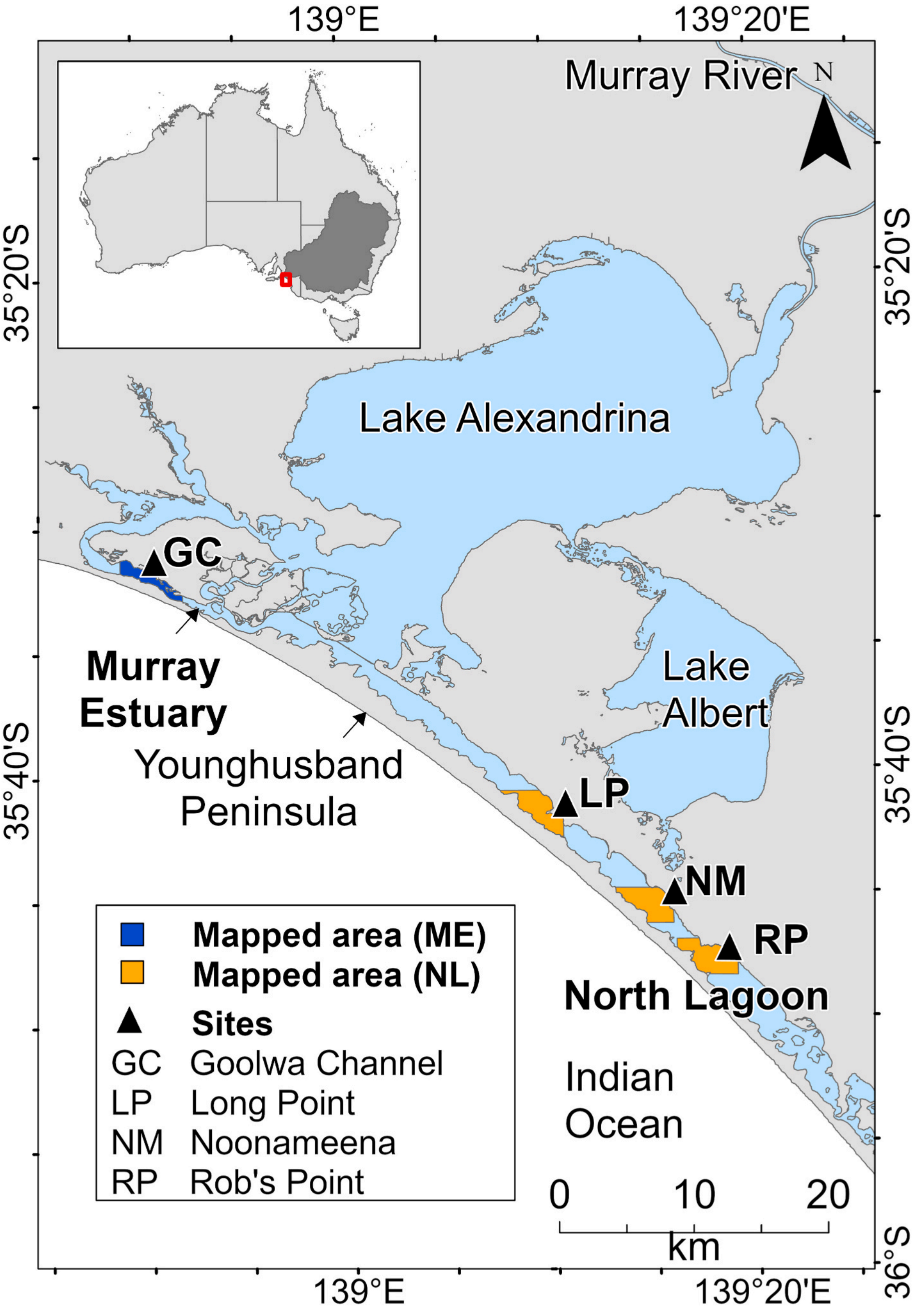


Fig. 1. Map of study areas and sites of *F. enigmaticus* reef classification and distribution undertaken in the Coorong, including the Murray Mouth and North Lagoon regions. The inset shows the location of the Coorong system (red-shaded area) at the terminus of the Murray-Darling Basin (MDB) catchment area (grey-shaded area) in Australia. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

distance from the Murray Mouth entrance were used respectively (Mosley et al., 2023). In addition, environmental conditions that could affect reef structures (pH, bicarbonate), relate to food availability for filter feeding (chlorophyll *a*, turbidity) and relate to rapid growth in eutrophic conditions (Trophic Index, TRIX) were sourced from Mosley et al. (2023), for later correlation with reef characteristics.

2.3. Reef detection

Advanced 3-D mapping techniques such as underwater photogrammetry (Rossi et al., 2021) were unsuitable to use in the Coorong, where high flows during this study period led to poor visibility (i.e., sediment resuspension and high-water turbidity). Fine-scale bathymetric LiDAR could provide an alternative approach (e.g., Bajjouk et al., 2020) but is a high-cost data collection option (Loh et al., 2019) and not suitable in coastal turbid environments (Dee et al., 2020). High resolution sonar is an alternative option to map polychaete reefs in turbid water (Brundu and Magni, 2021; Degraer et al., 2008), but in the Coorong reef occurrence is mainly restricted to shallower parts of the channel (<0.7 m water depth) that are not accessible (i.e., too shallow) for sonar mapping (e.g., Storlazzi et al., 2016). A remote sensing approach of readily available digital aerial imagery taken during a time of good water clarity (low freshwater flows) was used in this study, with resolution and spatial scale suitable for the detection of polychaete reefs across its current distribution range in the Coorong. Digital aerial imagery (R,G,B) from 2018 were obtained from the Department for Environment and Water (DEW), and used to spectrally detect *F. enigmaticus* reefs in shallow water, following a similar approach as Benger (2010). The digital aerial imagery used for this study was collected between May to August 2018 at 12.5 cm resolution, and orthorectified to the Geodetic Datum of Australia 1994, Zone 54.

Twenty spectral profiles across *F. enigmaticus* reefs were measured in each region of the Coorong (ME and NL) using ERDAS imagine (V16.6.2020). Each colour band (R,G,B) was statistically assessed for the profiles taken, and the one which yielded the greatest differentiation between reef and sediment, and lowest variation among reef pixels was determined. The ability to differentiate between reef and sediment was similar among all three colour bands (Supplementary Fig. S1, Table S2). The green band has previously been used in the detection of shallow water objects (Benger, 2010) and was subsequently chosen for spectral detection of reefs in the imagery. In each region, the illumination conditions between reef and sediment differed, and thus different optimal thresholds in the green band were determined for reef detection (Supplementary Tables S2–3).

2.4. *Image processing*

The 2018 digital imagery was processed in ArcGIS Pro (V 10.8.2). The area of imagery processed in the ME and NL were 250 ha and 2126 ha respectively. Approximately 15% of the total area was masked due to dark sediment or seagrass patches obscuring reef presence. Additionally, in the ME, the imagery was masked by elevations < -0.7 m AHD (Hobbs et al., 2019). The masked area excluded the deep channel areas of the estuary (−4.0 m to −0.7 m AHD) that were not suitable for reef detection by spectral means.

Digital polygons were extracted for the detected reefs by spectral means and filtered by area (m^2) to remove mis-classified reefs that were outside the minimum and maximum bounds from reef areas surveyed in the field. For the cross validation of reef detection in the processed imagery, 95 randomly sampled reefs across the ME and NL were geolocated with a dGPS in the field during 2022. Reef change was assumed negligible from the period between 2018 and 2022, where the environmental conditions (e.g., annual freshwater discharge) in the Coorong were relatively consistent, and no high flow, flood or drought events occurred (Mosley et al., 2023) that would have had a significant effect on growth or mortality of *F. enigmaticus*. Reef size in the 2018 imagery were compared to field measurements with a ground truth survey in 2022. Field measurements included the diameter (to the nearest 0.01 m) of individual geolocated reefs with recorded cardinal direction of measure (north to south or east to west).

2.5. *Reef classification*

A total of 200 polychaete reefs were classified in each region of the ME and NL, from ten 0.25 ha plots that were randomly generated across the imagery in each region. Reefs were visually assessed of their 2-D morphology (top-down view of their surface area) in the digital imagery. A classification scheme of 2-D reef morphologies in the 2018 digital imagery were cross validated against ground truth images taken in 2022 (Table 1) and high-resolution aerial images in 2020 obtained from Airborne Research Australia (Supplementary Figs. S2–5). For each reef classified, the diameter was digitally obtained from the imagery using ArcGIS Pro. The reef diameter was measured across the two widest edge points which passed through the reef centre.

Individual reef surface area (m^2) for each reef occurring in the same 0.25 ha plots were extracted from the polygons that were generated from the spectral detection approach. In addition, the sum of individual reef polygons per plot were used to assess reef density and reef percent coverage on a plot scale for each region of the ME and NL. Reef densities were extrapolated to reefs per hectare, based on the median reef density per plot.

Table 1
Description of *F. enigmaticus* reef classifications in the Coorong by their respective morphologies, and spatial occurrence.

Reef classification	Description of reef morphology	Spatial occurrence
Patch reef	*Form of a singular reef*	
Halo	A reef that has collapsed at the centre, leaving a hollowed interior.	ME
Irregular	A reef that is asymmetrical, having unequal diameters, when measured from two cardinal directions (perpendicular to one another).	ME, NL
Circular	A reef that is symmetrical, having equal diameters when measured from two cardinal directions (perpendicular to one another).	ME, NL
Aggregated reef	*Form of multiple coalesced reefs*	
Platform	Multiple patch reefs that have merged or fused together over time	ME, NL
Fringing	Multiple patch reefs that have fused with nearshore natural rock platforms	NL

To assess reef 3-D morphology of the different reef classes identified from the digital aerial imagery, supplementary field measurements of reef height (m) were taken using a measuring staff (0.01 m accuracy) in 2022. Reef height was taken from the edge of a reef at the seafloor to the highest point, and for each reef averaged across two measurements taken from the channel and shoreline edges of the reef.

2.6. *Spatial distribution of reefs*

To understand broad scale density patterns in *F. enigmaticus* reefs, spatial distribution maps were created in cross sections of the Coorong. Reef point data of *F. enigmaticus* were derived from the spectral detection of reefs in the ME and NL. As fringing reef are only present in the NL, their reef point data were excluded for a comparison of reef densities between regions. Reef polygon data were interpolated using kernal density estimation (KDE) (Silverman, 1986) in ArcGIS Pro using a planar method. KDE is a non-parametric analysis with few assumptions and has previously been applied to ecological data to approximate distribution patterns (e.g., Jourdan et al., 2022; O'Brien et al., 2012) and locate hot spots as regions of high density (Nelson and Boots, 2008). In each mapped cross section of the Coorong at sites GC, LP, NM and RP, interpolated data by KDE was used to show the spatial variation in reef density with a scale of individual reefs per hectare.

2.7. *Data analysis*

To statistically test the pixel values that yield the greatest spectral differentiation between reef and sediment in the ME and NL regions, a 2-way ANOVA with factors substrate type (reef, sediment) and colour band (R, G, B) was carried out. Tukey pairwise comparisons were used for significant interaction effects (Supplementary Table S2). To test for a significant difference in reef density per plot (0.25 ha) between regions of the ME and NL, a non-parametric Mann-Whitney *U* Test was used as data did not meet normality (Shapiro-Wilk Test). All the statistical tests were carried out in OriginPro 2021b, V 9.8.5.201.

To assess the relationship between reef characteristics (e.g., density, size, 2D morphology) and environmental conditions, distance-based ReDundancy Analysis (dbRDA) (McArdle and Anderson, 2001) were carried out using Primer 7 (Clarke and Gorley, 2015) and PERMANOVA+ (Anderson et al., 2008). Two overlays are presented in the dbRDA plot, one of the environmental conditions (salinity, temperature, chlorophyll *a*, bicarbonate, pH, TRIX, turbidity and water level), and second of the underlying pattern of reef characteristics (reef density and size of each reef class of circular, irregular, platform, fringing and halo).

3. Results

3.1. Environmental conditions

Across the distribution range of polychaete reefs in the Coorong, RP had the highest average salinity (75.56 ± 1.99) and lowest average water level (0.096 m ± 0.010), which was during summer (Fig. 2). Across all seasons, the most consistent and lowest salinities occurred at GC which were on average 24.30 ± 0.22 in summer and 19.97 ± 0.33 in spring (Fig. 2A). Seasonally higher water levels occurred in winter at LP and RP (0.415 m ± 0.008 and 0.429 m ± 0.010) along with lower average salinities at LP and RP (35.06 ± 0.26 and 51.85 ± 0.80) (Fig. 2A–C). Water temperature across the three sites showed a similar seasonal trend, with lowest average temperatures in winter (12 °C) and highest average temperature in summer (21 °C) (Fig. 2B).

RP is located the furthest away from tidal influence through the Murray Mouth (50 km) and flow speeds from discharge through the main Tauwitchere Barrage (36.5 km) (Fig. 1, Supplementary Fig. S6). In comparison, GC is the closest site to receive tidal influence through the Murray Mouth (5 km) and discharge from the Goolwa barrage (Fig. 1, Supplementary Fig. S6).

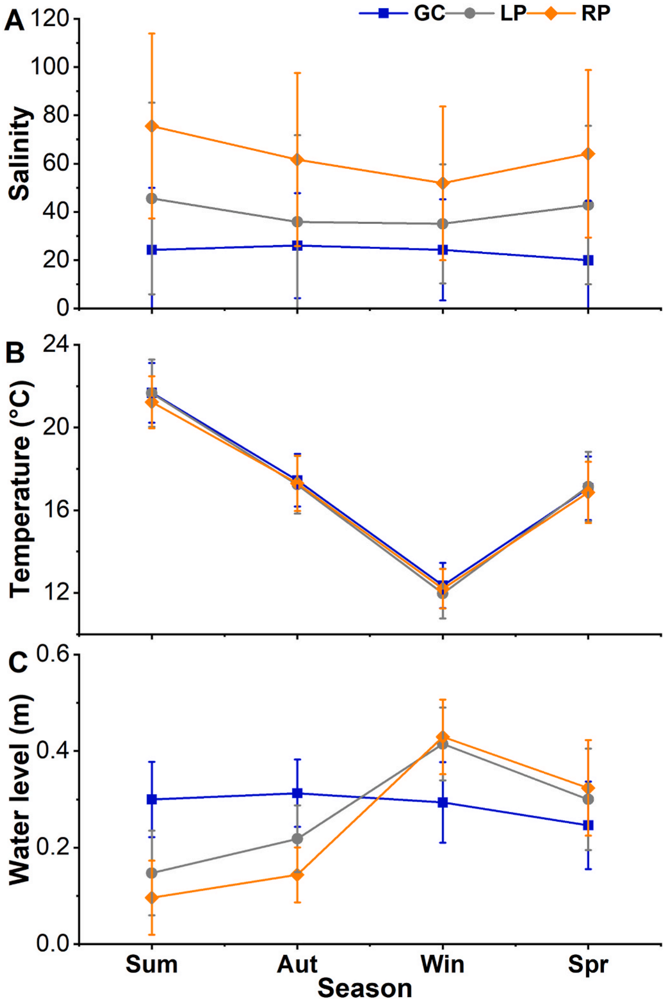


Fig. 2. Seasonal differences in average (±se) water conditions of A) salinity B) temperature (°C) and C) water level (m) at Goolwa Channel (GC), Long Point (LP) and Rob's Point (RP). Seasons include summer (December–February), autumn (March–April), winter (June–August), and spring (September–November). Data were sourced from WaterData SA and the seasonal mean ± se (symbols and bars) were calculated across flow years 2000–2022 based on available data.

3.2. Accuracy assessment

The ground truth survey verified *F. enigmaticus* reef presence in the 2018 imagery with reefs randomly sampled and geolocated in the field in 2022 (n = 95 reefs). Reef diameter from extracted reef polygons in the 2018 imagery positively correlated ($R^2 = 0.99$) with the field measured reef diameter (Fig. 3). In the 2022 field survey, living worms were detected from reefs in the estuary and lagoon, and new growth of tube structures was recorded on the outer rim of the reefs but often smothered by filamentous algae.

3.3. Reef classification

A total of five different reef types of *F. enigmaticus* reefs in the Coorong were identified from digital aerial imagery. Based on their morphology, the reef type was classified as either halo, irregular, circular, platform or fringing reef (Tables 1 and 2). In each region, patch reefs (halo, irregular or circular) and aggregated reefs (platform or fringing) were present, yet, aggregated reefs were more commonly encountered in the NL (Table 2). In the ME, the most common reef type observed were irregular reefs (71.5 % of reefs) which were on average 0.65 m in diameter and 0.19 m in height (Table 3). In comparison, the NL was characterised by large and circular reefs (49.5 % of reefs) that were on average 3.23 m in diameter and 0.71 m in height (Table 3). In the NL, platform reefs often consisted of 2–3 large circular reefs that were aggregated, reaching diameters of up to 18 m across, and 1.3 m in height (Table 3). Fringing reef only occurred in the NL, where natural limestone rocky platforms were present along the shoreline, that provided a hard substrate for *F. enigmaticus* to form reef aggregates (Table 3).

The average surface area (SA) per individual reef for the common reef classes (irregular, circular and platform) was greater in the NL than ME (Fig. 4). In each region, platform reefs contributed the most to SA coverage among reef classes, which were on average 25.04 ± 3.96 m^2 in the NL compared to an average of 2.20 ± 0.63 m^2 in the ME. In the ME, the SA of irregular and circular reefs were similar, with averages 0.21 ± 0.02 m^2 and 0.28 ± 0.04 m^2, respectively. A different pattern was identified in the NL, where circular reefs had a greater surface area compared to irregular reefs (3.52 ± 0.51 m^2 and 7.84 ± 0.76 m^2) (Fig. 4).

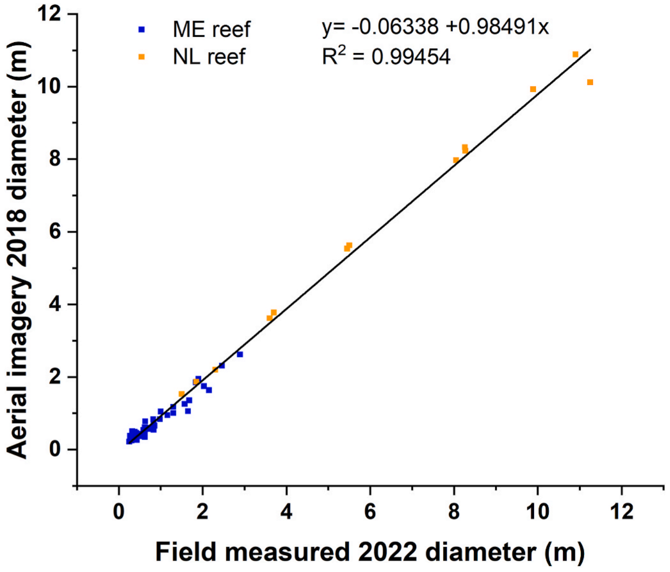


Fig. 3. Accuracy assessment of the 2018 digital aerial imagery for *F. enigmaticus* reef detection and size (N-S and E-W diameters) with geolocated reefs in the field in 2022 (n = 59 diameter measurements, n = 32 reefs).

Table 2

Classification of *F. enigmaticus* patch reef types in the Coorong, from comparisons between ground truth locations in 2022 and digital aerial imagery sourced from the Department for Environment and Water (DEW), 2018.

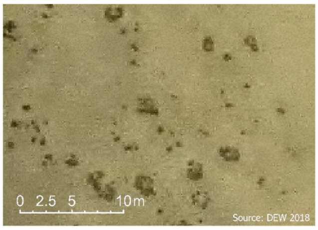
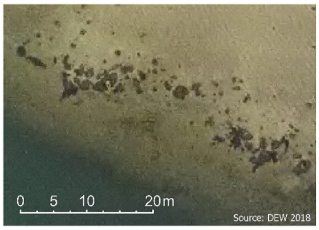
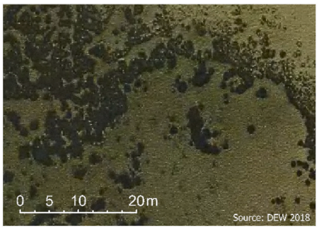
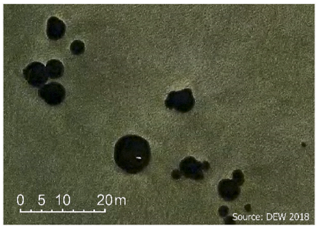
Classification	Ground truth image (2022)	Aerial photo (DEW, 2018)
Murray Estuary Circular with hollowed interior 'Halo' reef type		
Small 'irregular' reef type with some coalesced forming 'platforms'		
North Lagoon 'Circular reef type' amongst a 'fringing reef'		
Large 'circular reef type'		

Table 3

F. enigmaticus reef classification by morphology and diameter derived from digital aerial imagery of the Coorong in 2018 and reef height derived from field measurements in 2022 across the Murray Estuary and North Lagoon of the Coorong.

		Digital aerial imagery (2018) measurements			Field measurements (2022)		
Region	Reef Classification	Number of reefs measured	Average diameter (m)	Maximum diameter (m)	Number of reefs measured	Average height (cm)	Maximum Height (cm)
Murray Estuary	Halo	17	1.37 ± 0.17	3.20	4	20.29 ± 2.96	35.00
	Irregular	143	0.65 ± 0.02	1.82	204	18.97 ± 0.59	38.00
	Circular	30	0.65 ± 0.04	1.29	69	19.88 ± 0.46	48.00
	Platform	10	2.74 ± 0.56	6.85	34	24.28 ± 1.11	47.00
North Lagoon	Irregular	65	2.13 ± 0.17	5.76	1	50.00 ± 0	50.00
	Circular	99	3.23 ± 0.13	9.71	6	70.63 ± 0.07	110.00
	Platform	35	7.45 ± 0.65	17.98	3	106.67 ± 0.19	130.00
	Fringing	1	400.65 ± 0	400.65	0		

The median reef density in the ME was 56 reefs per 0.25 ha plot and significantly greater than the median reef density of 15.5 reefs per 0.25 ha in the NL ($U_{10,10} = 79$, $p = 0.031$) (Supplementary Fig. S7A). This would equate to 224 reefs per ha in the ME (range 4–1044 min to max) and 62 reefs per ha (range 0–228) in the NL. However, with the large size of reefs in the NL (Fig. 4), the percentage cover per plot showed a larger range, but was not significantly different from the percentage cover in the ME (Supplementary Fig. S7B). Percent coverage of reefs was low in both regions, with a median of 0.6% (range 0–4%) in the ME and 2.9% (range 0–14%) in the NL (Supplementary Fig. S7B).

3.4. Spatial distributions of reefs

Reef distribution in the Coorong varied spatially between regions (i.

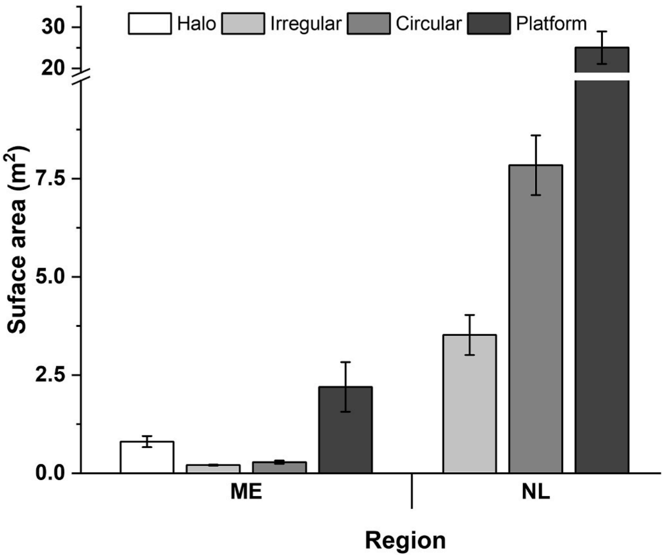


Fig. 4. Average surface area (m^2) of individual reef classes (halo, irregular, circular, platform) in each region of the Murray Estuary (ME) and North Lagoon (NL) of the Coorong, derived from reef detection in the 2018 digital aerial imagery.

e., ME versus NL), within regions (e.g., LP versus NM versus RP in the NL) and within specific locations (GC, LP, NM, and RP) (Figs. 5 and 6). The highest reef density in the ME was 525 reefs per hectare (Fig. 5). In the ME reefs were commonly distributed along the north-eastern shoreline and high densities occurred near the outflows of natural creeks (e.g., Shoal Bay, Rushy Island, and Swan Point) (Fig. 5).

The reef densities in the NL were lower than in the ME and varied across locations (Figs. 5 and 6). For the three investigated locations in the NL, the southern-most locality (RP) included some of the highest reef densities found (Fig. 6C). At RP, highest densities occurred on a sand spit situated on the Younghusband Peninsula side of the channel (Fig. 6C, Supplementary Fig. S4). A similar pattern of high reef density areas that coincided with sand spits created from aeolian sand drift on the peninsula also occurred at LP and NM, however, only reached up to 139 and 60 reefs per ha, respectively (Fig. 6A and B). At NM and RP, reef distribution is continuous along the eastern shoreline (up to 100 reefs per ha), with lower reef densities in the main channel section (1–10 reefs per ha) (Fig. 6B and C).

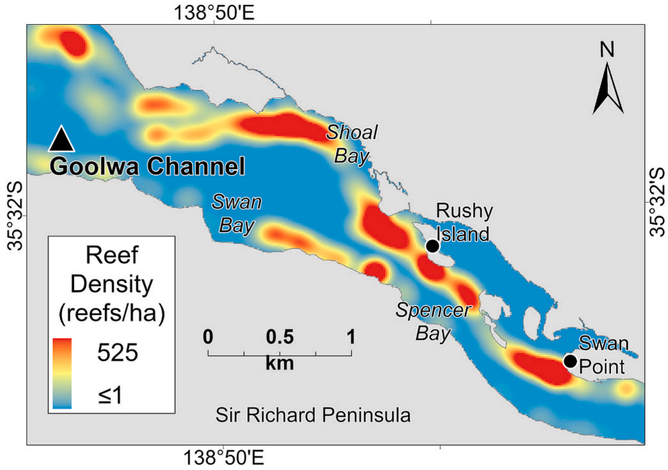


Fig. 5. Spatial analysis of the density of *F. enigmaticus* reefs in the Murray Estuary region of the Coorong in the Goolwa Channel. The scale shows reef density in reefs per hectare that were interpolated using Kernal Density analysis in ArcGIS Pro. Channel areas indicated in blue represent a density ≤1 reef ha^{-1}. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.5. *Effects of environmental conditions on reef density and size*

Distance based ReDundancy analysis (dbRDA) indicated correlations between reef characteristics (density and size) and environmental conditions, with the two first axis of the constrained ordination plot explaining 78.3 % of the total variation (Fig. 7). Reef density and halo reef size were drivers of the variation in reef characteristics at Goolwa Channel (ME), and were correlated with turbidity, temperature and water level (Fig. 7). In contrast to the ME, reef size of circular, platform and fringing types were driving variation in reef characteristics at NL sites (Fig. 7). Circular reef size was highly correlated with the NL site of Robs Point, and correlated with environmental conditions of chlorophyll *a*, TRIX, salinity and bicarbonate (Fig. 7). The water quality TRIX values were indicative of eutrophic waters (values > 6) and generally increased in a gradient towards the southern end of the North Lagoon (Fig. 8). The mean circular reef size positively correlated with the TRIX gradient, with the smallest reef size (0.9 m^2) and lowest TRIX value (7.3) in the GC and largest mean size of 27.3 m^2 and highest TRIX value (8.8) at RP (Fig. 8).

4. Discussion

This study provides evidence for extensive polychaete reefs built by *F. enigmaticus* in its Australian range, within the Coorong, a large temperate estuarine and lagoonal system. Classification and mapping based on a combined approach using remote sensing and field data differentiated five key types of polychaete reefs. In the Murray Estuary (ME) of the Coorong, polychaete reefs occur in high densities and small average sizes compared to the North Lagoon (NL) where reefs are on average larger in size but occur in lower densities. The distributions and morphologies of the reefs supported the hypothesis that reef size will increase and density will decrease along the environmental gradient of the Coorong at increasing distance from the main barrages and Murray Mouth (i.e., toward the most sheltered waters).

The reef formation and growth characteristics of *F. enigmaticus* is driven by environmental variables such as salinity, temperature, water depth, flow velocities, nutrients, and food availability (Fornós et al., 1997; Schwindt and Iribarne, 1998; Schwindt et al., 2004b). The preferred habitat of *F. enigmaticus* is within brackish and sheltered coastal lagoons, with reproduction and growth coinciding with salinities between 10 and 30 (Bianchi and Morri, 1996; Hartman-Schröder, 1967). In this study, the Goolwa Channel provided the most suitable habitat (i.e., brackish salinities) for *F. enigmaticus* growth and reproduction, and reef densities were highest, but reef sizes small. At the southernmost range of *F. enigmaticus* reefs in the Coorong, hypersaline conditions exceeded the previously known salinity range for *F. enigmaticus*, but reefs were larger in size. In some cases, high salinity does not impede recruitment and reef stability in serpulids, as observed in Prokopos Lagoon for *F. enigmaticus* in salinities of 38–42 (Ntzoumani et al., 2024) and in Baffin Bay for *Hydroides dianthus* in salinities of 36–46 (Breaux et al., 2023). The wide physiological adaptability of *F. enigmaticus* is also demonstrated by its recorded presence in hypersaline stromatolite pools in South Africa, with a salinity up to 54 (Rishworth et al., 2024). The overall pattern in the Coorong may reflect both current and past environmental conditions and events such as drought and flood. Freshwater flows through a complex of barrages are highly variable between years and are critical in maintaining connectivity and estuarine habitats in the Coorong (Webster, 2010).

The reef classification revealed that morphologies and sizes in the Coorong were similar to those found in Mar Chiquita for circular and platform reefs (Schwindt et al., 2004b), in Prokopos Lagoon in Western Greece for circular, irregular and halo reefs (Ntzoumani et al., 2024), and in Albufera of Menorca in the Western Mediterranean for fringing

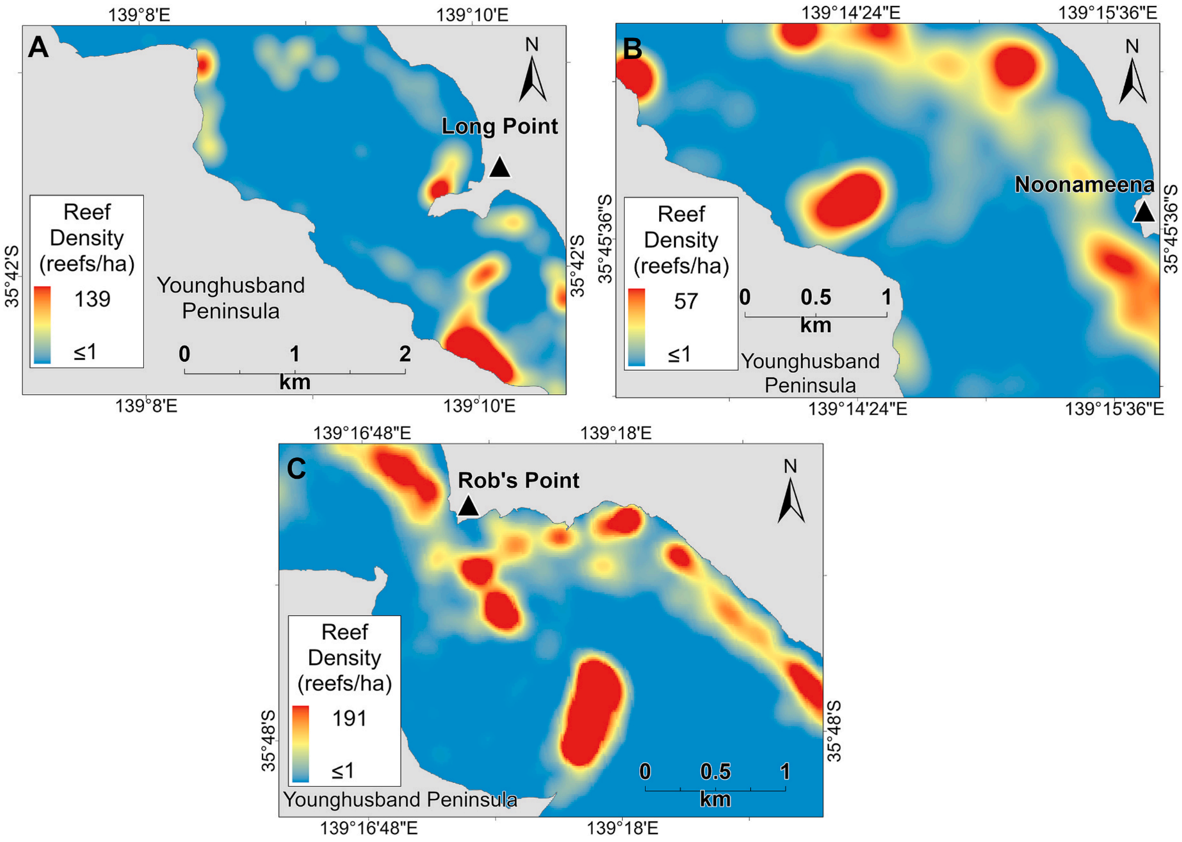


Fig. 6. Spatial analysis of the density of *F. enigmaticus* reefs in the North Lagoon region of the Coorong at locations of (A) Long Point, (B) Noonameena, and (C) Rob's Point. The scale shows reef density in reefs per hectare that were interpolated using Kernal Density analysis in ArcGIS Pro. High reef densities are indicated in red, and low reef densities are indicated in blue with ≤ 1 reef ha^{-1}. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

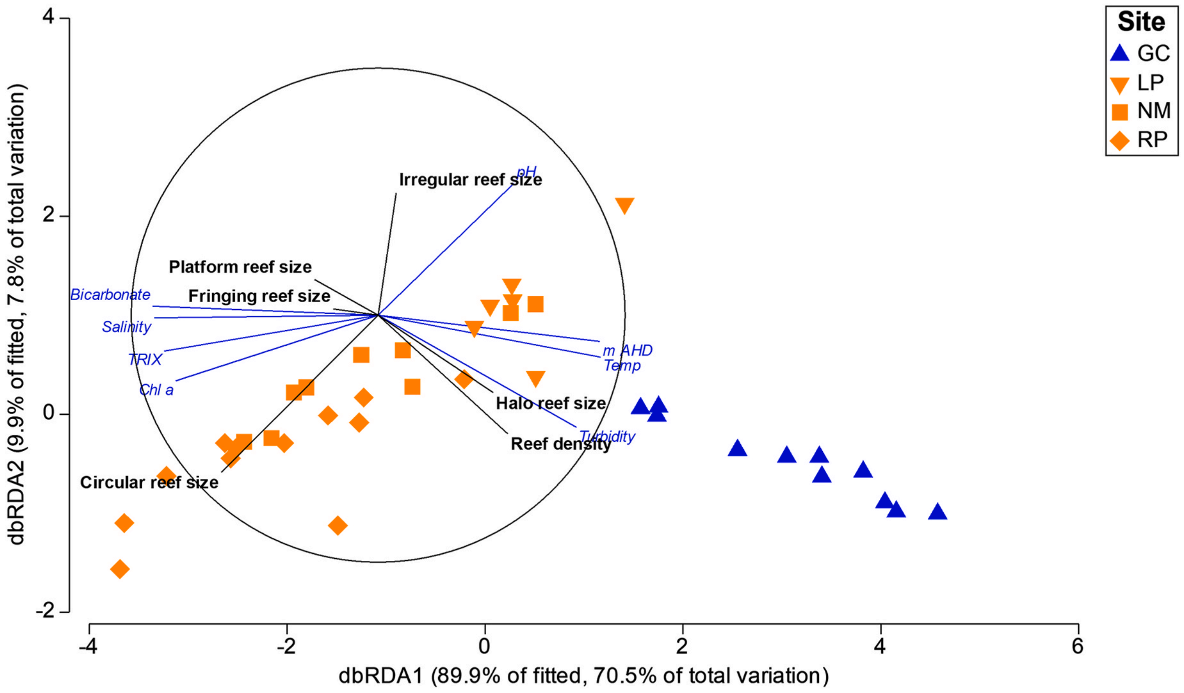


Fig. 7. Distance-based ReDundancy Analysis (dbRDA) correlating reef density and size of reefs (circular, irregular, platform, fringing and halo types) with mean environmental conditions in the Coorong. Environmental conditions include chlorophyll *a* (Chl a), TRIX (Trophic Index), temperature (temp), salinity, turbidity, water level (m AHD), pH and bicarbonate. Colours correspond to regions of the Coorong including blue symbols for the Murray Estuary sites and orange symbols for the North Lagoon sites. Environmental data were sourced from Mosley et al. (2023) and WaterData SA for the years 2000–2022. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

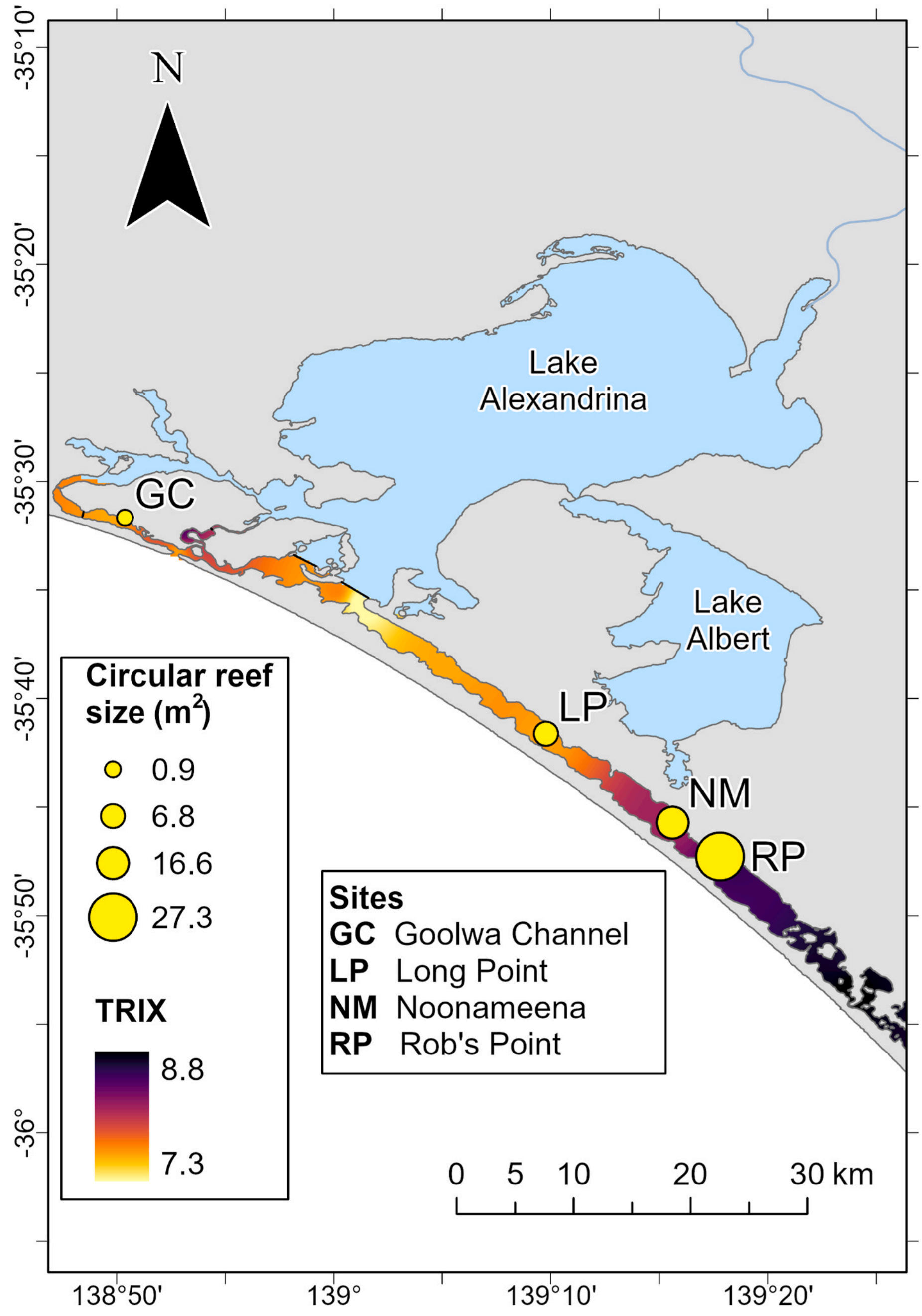


Fig. 8. Map of water quality for mean Trophic Index (TRIX) from 2000 to 2022 in relation to circular reef size for *F. enigmaticus* reefs in the Coorong. TRIX values > 6 indicate eutrophication, and TRIX data were obtained from Mosley et al. (2023).

reef (Fornós et al., 1997). In the ME, the common form of *F. enigmaticus* reefs were irregular and smaller in size (<0.7 m diameter and <20 cm in height). The small size may be reflective of younger reef formations, as the earliest photographic records of *F. enigmaticus* reefs in the ME were from 1960 (Dittmann et al., 2009). The reef distribution of *F. enigmaticus* was non-uniform, with a greater reef occurrence on the shallow intertidal mudflats of the channel in <1 m water depth. The small reef sizes and non-uniform distribution may also be attributed to disturbances from high flow velocities from tidal movements, but also freshwater release over the nearby barrages into the narrow channel. Examples of impacts from flood events on *F. enigmaticus* reefs include high turbidity disrupting the settlement of larvae (Kupriyanova et al., 2001), sedimentation causing the break-up of the oldest, central parts of reefs (Schwindt and Iribarne, 1998; Keene, 1980) and, in some cases, mass mortality of adult worms (Aliani et al., 1995). In comparison, disturbances to reefs during times of drought could include increased salinities from a lack of freshwater flows (e.g., in the Coorong, Benger, 2010) or closing of the estuary mouth (e.g., Wilson Inlet, Styan et al., 2017).

Platform reefs in the estuary consisted of merged individual patch reefs, which were elongated in the main flow direction, like reefs subject to uni-directional flow described by Schwindt and Iribarne (1998). The halo morphology of *F. enigmaticus* reefs, also referred to as micro-atoll like (Fornós et al., 1997), has been observed in other coastal lagoons (Keene, 1980; Ntzoumani et al., 2024; Schwindt and Iribarne, 1998), and was also found in the Coorong. The halo develops when accumulation of sediments inside the reef causes the mortality of the oldest worms and subsequently collapse in the centre. Halo reefs indicate that previous disturbances have occurred and may be older reef forms (Fornós et al., 1997; Keene, 1980; Ntzoumani et al., 2024; Schwindt and

Iribarne, 1998).

In the Coorong NL, large circular *F. enigmaticus* reef formations (on average 3.2 m diameter, 0.7 m height) may reflect long-term growth with rapid growth periods (i.e., brackish salinities, high nutrients) and fewer disturbances (i.e., lower flow velocities) than in the ME. In addition, shallow water depths combined with uniform flow can explain circular reef formations in *F. enigmaticus* (Schwindt et al., 2004a). The maximum diameter of a circular reef recorded in the NL was up to 11 m, exceeding the maximum diameter of 7 m from Mar Chiquita in Argentina (Schwindt et al., 2004a). Geddes and Butler (1984) observed 'large mounds' of living reefs of *F. enigmaticus* in the littoral areas of the NL in 1983. This may indicate that a main growth phase of reefs commenced in the early 1980's, coinciding with the start of reduced flushing of the Coorong lagoons (Mosley et al., 2023). Long term water quality data over the last two decades indicate that reduced flushing has led to high concentrations of salinity, total nutrients and phytoplankton (Mosley et al., 2023). In this study, key environmental drivers of circular reef formations included salinity, bicarbonate, chlorophyll *a* and TRIX. The positive correlation between circular reef size and TRIX values in the Coorong suggest that the eutrophic conditions in the Coorong could have led to increased food availability for suspension feeding by *F. enigmaticus*, intensified growth and large reef formations that are now dominant. Examples from other coastal lagoons suggest that *F. enigmaticus* has the highest growth rates and biomass under eutrophic conditions (Keene, 1980; Zaouali and Baeten, 1983).

In the NL, platform reef morphologies of *F. enigmaticus* were common and widespread. Platform reefs may consist of merged circular bioherms, which have also been described as 'fused reef' in the Mar Chiquita (Schwindt and Iribarne, 1998; Schwindt et al., 2004b). In the Coorong lagoon, platform reefs were common in the deeper water sections, which may reflect a relationship between reef diameter and height to achieve reef stability. The fringing reef forms of *F. enigmaticus* which were widespread in littoral areas of the Coorong NL had formed on shallow limestone rocky platforms. Fringing reefs are common where there is an availability of rocky substrate and they can reach several m^2 in size, often growing in a horizontally protruding direction (i.e., along the shoreline) in the littoral zone (Fornós et al., 1997; Obenat and Pezzani, 1994).

Previous mapping studies in coastal estuaries and lagoons of *F. enigmaticus* reef distribution have shown that individual reef density may vary with substrate availability (Bezuidenhout and Robinson, 2020; Bianchi and Morri, 1996), benthic assemblages (Brundu and Magni, 2021), and growth rates over time (Schwindt et al., 2004b). In the Coorong, the reef density (median of 224 reefs per ha) observed in the ME was lower than the density in the Mar Chiquita coastal lagoon in Argentina (370 reefs per ha). However, the reef classification revealed that morphologies and sizes (circular and platform reefs) were similar to those found in Mar Chiquita (Schwindt et al., 2004b). In the Coorong, higher reef densities were found, although these were seen to occur in localised patches. In the ME up to 525 reefs per ha occurred near natural creek outflows, which may indicate localised hotspots for primary productivity from nutrient run off that could facilitate rapid *F. enigmaticus* colonization and growth. Abundant establishment substrates or frequent disturbances causing reefs to break apart over time could also contribute to a higher density.

The highest patch densities in the NL reached up to 191 reefs per ha and occurred on sand spits on the peninsula side of the channel. Rapid rates of coastal erosion coupled with aeolian sand sheet transgression inland is occurring on the Younghusband Peninsula (Hesp et al., 2022), which may explain the recent formation of sand spits on the peninsula side of the Coorong lagoons. The small but abundant *F. enigmaticus* patch reefs on sand spits may indicate relatively recent expansions of their distribution, facilitated by ideal conditions for *F. enigmaticus* growth such as shallow water depths and slower currents. The prevalence of *F. enigmaticus* on peninsula sand spits in the hypersaline southern sections of the NL may be linked to locally reduced salinities from freshwater soaks (Bickerton and Winter 2001). Similarly, reefs located along the eastern shorelines of the NL may also benefit from localised groundwater discharges (Haese et al., 2009).

In the main channel of the NL, reef densities were lower (1–10 reefs per ha) and similar to densities found for serpulid reefs (*F. enigmaticus* and *Hydroides*) in Mediterranean lagoons in Italy (8–13 reefs per ha) (Brundu and Magni, 2021). Physical damage to serpulid reefs can cause mass spawning and further spread (Kupriyanova et al., 2001). Disturbance from recreational boat traffic has facilitated the spread of *Hydroides elegans* (Serpulidae) in the Mediterranean (Ferrario et al., 2024). The proliferation of reefs within the main channel of the NL may be similarly linked to boat traffic and propellor strikes to existing reefs. Anthropogenic disturbances to estuaries (e.g., increased boat traffic, nutrient run off, reduced freshwater inflow) may have implications for the distribution and ecological functions of polychaete reefs.

5. Conclusion

The classification and mapping of *F. enigmaticus* undertaken within this study has shown that polychaete reefs are extensive throughout the Coorong, a large temperate estuarine and lagoonal system. The reefs built in the Coorong by *F. enigmaticus* are some of the largest described for this species, compared to other estuaries and lagoons worldwide. Our findings elucidate that *F. enigmaticus* reefs are expanding in range across the Coorong, with potential effects on ecological health and functioning of this Ramsar listed wetland of international importance. We provide a benchmark study of the distribution and sizes of *F. enigmaticus* reefs across an environmental gradient, that could be informative for the management of flow and eutrophication in the Coorong system and other estuaries and coastal lagoons with *F. enigmaticus* growth.

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CRediT authorship contribution statement

Laura Schroder: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Orlando Lam-Gordillo:** Writing – review & editing, Methodology. **Sabine Dittmann:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

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.

Data availability

All the data used is presented in the article and supplementary materials.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.108905.

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Chapter 3. History of polychaete reefs in the Coorong, South Australia

Dried *F. enigmaticus* tubes from a reef core collected in the Coorong. Photo credit: Laura Schroder.

Abstract

Ficopomatus enigmaticus is a prolific reef-building polychaete, known to build reefs up to several metre in diameter and height in brackish and sheltered coastal environments. Globally, *F. enigmaticus* is a well-known marine invasive species with a putative native range in Australia. In a large temperate estuary in Southern Australia (The Coorong), unknown fossil serpulid mixed with bryozoan mats have previously been dated at 700 BP, yet the history of *F. enigmaticus* reefs throughout the system remain unknown. This study provided a new approach to determine the history of *F. enigmaticus* reefs in the Coorong using radiocarbon dating of reef cores from large platform reefs up to 10 m in diameter and 0.8 m in height. Two polychaete reef cores of 80 cm depth were radiocarbon dated from multiple depth layers along the core. Core 1 and Core 2 showed evidence of modern carbon ($F^{14}C>1$, n=21 depths), and a bomb-pulse signal were detected in Core 2 ($F^{14}C<1$, n=1 depth and $F^{14}C>1$, n=10 depths). Results indicate that reef formation in *F. enigmaticus* occurred post 1955, which likely coincided with large changes in the Coorong such as barrage construction, diminishing freshwater flows and eutrophication since the 1940s. The environment of the modern Coorong supports extensive *Ficopomatus enigmaticus* reefs, yet further work is needed to identify whether *F. enigmaticus* has since replaced a native serpulid such as the unidentified fossil serpulid known from Sub-Recent bryozoan-serpulid buildups in the Coorong.

Key words: Carbon 14, Bomb-pulse, Serpulidae, *Ficopomatus enigmaticus*

3.1 Introduction

Reef building polychaetes (RBP) are ecosystem engineers of coastal and shallow water environments, which can provide important ecosystem services like water filtration, sediment stabilisation and nutrient cycling (Bruschetti, 2019). Polychaetes of the family Sabellariidae and Serpulidae are tube-dwelling and produce sand or calcareous tubes respectively (Giangrande et al., 2020). The gregarious nature of RPB reflects their ability to form complex three-dimensional reefs consisting of multiple generations of intertwined tubes, if given an initial hard substrate like shell or rock to settle on (Giangrande et al., 2020). The growth rates of polychaete reefs vary spatially and temporally and depend on environmental factors such as salinity, water temperature, nutrient availability, water level height and current speeds (Bianchi and Morri, 1996; Fornós et al., 1997; Hartmann-Schröder, 1967; Schwindt et al., 2004a). Sabellarid reefs are highly dynamic, undergoing cyclical phases of growth and destruction (Aviz et al., 2025; Franzitta et al., 2022; Ventura et al., 2024). In comparison, serpulid reefs are more persistent and stable structures that can last for several decades (Montefalcone et al., 2022). Serpulid reef growth can be rapid under favourable conditions (i.e., low current speeds, high nutrient rich water) (Schwindt et al., 2004b), and could provide records of environmental changes similar as for other biogenic reefs (Gillies et al., 2020; Erler et al., 2020). Interpreting chronological records in reefs requires knowledge of the age of the reef along depth strata (e.g., Erler et al., 2020; Erler et al., 2016). Yet for serpulid reefs, there are only few examples investigating ages from the most basal part of the core (e.g., Smith et al., 2005).

Globally, *Ficopomatus enigmaticus* (Polychaetea, Serpulidae) (Fauvel 1923) is one of the most prolific reef-building polychaetes and can be highly invasive in coastal lakes, lagoons and estuaries. An Australian origin for *F. enigmaticus* was proposed by Dew (1959), but remains speculative given the earliest observations were recorded after European arrival in the early 1930s. Recent molecular analysis of *F. enigmaticus* suggests there are three putative species across Southern Australia (Styan et al., 2017) and raises uncertainty of an Australian origin of the *F. enigmaticus* sensu lato group (Kupriyanova et al., 2023). The widespread distribution of *F. enigmaticus* has been intensified with anthropogenic vectors such as the international shipping trade, for example to the Mediterranean (Bianchi and Morri, 1996; Brundu and Magni, 2021; Fornós et al., 1997; Ntzoumani et al., 2024), South America (Schwindt et al., 2004a; Schwindt et al., 2004b), South Africa (Bezuidenhout and Robinson, 2020; Davies et al., 1989; McQuaid and Griffiths, 2014), North-Western France (Charles et al., 2018), Atlantic (Costa et al., 2019), and Baltic Sea (Hille et al., 2021). In coastal lagoons in the Mediterranean, reefs of *F. enigmaticus* have remained stable for several decades, for example, they have occurred in Italy since 1919 (Brundu and Magni, 2021; Gravina et al., 2020). Similarly, reefs of *F. enigmaticus* have been established for decades in the Mar Chiquita coastal lagoon in Argentina since their introduction over 60 years ago (Schwindt et al., 2004b). For a different serpulid species, *Galeolaria hystrix*, reefs were dated up to 50 years old in New Zealand (Smith et al., 2005). In some of the most highly eutrophic coastal lagoons and estuaries in the world, *F. enigmaticus* reefs can remain stable for decades (Brundu and Magni, 2021; Ntzoumani et al., 2024; Davies et al., 1989), while water quality improvements (e.g., increased water circulation and decreased organic matter), can cause a complete disappearance of *F. enigmaticus* reefs (Diawara et al., 2008). In temperate regions of the Indian Ocean, the putative native range of *F. enigmaticus* (Dew, 1959), there are few lines of evidence for ages of *F. enigmaticus* reefs, and whether they proliferated with anthropogenic impacts. Thus, the age of *F. enigmaticus* reefs in southern temperate estuaries remains a key knowledge gap.

Paleontological data can provide an important insight into past records of serpulid reefs (e.g., Ippolitov et al., 2014; Georgieva et al., 2019) and may be an alternative approach for resolving the establishment times of *F. enigmaticus,* such as for estuaries in Southern Australia. The calcareous tubes secreted by *F. enigmaticus* are made up of calcite (98% Wt%) and magnesium carbonate, and fossil tubes can be identified by distinctive features of their external and internal tube morphology (Aliani et al., 1995; Smith et al., 2013). In the Mar Chiquita lagoon, fossil serpulids from mid-Holocene sediments were radiocarbon dated 6,300 BP and showed resemblance to Hydroides but not *F. enigmaticus* (Ferrero et al., 2005). In Southern Australia, significant build-up of fossil serpulids intergrown with brozoans (*Membranipora aciculata*) were found in the Coorong and radiocarbon dated 700 BP (Bone and Wass, 1990). However, Bone and Wass (1990) did not describe the species of fossil serpulid, which raised uncertainty about whether they were *F. enigmaticus* or not. While serpulids were present in the Coorong in the past, the history of current *F. enigmaticus* reefs is unknown.

The Coorong is a large temperate estuarine and lagoonal system in Southern Australia, with a dynamic salinity gradient driven by freshwater flows from the Murray River, at the end of Australia's largest catchment basin (Webster, 2010). Since the late 1930s man-made barrages have regulated freshwater flows from the Murray River via the Lower Lakes into the Coorong. The Coorong is characterized by an estuary and two geographically split lagoons that stretch over 100 km, the North and South Lagoon. The earliest published records of living *F. enigmaticus* in the Coorong were by Geddes and Butler (1984), who found large populations in the North Lagoon. The large circular reefs now present in the North Lagoon are up to 11 m in diameter and the largest recorded globally (Chapter 2; Schroder et al., 2024). However, the history of *F. enigmaticus* in the Coorong remains unknown and the determination of reef ages could provide insight into whether reef growth coincided with the start of extreme salinisation and eutrophication in the Coorong over the last two decades (Mosley et al., 2023).

This study seeks to determine the history of large platform and circular *F. enigmaticus* reefs from the Coorong, using modern radiocarbon dating approaches. Previous investigation along the spatial gradient of the Coorong revealed that polychaete reef size was correlated with low water levels, eutrophic and hypersaline conditions (Schroder et al., 2024) and that these conditions have become more prevalent in recent decades (Mosley et al., 2023). It was hypothesised that *F. enigmaticus* reefs are modern in radiocarbon age and that reef expansion coincided with the start of large environmental changes in the Coorong (i.e., eutrophication). Outcomes of the study will provide novel insight into *F. enigmaticus* reef ages from a southern temperate estuary. If *F. enigmaticus* reef proliferations coincided with major environmental changes in the modern Coorong, then results will be of relevance for the management of a Ramar listed wetland of international importance. Furthermore, outcomes will include a novel insight into the use of radiocarbon dating in reef cores obtained from reef-building polychaetes.

3.2 Methods

3.2.1 Study area

Polychaete reefs (*Ficopomatus enigmaticus*) were sampled in the Coorong, a Ramsar listed wetland of international importance, at the terminus of the Murray-Darling Basin in Australia (Figure 3.1). Freshwater derived from the River Murray enters Lakes Alexandrina and Albert and flows through constructed barrages to the Coorong and out to the open sea through the Murray Mouth. The 'Murray Estuary' (ME) is the narrow channel (500 m width and 6 m average depth) in the Coorong, in the vicinity of the Murray Mouth. The ME is microtidal, ranging from ~ 0.4 to ~1.2 m during neap and spring tides respectively (Webster, 2010).

The Coorong consists of two connected shallow lagoons, the North Lagoon (NL) and South Lagoon (SL) which stretch over 100 km of the coast, protected from the open ocean by the Younghusband Peninsula. The NL constitutes 85 km^2 with an average channel width of 1.5 km (Webster, 2010) and geographically ends at a main constriction point (Parnka Point), the start of the SL. The typical salinity gradient for the Coorong increases from brackish waters in the ME to hypersaline in the SL, but varies with frequency, volume, and timing of freshwater inflows from the River Murray (i.e., flow regime) (Mosley et al., 2023). Water depths are generally shallow in the NL and SL, on average 1.2 and 1.4 m, respectively, and fluctuate with flow regime, wind seiches and evaporation (Webster, 2010). Water levels are typically lower in the summer, and higher in the winter (Mosley et al., 2023). El Ni*ñ*o (dry) and La Ni*ñ*a (wet) weather patterns affect the rainfall in the catchment which can result in drought or flood events (Ryan, 2018).

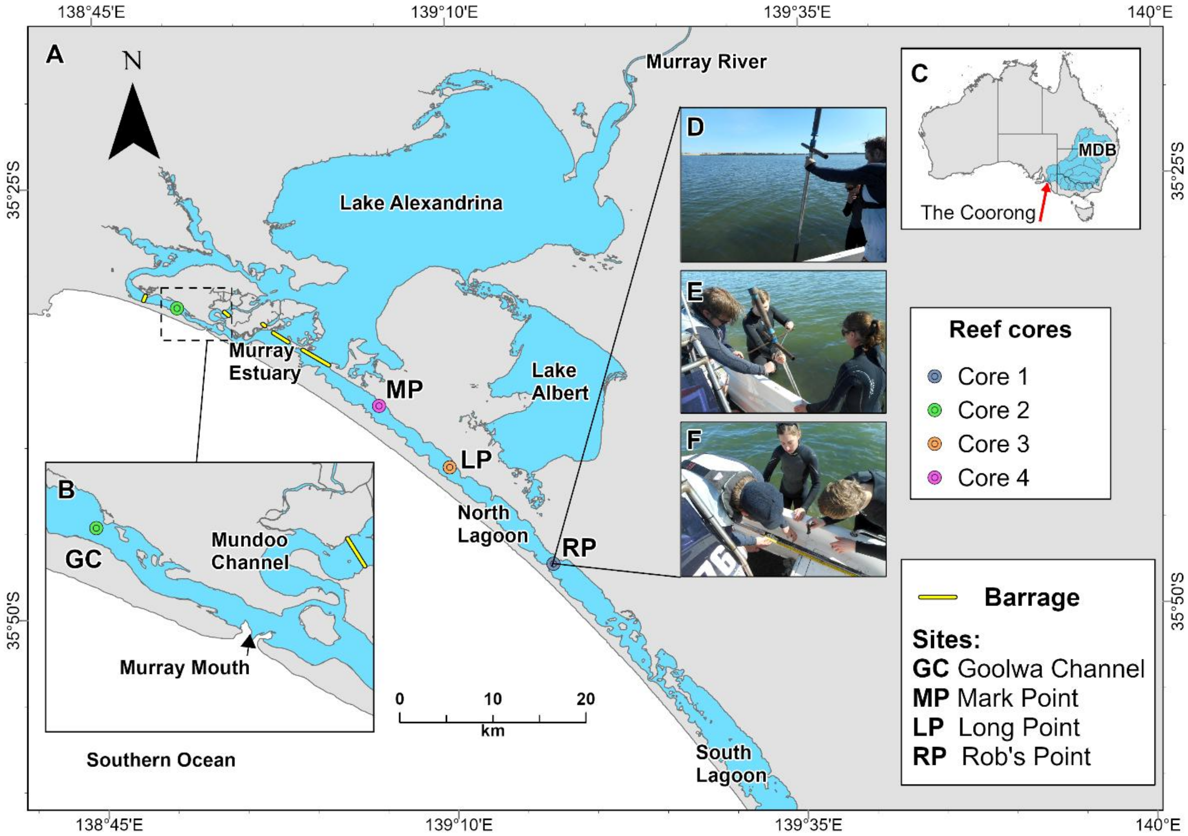

Figure 3.1. A–B) Location of the reef coring sites in the Murray Estuary and North Lagoon of the Coorong. Cores used for radiocarbon dating were from Rob's Point (RP, Core 1), the Goolwa Channel (GC, Core 2), Long Point (LP, Core 3) and Mark Point (MP, Core 4). The inset **C)** shows the location of the Coorong in Southern Australia in relation to the catchment area of the Murray-Darling Basin (MDB). **D–F)** Field sampling using a stainless-steel gouge sediment auger to core into *F. enigmaticus* reefs from a small boat. Map **A)** and **B)** source: WaterConnect, Government of South Australia[4]. Map **C)** No source acknowledged[5]

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[4] River Murray shapefile (CC BY 4.0) was downloaded from https://www.waterconnect.sa.gov.au/Systems/SitePages/Spatial%20Data.aspx (accessed 28/2/2025)

[5] Murray Darling Basin (no attribution required) web map downloaded at https://www.arcgis.com/home/item.html?id=152cd62c03c04302a1bd2def758c3e1b

3.2.2 Collection of polychaete reef cores

A 1 m length stainless steel gouge sediment auger and weighted post dropper were used to core into the middle of a reef, reaching a depth equal to or greater than the height of the reef above the seafloor (Figure 3.1.D–F). The auger was carefully lifted into a small boat, and complete cores were immediately measured then sectioned into depth intervals. Depth intervals included every 2 cm from the top of the core to 30 cm depth, then below this every 5 cm. The scraper was rinsed between each sectioning with MQ (Milli-Q^{TM}) water to avoid cross-contamination between layers. Samples were stored at -20 °C until laboratory processing.

Core 1 was taken from a large circular reef at Rob's Point in the North Lagoon, to depth of 80 cm (Table 3.1; Figure 3.2; Appendix B Figure S1). Intact polychaete tube casings (*F. enigmaticus*) were consolidated throughout all of Core 1. In the upper surface of core 1, a black anoxic sediment layer amongst the polychaete casings was present from 0–17 cm (Figure 3.2).

Core 2 was taken from a large platform reef at the Goolwa Channel in the Murray Estuary (Table 1; Figure 3.2; Appendix B Figure S1). Core 2 was characterised by intact polychaete tube casings (*F. enigmaticus*) which were consolidated to a depth of 24 cm and broken to a depth of 65 cm. A black anoxic sediment layer was present to 10 cm depth, and bivalve shells including *Spisula trigonella, Hiatula alba* and *Arthritica semen* were present amongst the polychaete tube casings in two depth intervals of 0–12 cm and 35–65 cm (Figure 3.2).

Core 3 was taken from a small living reef at Long Point in the North Lagoon to a depth of 15 cm (Table 1). Core 4 was taken from a medium sized circular reef at Mark Point in the North Lagoon and included polychaete tube casings (*F. enigmaticus*) consolidated throughout the core to a depth of 84 cm, but were not complete (i.e., section missing from 59–65 cm).

Table 3.1. Reef core details, including classification and dimensions of *F. enigmaticus* reefs sampled and collection date and length of the reef core taken.

Reef sampled	Reef core (Location)	Collection date	Reef classification	Cardinal diameter 1 (north south) (m)	Cardinal diameter 2 (east west) (m)	Reef height (m)	Core length (m)
	Core 1 (RP)	6/9/2022	Circular reef	9.89	8.26	0.8	0.80
	Core 2 (GC)	29/3/2023	Platform reef	6.40	2.50	0.5	0.67
	Core 3 (LP)	25/10/2023	Irregular reef (living)	0.50	0.40	0.20	0.15
	Core 4 (MP)	21/03/2024	Circular reef	4.60	4.45	0.8	0.84

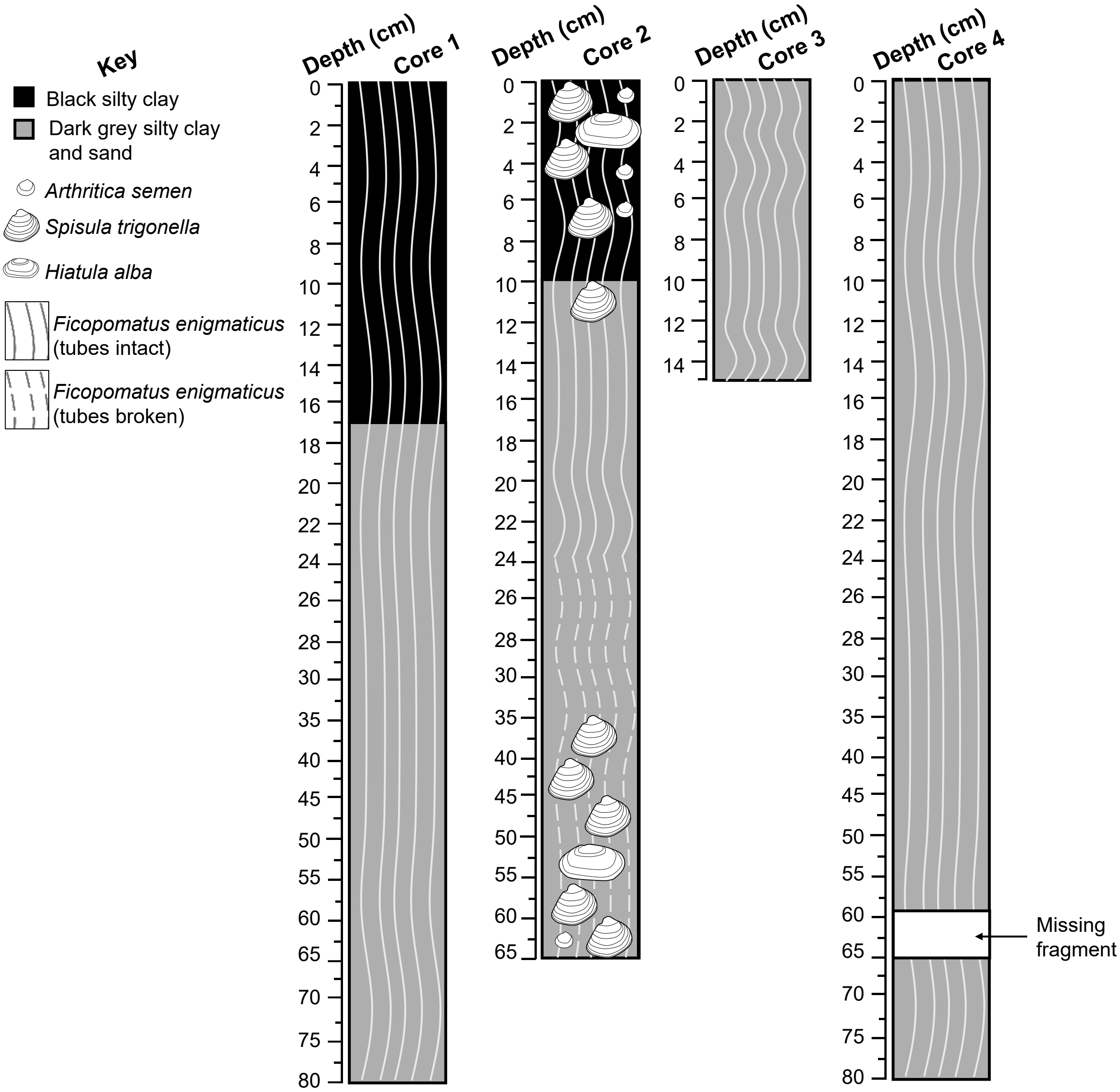


Figure 3.2. Schematic diagram of polychaete reef cores 1–4 in the Coorong. The core intervals with intact or broken *F. enigmaticus* tubes are shown, along with bivalve shells. Note the bivalve shells are not drawn to scale.

3.2.3 Polychaete reef ageing approach

Polychaete (*F. enigmaticus*) reefs consist of intertwined skeletal tubeworm casings with evident growth rings (Schwindt et al., 2004b). The age of *F. enigmaticus* reefs cannot be determined from its dimensions (i.e., height, diameter) or growth rings as rates of growth vary spatially and temporally with the environmental conditions experienced (Bianchi and Morri, 1996; Schwindt et al 2004b). Instead, the skeletal tubeworm casings of serpulids may provide an opportunity to age reefs through methods such as radiocarbon dating, as previously used (Georgieva et al., 2019; Bone and Wass, 1990; Smith et al., 2005). A radiocarbon dating approach of reef cores collected from known *F. enigmaticus* reefs in the Coorong was used in this study to determine reef ages.

3.2.4 Cleaning of polychaete tube casings

Pre-treatment methods for cleaning the polychaete tube casings were adapted from FORAMS (Foraminifera shells) or coral reef studies (Erler et al., 2020; Ren et al., 2009; Ren et al., 2017). Each sample was sieved over a 0.5 mm mesh with MQ (Milli-Q^{TM}) water, and individual tubeworm casing manually separated with forceps into a centrifuge tube filled with MQ water. Samples were then transferred into an ultrasonication bath (Soniclean 160HT) filled with MQ water and heated on low temperatures (40 °C) for 30 minutes. Ultrasonication was repeated 2 times, with centrifuge tubes filled again with MQ water and then with 2 % sodium hexametaphosphate solution (pH=8). Samples were soaked in centrifuge tubes filled with 6-12.5% sodium hypochlorite for 18 hours. Three rinsing steps were carried out with MQ water and individual tube casings were manually separated from broken fragments with forceps. Individual tube casings were inspected under a stereo microscope selecting a specimen (~20 mg) from each depth interval and gently scraping off any encrusting bryozoans from the tube surface. Samples were oven dried overnight for 15 hours at 40 °C or until a constant weight was reached.

3.2.5 Radiocarbon dating

Twenty-three samples (*F. enigmaticus*) and two shell (*Spisula trigonella*) samples were radiocarbon dated at the Australian National University (ANU), and one tubeworm sample (*F. enigmaticus*) was dated at Australia's Nuclear Science and Technology Organisation (ANSTO). In Core 1, polychaete tube casings were dated from depths of 1, 5, 11, 15, 21, 25, 32.5, 42.5, 52.5, 72.5 and 77.5 cm, In Core 2, polychaete tube casings were dated from depths of 1, 5, 11, 17, 19, 21, 23, 32.5, 47.5, 52.5, 62.5 cm and shell were dated from depths of 52.5 and 72.5 cm. Two additional samples of polychaete tube casings were dated included a living reef (Core 3) and a North Lagoon reef at 82.5 cm depth (Core 4) (Table 3.1).

The samples analysed at ANU were prepared following methods for carbonates by Wood et al. (2023). A sub-sample (5–10 mg) was crushed into small chunks, which were cleaned in diluted HCl (0.1 M) at 80°C to remove 20% weight, then rinsed in ultrapure water and dried. The cleaned sub-sample was converted to graphite in a two-step process: firstly, it was converted to carbon dioxide, then it was reacted with hydrogen using an Fe catalyst and heating to 560°C. Graphitized samples were analysed on a single stage accelerator mass spectrometer (SSAMS) at the ANU Research School of Earth Sciences (Fallon et al., 2010). One sample (Core 1 at 77.5 cm depth) analysed at ANSTO, was prepared by aggressive cleaning with etching of ~15% of surfaces by mass and ran through a VEGA (1MV mass accelerator) for isotopic ratio determination with IRMS measurement following procedures described in Wilcken et al. (2015). Radiocarbon concentrations are presented as unrounded $F^{14}C$ values (fraction of modern carbon) (i.e., $F^{14}C$ =pMC/100, where pMC is the percent of modern carbon) and not as calendar ages. In radiocarbon concentration calculations, the atmospheric ^{14}C values in 1950 are conventionally set to 1 fraction of modern radiocarbon (i.e., $F^{14}C=1$ and pMC=100) (Donahue et al., 1990; Hua, 2009). All apart from one sample was modern (post-bomb) in radiocarbon age ($F^{14}C>1$), thus no marine reservoir correction (ΔR) was applied (Reimer and Reimer, 2006) (Appendix B Table S1). The atmospheric calibration dataset (e.g., Southern Hemisphere Zone 1-2) (Hua et al., 2022) was not used to convert radiocarbon concentrations to calendar year, given a potential lag time and uptake in the polychaete reef cores. Atmospheric ^{14}C began to rise at the start of global nuclear testing in the 1950s (Hua et al., 2022), but in the Southern Hemisphere, the rise occurred around 1955–1956 (Hua et al., 2022). Thus, a conservative benchmark of 1955 was used to interpret the oldest radiocarbon age of modern samples (post-bomb).

3.3 **Results**

3.3.1 Radiocarbon dating

All polychaete tube casings in this study (excluding one sample) showed evidence of modern carbon ($F^{14}C>1$), suggesting reef growth occurred post 1955. $F^{14}C$ values ranged from 0.9977 ± 0.0020 to 1.1335 ± 0.0022. The $F^{14}C$ values are presented in Figure 3.3 and Table 3.2.

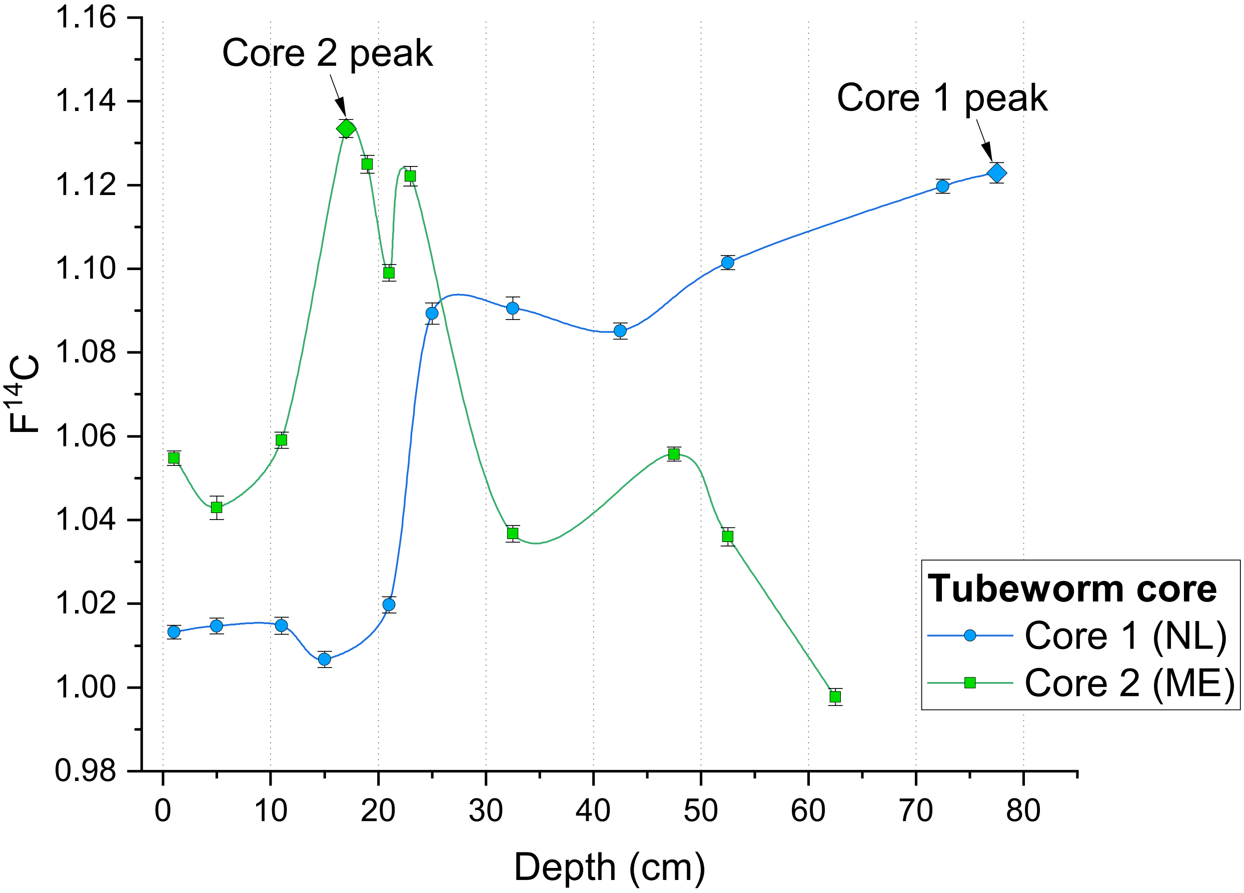


Figure 3.3. Measured $F^{14}C$ of *F. enigmaticus* relative to depth (cm) from the surface of the polychaetecore, for cores 1 and 2 taken in the North Lagoon (NL) and Murray Estuary (ME) of the Coorong. Radiocarbon measurements were taken at the ANU Radiocarbon Facility (Fallon et al., 2010).

Table 3.2. Additional $F^{14}C$ measurements of *F. enigmaticus* from core 3 (living) and core 4 (82.5 cm depth), and *Spisula trigonella* from core 2 at 47.5 cm and 62.5 cm depth. Radiocarbon measurements were taken at the ANU Radiocarbon Facility (Fallon et al., 2010).

Laboratory code	Sample ID	Material dated	F14C	Calibrated age (yr cal BP)
S-ANU77016	Core3_living	*Ficopomatus enigmaticus*	1.0016 ± 0.0021	Modern
S-ANU77017	Core4_TW_82.5cm	*Ficopomatus enigmaticus*	1.0936 ± 0.0019	Modern
S-ANU77012	Core2_S_47.5cm	*Spisula Trigonella*	1.0286 ± 0.0019	Modern
S-ANU77014	Core2_S_62.5cm	*Spisula Trigonella*	1.1208 ± 0.0019	Modern
S-ANU77018	Marble 14C free		0.0020 ± 0.0001	50040 ± 258

3.3.2 Core 1

In core 1, polychaete tube casings from all depth's radiocarbon dated in the core had $F^{14}C$ values >1 (Figure 3.3). The $F^{14}C$ values in core 1 were lowest in the shallow depths of the core (i.e., <21 cm depth) with the range in mean values between 1.00–1.01. At 21 cm depth, $F^{14}C$ was 1.01 ± 0.0019 and increased to 1.09 ± 0.0027 at 25 cm depth. The maximum $F^{14}C$ in core 1 was 1.12 ± 0.0024 at the base of the core (77.5 cm depth) but did not show evidence of a bomb pulse peak (i.e., no inflection point) (Figure 3.3).

3.3.3 Core 2

Core 2 showed evidence for a bomb-pulse signal. In shallow depths of the core (i.e., <12 cm depth), $F^{14}C$ mean values ranged between 1.04–1.06. At 11cm depth, $F^{14}C$ was 1.0591 ± 0.0020, and increased to 1.1335 ± 0.0022 at 17 cm. At 17 cm depth, a peak in $F^{14}C$ was observed (i.e., bomb-pulse), which would coincide with an age of approximately in the 1965s.

From 17 cm depth, $F^{14}C$ declined at 19 cm and at 21 cm, however a second peak in $F^{14}C$ occurred at 23 cm depth (1.1221 ± 0.0024). At 32.5 cm depth, $F^{14}C$ sharply declined to 1.0367 ± 0.0020, but increased to 1.0557 ± 0.0017 at 47.5 cm depth. From 47.5 cm depth onwards in the core $F^{14}C$ values declined. In the deepest section of the core, the lowest $F^{14}C$ value was at 62.5 cm depth (0.9977 ± 0.0020), which would coincide with an age of approximately in the 1955s. *Spisula trigonella* shell dated at depth layers of 47.5 and 62.5 cm varied in $F^{14}C$ values to the polychaete tubes at the same depth layer, but $F^{14}C>1$ for both shell samples (Table 3.2).

3.3.4 Core 3 and core 4

Core 3 was a recent living sample collected in October 2023, with a $F^{14}C$ values of 1.0016 ± 0.0021. Core 4 was sampled at the base of the core at 82.5 cm depth and had a $F^{14}C$ 1.0936 ± 0.0019 (Table 3.2).

3.4 Discussion

Ficopomatus enigmaticus is one of the most prominent providers of polychaete reefs in brackish and sheltered waters, and this study was the first to investigate the history of reefs from a large temperate estuary in southern Australia. Radiocarbon (^{14}C) dating results revealed that two large platform and circular polychaete reefs sampled from the Coorong were modern in age, supplementing the earliest observations of *F. enigmaticus* in Australia in the 1930s (Dew, 1959). Given fossil evidence of extensive serpulid buildups in the Coorong, and radiocarbon dated 700 years or older (Bone and Wass, 1990), consideration needs to be given as to whether *F. enigmaticus* is native to the Coorong or has since replaced a native serpulid species. This study provided new evidence showing large *F. enigmaticus* reefs, for example a circular formation 10 m in diameter and 0.8 m in height, are relatively recent and formed over the last 70 years in the modern Coorong estuary and North Lagoon.

3.4.1 Detection of radiocarbon in polychaete reef tubes

Marine polychaetes belonging to the family Serpulidae, such as *F. enigmaticus,* exhibit biomineralization and produce a calcium carbonate habitation tube (Smith et al., 2013). Tube building is achieved in *F. enigmaticus* via a collar glands (Aliani et al., 1995), and as for other Serpulidae, a calcium secreting gland requires either the uptake of ions from seawater or ingestion of ions (Smith et al., 2013; Neff, 1969). *Ficopomatus enigmaticus* is an efficient filter feeder consuming small particles (2-12 um) such as organic detritus or flagellates from the water column (Davies et al., 1989). Stable isotope analyses for $\delta^{13}C$ have indicated a good correlation between the particulate organic matter (POM) in the soft tissue of the worm and the carbonate tube (Lojen et al., 2014).

Radiocarbon (^{14}C) can be dissolved as $^{14}CO_2$ in seawater, where it is taken up by phytoplankton through photosynthesis and passed through the food chain (Quarta et al., 2021). In the recently alive tube of *F. enigmaticus* from the Coorong, the $F^{14}C$ value (1.0016 ± 0.0021) was similar to $F^{14}C$ of current atmospheric conditions (1.0195 ± 0.0001 in 2019) (Hua et al., 2022). The transfer of ^{14}C between the atmosphere and tubes of *F. enigmaticus* may reflect the filtered particulate organic matter consumed by the polychaete at the time of tube building, and high air to surface CO_2 water exchange rates in the shallow water environment.

3.4.2 Bomb pulse signal in polychaete reef core

Atmospheric ^{14}C began to rise at the start of global nuclear testing in the 1950s (Hua et al., 2022). In the Southern Hemisphere, the rise occurred around 1955–1956 and peaked in 1965 where $F^{14}C$ nearly doubled (Hua et al., 2022). In South Australia, British atomic tests were conducted at Maralinga starting in 1952 (Simon and Bouville, 2002). The Maralinga bomb testing were small blasts, and overall did not influence the Southern Hemisphere ^{14}C (Kern, 2020), but there was a plume from a third explosion in 1956 where acid rain and winds fell over Adelaide (Marston, 1958). A bomb-pulse signal was detected in the Murray Estuary polychaete reef core from this study, although a diluted peak signal in comparison to the atmospheric $F^{14}C$ modelled for the Southern Hemisphere, which is expected given a potential lag time in the bomb-pulse signal (e.g., Grammer et al., 2015; Markowska et al., 2019). Nevertheless, the signal of a bomb-pulse, provides evidence for the oldest and deepest part of the core to be no older than 1955–1956.

3.4.3 Comparison of polychaete reef cores

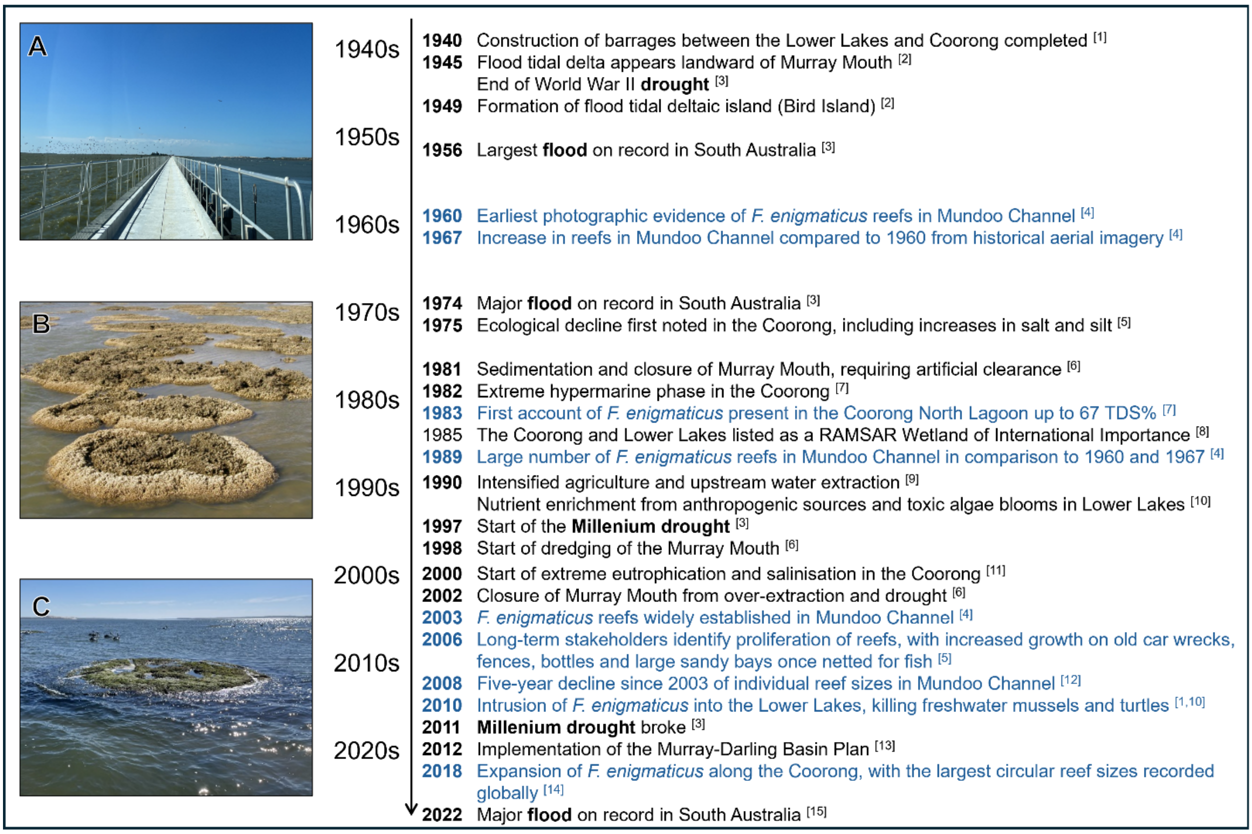
There were some dissimilarities when comparing patterns in $F^{14}C$ along depths of the two polychaete cores. Firstly, in the North Lagoon polychaete reef core there was no observed bomb-pulse signal. In the deepest section of the North Lagoon core $F^{14}C$ values were, however, close to reaching the peak in the Murray Estuary core. This may suggest that there was a potential reservoir effect between the estuary and lagoon in the Coorong (e.g., Disspain et al., 2017), or that the North Lagoon reef was younger and started growing soon after the bomb-peak. Another key difference between the two polychaete reef cores was that $F^{14}C$ dropped to much lower values in the shallow sections of the North Lagoon core, but the drop in $F^{14}C$ in the 0–10 cm of the Murray Estuary core was not as pronounced. As polychaete reef cores were taken from the middle of each reef, it could imply that the middle of the Murray Estuary reef died off before the North Lagoon reef and no further growth occurred. *F. enigmaticus* reef growth is dependent on various environmental factors (e.g., temperature, salinity, nutrients, flow speed), however they grow outwards in centric rings where the maximum height of the reef is determined by the water level height at the time (Schwindt et al., 2004b; Fornos et al., 1997). Thus, the relatively low $F^{14}C$ values at the surface of the North Lagoon core may reflect more recent growth with higher flows since the Millennium Drought, which would have led to higher water levels and increases in reef height.

A pattern in both polychaete reef cores were rapid inclines or declines of F^{14}C values for small increments in depth. This pattern may reflect a hiatus in reef growth, for example if environmental change caused the reef to die off until favourable conditions allowed re-growth. Since the 1950s, there have been several major flood events (high flow velocities and fresh conditions), droughts (hypersalinity and low water levels) that could have caused hiatus of *F. enigmaticus* reefs within the Coorong (Figure 3.4).

In both cores, smaller troughs and peaks in F^{14}C were evident, contributing to irregularities in the general curve trends of F^{14}C by depth. These irregularities may represent a natural occurrence and reflect non-linear growth patterns in *F. enigmaticus* reefs. A common phenomenon in *F. enigmaticus* is population bursts and crashes that consolidate the reef framework and aid in stability (Thomas & Thorp, 1994; Montefalcone et al., 2022). Disturbances can also lead to mortality in the reef, resulting in the mass release of larvae and subsequent rapid juvenile growth (Kupriyanova et al., 2001). For instance, in the Magra estuary, aperiodic river floods cause reef dieback, clearing space for new recruitment by juveniles within reefs (Aliani et al., 1995). Therefore, a singular growth layer or depth interval from the reef may be characterised by tightly packed tubes from multiple generations of worms.

3.4.4 Ecological changes in the modern Coorong

The modern radiocarbon dates of *F. enigmaticus* reefs in the Coorong provide evidence to support that their initial growth phase likely coincided with the start of major ecological changes which occurred in the Coorong since the 1940s (Figure 3.4).



1940 Construction of barrages between the Lower Lakes and Coorong completed [1]
1945 Flood tidal delta appears landward of Murray Mouth [2]
End of World War II **drought** [3]
1949 Formation of flood tidal deltaic island (Bird Island) [2]
1956 Largest **flood** on record in South Australia [3]
1960 Earliest photographic evidence of *F. enigmaticus* reefs in Mundoo Channel [4]
1967 Increase in reefs in Mundoo Channel compared to 1960 from historical aerial imagery [4]
1974 Major **flood** on record in South Australia [3]
1975 Ecological decline first noted in the Coorong, including increases in salt and silt [5]
1981 Sedimentation and closure of Murray Mouth, requiring artificial clearance [6]
1982 Extreme hypermarine phase in the Coorong [7]
1983 First account of *F. enigmaticus* present in the Coorong North Lagoon up to 67 TDS% [7]
1985 The Coorong and Lower Lakes listed as a RAMSAR Wetland of International Importance [8]
1989 Large number of *F. enigmaticus* reefs in Mundoo Channel in comparison to 1960 and 1967 [4]
1990 Intensified agriculture and upstream water extraction [9]
Nutrient enrichment from anthropogenic sources and toxic algae blooms in Lower Lakes [10]
1997 Start of the **Millenium drought** [3]
1998 Start of dredging of the Murray Mouth [6]
2000 Start of extreme eutrophication and salinisation in the Coorong [11]
2002 Closure of Murray Mouth from over-extraction and drought [6]
2003 *F. enigmaticus* reefs widely established in Mundoo Channel [4]
2006 Long-term stakeholders identify proliferation of reefs, with increased growth on old car wrecks, fences, bottles and large sandy bays once netted for fish [5]
2008 Five-year decline since 2003 of individual reef sizes in Mundoo Channel [12]
2010 Intrusion of *F. enigmaticus* into the Lower Lakes, killing freshwater mussels and turtles [1,10]
2011 **Millenium drought** broke [3]
2012 Implementation of the Murray-Darling Basin Plan [13]
2018 Expansion of *F. enigmaticus* along the Coorong, with the largest circular reef sizes recorded globally [14]
2022 Major **flood** on record in South Australia [15]

Figure 3.4. Timeline of changes that have occurred in the Coorong since the 1940s including major flood and drought events, and observations of *F. enigmaticus* reefs. **A)** Coorong barrages **B)** exposed *F. enigmaticus* reefs in the North Lagoon of the Coorong during the Millenium drought **C)** modern *F. enigmaticus* reefs in the North Lagoon of the Coorong taken in 2022. Anecdotal and documented changes of *F. enigmaticus* reefs are highlighted in blue text. [6]

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[1] [1] Kingsford et al., 2011, [2] James et al., 2015, [3] Ryan, 2018, [4] Dittmann et al., 2009, [5] Phillips and Muller, 2006, [6] Bourman et al., 2018, [7] Geddes and Butler 1984, [8] Leblanc et al., 2012, [9] Codd et al., 1994, [10] Department for Environment and Heritage, 2000, [11] Mosley et al., 2023 [12] Benger, 2010, [13] Rumbelow 2018, [14] Schroder et al., 2024, [15] Mosley et al., 2024.

Post-European settlement in South Australia resulted in urbanisation, which adversely affected the Coorong by diminishing the natural freshwater flows from the River Murray to the Lower Lakes from approximately 13,000 GL per annum to 6,000 GL per annum (Chiew et al., 2020). In the 1940s, five barrages were constructed to separate the Coorong estuary from the Lower Lakes in order to mitigate against seawater intrusion into the Lower Lakes. Instances of a more sheltered environment in the Murray Estuary following barrage construction include a reduction in the size of the Murray Mouth and the formation of a flood tidal deltaic island (Bourman et al., 2018). Within the Coorong estuary, the sheltered waters of the Goolwa Channel and Mundoo Channel likely provided a favourable habitat for *F. enigmaticus* reefs. The estimated age of the Goolwa Channel reef (~1950s) aligns with the first detection of reefs in Mundoo Channel, which was recorded in historical aerial imagery from 1960 (Dittmann et al., 2009; Benger, 2010). The main establishment phase of *F. enigmaticus* in the Coorong lagoon is suggested to have begun from the 1960s onwards, following a significant flood event in 1956 that may have inhibited *F. enigmaticus* growth.

Ecological decline in the Coorong was first noted in the 1970s and escalated in the 1990s, when there were increases in salinity and sedimentation in the ecosystem (Figure 3.4). The first record of *F. enigmaticus* in the Coorong from ecological surveys was in 1983 (Geddes and Butler, 1984), which coincided with increasing hypersalinity throughout the Coorong. During this time, the establishment of *F. enigmaticus* in the Coorong was evident as large mounds throughout the North Lagoon, with living worms in salinities up to 67 TDS % (Geddes and Butler, 1984). Lower water levels and sedimentation in the North Lagoon since the 1970s could have facilitated the establishment of *F. enigmaticus reefs*, and align with their modern age (i.e., post 1955) found in this study. By 1989, it was evident that reefs were widely established in the Mundoo Channel, and reef density increased over time based on comparisons of aerial imagery between 1960, 1967 and 1989 (Dittmann et al., 2009).

Ecological decline in the Coorong in the early 2000s was escalated due to the Millennium drought, which brought minimal to no freshwater flows into the Coorong (Kingsford et al., 2011). During this period, long term-stakeholders had already identified an increased proliferation of reef growth in the Coorong, for example where large sandy bays could no longer be netted for fish (Phillips and Muller, 2006). Also, the intrusion of estuarine water into the Lower Lakes facilitated larval spread of *F. enigmaticus*, which had implications for fouling on boats and infrastructure, and causing mortality of freshwater mussels and turtles (Kingsford et al., 2011; Dittmann et al., 2009). Two decades of declining ecological health was reflected by extreme eutrophication and salinisation in the Coorong (Mosley et al., 2023). *Ficopomatus enigmaticus* is known to proliferate under eutrophic conditions, and evidence from the classification and mapping of *F. enigmaticus* reefs in modern times suggests a widespread distribution of reefs and large circular reefs in the more eutrophic parts of the Coorong (i.e., southern sections of North Lagoon) (Schroder et al., 2024). Thus, the results from this study suggest that past environmental conditions would have determined growth rates and thus reef sizes.

3.4.5 Limitations and future directions for polychaete reef ageing using radiocarbon dating

Polychaete reef cores included a representation of two reefs from the Murray Estuary and North Lagoon. Although there was a sufficient spread of samples along the depth of the core, additional reef replicates from each region of the Coorong may have provided a greater understanding of whether there was a stronger reservoir effect in the Lagoon versus estuary (i.e., more flushing in the estuary). Each reef core was taken from the middle of a reef. However, vertical reef growth is constrained by water depth (Fornos et al., 1997). Horizontal cores may have provided an additional insight into growth over time, as reefs grow outwards in concentric rings from the middle (Schwindt et al., 2004b). Future application of radiocarbon dating of modern polychaete reefs should seek to acquire time points from reefs of known age if possible, to better untangle chronological timestamps along the depth of a polychaete core taken.

3.4.6 Comparisons of polychaete reef ages in different estuaries

Across other estuaries in Australia, the history of polychaete reefs such as reef age has not yet been determined. However, there are some early observations of *F. enigmaticus* that can be compared to the establishment times of *F. enigmaticus* from the Coorong found in this study. The earliest record of *F. enigmaticus* was from the Cook's River (NSW) in 1910 (Dew, 1959) and *F. enigmaticus* was thought to be widely distributed in Australia by the 1930s (Allen, 1953). By the 1950s occurrences of *F. enigmaticus* were also reported from Western Australia (the Swan River) and South Australia (Allen, 1953). Reefs of *F. enigmaticus* from the Coorong, such as those investigated in this study, may therefore be recent examples of polychaete reefs in Australia. Future investigations on comparing polychaete reef ages to those found in other

Australian estuaries such as the Swan River or Cook's River may compliment the understanding of the distribution and history of *F. enigmaticus* in Australia.

Polychaete reefs can persist in the environment for many decades, and the potential ages of *F. enigmaticus* reefs in this study align with observations of polychaete reefs from other parts of the world. For example, *F. enigmaticus* reefs from the Mar Chiquita coastal lagoon in Argentina are known from the last 60 years, and it is hypothesised they could be many decades old if they have persisted since their early introduction (Schwindt et al., 2004b). For polychaete reefs built by a different serpulid species, *Galeolaria hystrix*, in New Zealand, reefs were radiocarbon dated and found to be up to 50 years old (Smith et al., 2005). Further radiocarbon dating of *F. enigmaticus* reefs from other estuaries of the world could identify environmental drivers of reef preservation or assist in understanding reef size and morphology in relation to reef age and history.

3.5 Conclusion

Radiocarbon dating in this study provided evidence that the sampled *F. enigmaticus* reefs have recently established in the Coorong estuary and North Lagoon. This compliments the previous classification and mapping of *F. enigmaticus* reefs in the modern Coorong (Schroder et al., 2024) and coincides with eutrophic conditions observed in the modern Coorong (Mosley et al., 2023). The determined history of *F. enigmaticus* reefs in the Coorong reflect that reef growth can be rapid under eutrophic conditions (e.g., Ntzoumani et al., 2024). The large circular reef sampled in this study with a diameter up to 10 m, likely formed in approximately the last 70 years. The duration for which the sampled *F. enigmaticus* reefs have been established in the Coorong are comparable to those in the Mar Chiquita coastal lagoon in Argentina (Schwindt et al., 2004b). However, further research is required to elucidate whether fossil serpulids in the Coorong, radiocarbon dated 700 BP in the Coorong by Bone and Wass (1990) could have been of *F. enigmaticus* or whether *F. enigmaticus* replaced a native fossil serpulid species, as seen in Argentinean estuaries (Ferrero et al., 2005). The anthropogenic changes which have occurred in the Coorong since the 1940s have likely contributed to the establishment and proliferation of *F. enigmaticus* reefs in the estuary and North Lagoon.

Chapter 4. Estuarine fish dynamics associated with polychaete reefs and environmental stressors

A fyke net set near polychaete reefs in the Coorong. Photo credit: Laura Schroder.

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4.2 Author contributions

Laura Schroder: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Data curation. **Orlando Lam-Gordillo**: Conceptualization, Methodology, Writing – review & editing. **Qifeng Ye:** Conceptualization, Methodology, Supervision, Writing – review & editing. **Sabine Dittmann**: Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

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Estuarine fish dynamics associated with polychaete reefs and environmental stressors

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ABSTRACT

Biogenic reefs serve as important habitats for fish, yet reef-building polychaetes and their functional role for associated estuarine fish communities is not well understood. The aim of this study was to investigate the ecological role of one of the most prominent providers of polychaete reefs, *Ficopomatus enigmaticus,* in a large temperate estuary in Southern Australia (the Coorong). Fish communities were compared between *F. enigmaticus* reef and non-reef habitats. The fish community included 22 native species, and dissimilarity between the reef versus non-reef habitats was driven by the abundances of particular estuarine species. The fish community from the reef habitat were characterised by higher abundances of estuarine species of gobies (*Pseudogobius olorum*, *Arenigobius bifrenatus*, *Tasmanogobius lasti*, *Afurcagobius tamarensis*), smallmouth hardyhead (*Atherinosoma microstoma*), and black bream (*Acanthopagrus butcheri*). The functional roles of *F. enigmaticus* reefs serve as either shelter or feeding habitats for estuarine fish especially during the juvenile life stage. An extreme flood event, one of the highest on record, lowered salinities throughout the estuary and lagoon. Temporal variations in fish communities of both reef and non-reef habitats from the estuary and lagoon were explained by stressors of the flood, heatwave and invasive species, and environmental conditions including the total monthly flow, water temperature and transparency. Reefs built by the polychaete *F. enigmaticus* deliver ecosystem functions that benefit fish communities and merit conservation.

1. Introduction

Freshwater flows are crucial for supporting biodiversity by maintaining salinities, habitat connectivity and nutrient availability in the mixing zone between riverine and oceanic waters (Beck et al., 2009). Estuarine fish communities are dynamic in nature and primarily influenced by the flow regime. Biogenic structured habitats like reefs can increase habitat heterogeneity to support fish diversity and biomass (Peterson et al., 2003; Crawford et al., 2019; Martínez-Baena et al., 2022; Bishop et al., 2023). The habitat provisioning role of typical biogenic reefs (e.g., shellfish) for estuarine fish can include improvements to water quality, sediment stabilization, food availability and shelter (Sheehan et al., 2015; Stewart-Sinclair et al., 2020; Witte et al., 2024). Reef building polychaetes (RBP) can offer similar ecosystem provisions as typical reef builders through their gregarious nature of tube building (Bruschetti, 2019; Giangrande et al., 2020). Yet, the structural complexity of polychaete reefs and their functional role for associated fish communities is poorly understood (Montefalcone et al., 2022). Estuaries are vulnerable to anthropogenic threats (e.g., hyper salinity, acidification, sea level rise) which could have cascading negative impacts on foundation species (such as RBP) into the future (Mahoney and Bishop, 2017; Wernberg et al., 2024).

The effects of biogenic reefs on fish can vary with patch size, edge effects and environmental context (Graham and Nash, 2013), but for polychaete reefs these are less well understood (Bruschetti, 2019; Montefalcone et al., 2022). For example, juvenile fish density, growth and condition were positively correlated with reef complexity (i.e., worm densities) provided by sand masons (Sabellariidae) (Zalmon et al., 2010; Ventura et al., 2024). Patch edges of *Chaetopterus* sp. were dominated by the goby species *Rhinogobiops nicholsii* (Zalmon et al., 2010). Similarly, for the sand mason *Lanice conchilega,* the abundance of demersal fish (e.g., gobies and flatfish) were positively correlated with reefs, which reflected their macroinvertebrate prey availability in the vicinity of reefs (De Smet et al., 2015). Yet, a different pattern was

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observed in the hyperbenthos where juvenile fish abundance was correlated with the environmental context in the vicinity of reefs (e.g., total organic matter, chlorophyll *a*, and suspended particulate matter) (De Smet et al., 2015). While fish associations with sand mason reefs (i.e. low relief reefs) are emerging (e.g., Chong et al., 2021; Ventura et al., 2024), there is still a knowledge gap on fish associations with serpulid reefs (i.e., high relief and calcareous reefs).

There are few quantitative studies on fish associations with serpulid reefs (Montefalcone et al., 2022). For example, for *Serpula vermicularis* reefs in Scotland, underwater video stations recorded 13 associated fish species seeking refuge or foraging in the vicinity of reefs (Poloczanska et al., 2004). Trophic interactions included gobies (*Pomatoschistus* spp.) preying on feeding crowns of the tubeworm *S. vermicularis,* and wrasses (*Crenilabrus melops* and *Labrus bergylta*) feeding on reef associated epifauna (Poloczanska et al., 2004). The fish community of reefs constructed by a different serpulid, *Galeolaria hystrix* in New Zealand, were characterised by six fish species including the blue cod (*Parapercis colias*) and spotted wrasse (*Notolabrus celidotus)* (Smith et al., 2005). However, in coastal ecosystems (i.e., estuaries and lagoons) the fish community associated with serpulid reefs remain understudied (e.g. Palmer et al., 2021). For serpulid reefs, increased knowledge on their role as habitat for fish fauna will contribute to a greater understanding of their ecosystem functions and services.

The cosmopolitan tubeworm, *F. enigmaticus* (Fauvel, 1923)*,* is one of the most prominent provider of serpulid reefs in brackish and sheltered coastal waters. The true origin of the species remains unclear (Styan et al., 2017; Tovar-Hernández et al., 2022; Kupriyanova et al., 2023). The putative native distribution range of the species includes temperate regions of the Indian Ocean (Ten Hove and Weerdenburg, 1978). *F. enigmaticus* reefs vary in structural complexity such as small irregular clumps up to a metre in diameter, circular formations several metre in diameter, and platforms from several circular fused reefs (Schroder et al., 2024). Reefs alter the hydrodynamics and could offer refuge for fishes away from high-speed current flows (e.g., Schwindt et al., 2004). Reefs offer smaller crevices and edges that are used for fish to shelter in (e.g., Por and Dor, 1975). However, fish may be deterred when birds rest upon reefs (e.g., Bruschetti et al., 2009). *Ficopomatus enigmaticus* is one of the most prolific serpulid reef builders found in many parts of the world in temperate climates (Alvarez-Aguilar et al., 2022), adding complexity to soft sediments and modifying the abiotic environment (Schwindt et al., 2004). Yet, there are no previous studies which have quantified fish associations with *F. enigmaticus* reefs.

The Coorong is a large temperate estuary and lagoon system which stretches over 100 km of the coastline in Southern Australia. In the Coorong, biogenic reefs built by *F. enigmaticus* have an expansive distribution. Fossil serpulids intergrown with bryozoans occur in the Coorong, and were radiocarbon dated at 700 BP, but it remains unknown whether they were or not *F. enigmaticus* (Bone and Wass, 1990). Modern reefs of *F. enigmaticus* in the Coorong reach large sizes, with individual circular reefs recorded up to 11.3 m in diameter (Schroder et al., 2024). In the estuary part of the Coorong, the average reef density is 224 reefs ha^{-1}, whereas the reef density is lower in the lagoon, 62 reefs ha^{-1} on average (Schroder et al., 2024). The distribution of *F. enigmaticus* reefs in the Coorong provided a unique opportunity for investigating the ecological patterns of fish community associations with serpulid reefs.

Fish communities in the Coorong are primarily driven by salinity. Salinity changes occur both spatially and temporally which are reflective of the frequency, volume and timing of freshwater inflows (i.e., flow regime) (Hossain et al., 2017a; Ye et al., 2020, 2021). The freshwater inflows to the Coorong are derived from the Murray River, which is part of Australia's largest catchment basin, the Murray-Darling Basin (MDB). Flow year (i.e., water year) describes the year which starts in July, when winter rainfall occurs in the MDB catchment, with freshwater inflows typically reaching the Coorong during September to January and ends in June (Rumbelow, 2018; Stewardson and Guarino, 2018). Flow regimes have important implications for how particular fish species utilise the estuary to complete their life-histories (Whitfield, 1999; Potter et al., 2015) or provide environmental cues for fish spawning (e.g., Sakabe and Lyle, 2010).

Major flood events can cause disturbances to estuarine fish communities (e.g., Henderson et al., 2024), due to increases in water flow, water levels and turbidity, and drastic decreases in salinity and dissolved oxygen (Nishijima et al., 2013; Thibault de Chanvalon et al., 2016; Mayjor et al., 2023). Environmental stressors are also important to consider when interpreting the complex nature of patterns in temperate estuarine fish communities (e.g., Whitmarsh et al., 2020). Pollution including effluent input, heatwaves causing hypoxia in shallow water and floods causing fresh conditions are examples of environmental stressors on the fish community (Whitmarsh et al., 2020; Zamora-López et al., 2023; Henderson et al., 2024). Invasive freshwater fish can become more abundant after floods, which can negatively impact upon the native fish community through competition and predation (Havel et al., 2015). European carp (*Cyprinus carpio*) is one of the most widespread invasive freshwater fish species found in the MDB and can become abundant in the river following flood events (Bice et al., 2014; Forsyth et al., 2013). Invasive fish were considered as a stressor in the present study and not included as part of the estuarine fish community.

This study investigated the fish communities in the Coorong, with a primary aim to assess the species composition and abundance of fish associated with polychaete reefs built by *F. enigmaticus*. Polychaete reef habitats are expansive in the Coorong, but occur in spatial patches (Schroder et al., 2024). It was hypothesised that (1) the total abundance and diversity of fish is higher in polychaete reef than non-reef habitat, and (2) the fish community structure differs between polychaete reef and non-reef habitats. An extreme flood event during the study period also allowed a secondary aim, which was to investigate temporal variations in fish community structure in response to changed environmental conditions (e.g., lower salinities) and stressors (e.g., high abundances of invasive species).

2. Methods

2.1. Study area

A case study was conducted in the Coorong, a Ramsar listed wetland of international importance at the terminus of the MDB in Australia (Fig. 1). Freshwater from the River Murray enters the Lakes Alexandrina and Albert and flows through constructed barrages to the Coorong and open sea. The area (approximately 20 km^2) in the vicinity of the Murray Mouth is referred to as the 'Murray Estuary' (ME) and is a narrow channel (~500 m width and 6 m average depth). The tides in the ME are semi-diurnal with a moderate diurnal inequality and range from ~0.4 to ~1.2 m during neap and spring tides, respectively (Webster, 2010).

Adjacent to the ME, the Coorong lagoons stretch over 100 km as two shallow connected lagoons, the North Lagoon (NL), and South Lagoon (SL), which are protected from the open ocean by the Younghusband Peninsula (Gibbs et al., 2018). The NL constitutes 85 km^2 with an average channel width of 1.5 km (Webster, 2010) and ends at a main constriction point (Parnka Point) separating it from the SL. The typical salinity gradient for the Coorong increases from brackish waters in the ME to hypersaline in the SL, but varies with frequency, volume, and timing of freshwater inflows (i.e., flow regime) from the River Murray (Mosley et al., 2023). Water depths are generally shallow in the NL and SL, on average 1.2 and 1.4 m, respectively, and fluctuate with flow regime, wind seiches and evaporation (Webster, 2010). Water levels are typically lower in summer (December, January and February), and higher in winter (June, July and August) (Mosley et al., 2023). El Niño (dry) and La Niña (wet) weather patterns affect the rainfall in the catchment which can result in drought or flood events (Ryan, 2018).

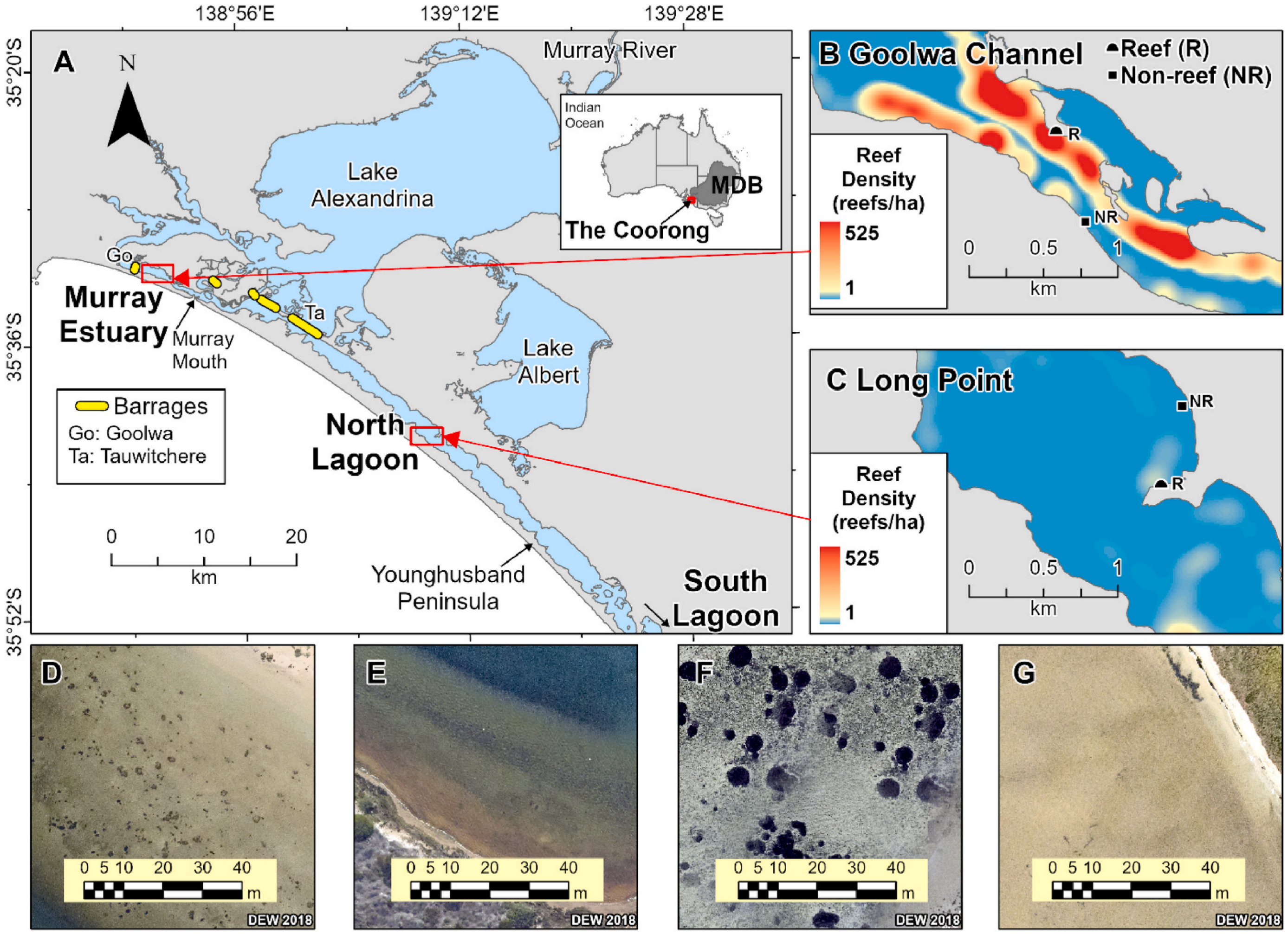

Fig. 1. A) The Coorong estuary at the terminus of the Murray-Daling Basin (MDB) in Australia (source: Data.SA, 2025), and fish survey sites in relation to polychaete reef habitats at **B)** Goolwa Channel in the Murray Estuary (ME) of the Coorong (source: Schroder et al., 2024) and **C)** Long Point in the North Lagoon (NL) of the Coorong (source: Schroder et al., 2024). Habitat types are shown as digital aerial imagery sourced from the Department of Environment and Water (DEW, 2018), which include **D)** ME reef, **E)** ME non-reef, **F)** NL reef and **G)** NL non-reef habitats.

2.2. *Reef and non-reef habitats*

Polychaete reefs occur throughout the ME and NL, but not in the hypersaline waters of the SL (Schroder et al., 2024). The polychaete reef habitats (hereafter 'reef habitats') were investigated in the ME and NL at 3.9 km and 17.8 km distance respectively from the nearest barrage (Goolwa Barrage for ME and Tauwitchere Barrage for NL) (Fig. 1).

Reef habitat in the ME was characterised by small sized reefs (0.8 m average diameter, 0.2 m average height) that were irregular, halo or platform types, which occur in high densities (525 reefs ha^{-1}, Fig. 1A) with approximate total reef coverage of 264 m^2 ha^{-1}. The NL reef habitat included large (1.5 m average diameter, 0.5 m average height) and mostly circular or platform type reefs in lower densities (139 reefs ha^{-1}, Fig. 1B) with approximate total reef coverage of 246 m^2 ha^{-1}. The polychaete reefs in the ME and NL were occasionally covered by filamentous algae and not all tubes were inhabited by living *F. enigmaticus*. In the ME, reefs are temporarily exposed at low tide, whereas in the NL, reefs are permanently covered unless water levels drop below 0.3 m in Australian Height Datum (AHD). A non-reef habitat was used as a control site, consisting of unstructured soft sediments with fine to medium sand (57–80 %) located at least 0.5 km away from high density reef areas (Fig. 1).

2.3. *Survey design and flood event*

In each region (ME and NL), fish surveys were carried out at two sites (herein 'habitats'), a reef habitat and non-reef habitat, located at least 0.5 km apart. Fish surveys coincided with a major flood in October 2022 and peaked in the Coorong (Fig. 2) during January 2023 (Fig. 2). In the flow year 2022 (i.e., July 2022 to June 2023, herein '2022') high rainfall in the upper MDB caused the third highest flood since records started in 1890, and the highest flow rates to reach the Lower Lakes and Coorong since 1956 (Mosley et al., 2024; Ryan, 2018). The start of the fish surveys occurred in spring (October) and summer (late November to December) during the onset of the very high flows reaching the Coorong (Fig. 2; Table S1). The first autumn fish survey (March to early April) occurred immediately after the main flood peak (Fig. 2; Table S1). Subsequently, the fish surveys were repeated in the spring (October), summer (December) and autumn (March) for a second flow year in 2023 (i.e., July 2023 to June 2024, herein '2023') (Fig. 2; Table S1).

2.3.1. *Fish sampling methods*

Fish communities were sampled with single wing fyke nets (5.6 m long with circular hoops of 0.6 m funnel, 3 m long single wing with 0.6 m height and weights to reach the bottom, and 8 mm mesh). For logistic reasons, fyke nets were set in consecutive weeks in the ME and NL for every seasonal survey (see Table S1 for survey dates). In each region,

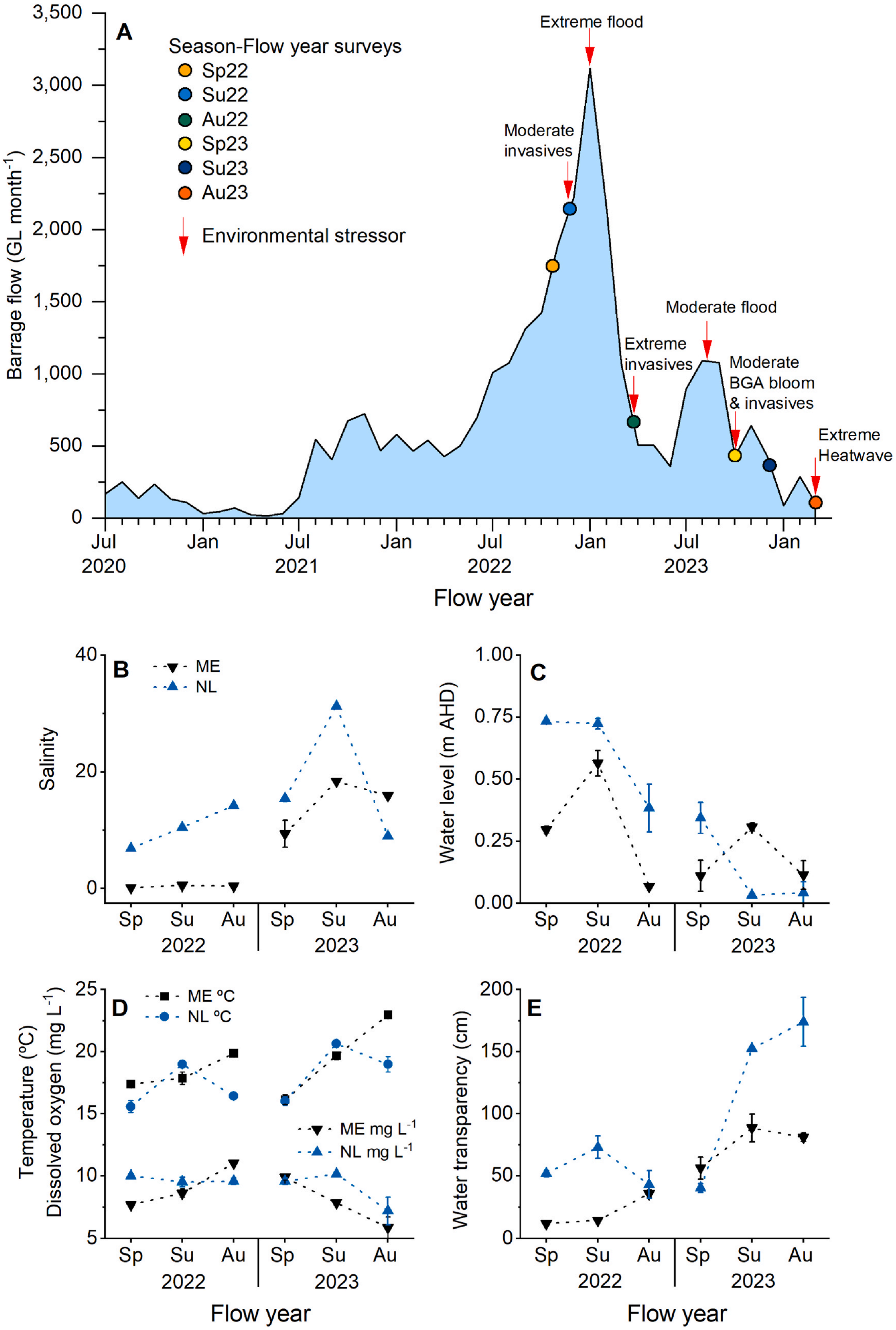

Fig. 2. A) Barrage flow (GL month^{-1}) of freshwater entering the Coorong across all barrages for flow years from 2020 to 2023. Fish survey start dates are indicated by dots and show seasonal surveys conducted in spring, summer, and autumn in flow years 2022 and 2023. Stressors which coincided with surveys are indicated by red arrows, and blue-green algae bloom was abbreviated as BGA. The mean ± s.e. of other environmental conditions during seasonal fish surveys in the Murray Estuary (ME) and North Lagoon (NL) shown are **B)** salinity, **C)** water level (m AHD), **D)** temperature (°C) and dissolved oxygen (mg L^{-1}) and **E)** water transparency (cm). Data presented from **A–D)** WaterData SA (DEW, 2024).

reef and non-reef habitats were sampled simultaneously. Four nets were set in the reef habitat around different reefs, and four nets set in the non-reef habitat, spacing nets 10–15 m apart. Net deployments were made overnight (~15 h duration), and methods repeated for a second sampling night. This obtained 8 replicates per habitat per survey in each region. The ME fish surveys coincided with spring tides where nets were set during an afternoon low tide (0.3–0.5 m depth) to sample fish moving into shallow areas during high tide overnight. During the NL surveys, nets were set in the same locations but water depths varied from 0.6 to 0.8 m during the flood to 0.3–0.5 m depth after the flood. Fish catch from each replicate (net) were retrieved the following morning and transferred to aerated holding containers for sorting. Fish species and numbers were recorded, with all taxa identified to species except carp gudgeons which were identified to genus level (*Hypseleotris*) (Lintermans, 2007). Total length (TL) measurements of all individuals of fish species were taken to the nearest mm, except for highly abundant species, where a subsample of 40 individuals were measured. All native fish were returned alive to the same location of capture. Individuals of invasive species were euthanised with an overdose of AQUI-S solution.

2.3.2. *Environmental data and stressors*

Environmental data were recorded to account for spatial changes in the estuarine habitat in the Coorong driving the dynamics and composition of fish communities. In the field, dissolved oxygen (DO, mg L^{-1}) was measured at approximately 20 cm depth below the water surface using a Hanna DO meter (model HI9146), and water transparency (cm) was measured with a Secchi disk. Three replicate measurements for each environmental parameter were taken at the reef and non-reef habitat over the same two consecutive days when fyke nets were set. Water quality measurements were similar between reef and non-reef habitats and were averaged by region for each survey. Other surface water data including conductivity, water level (m AHD) and temperature (°C) were obtained from WaterData SA (https://water.data.sa.gov.au), for the ME (Goolwa Channel logger A4261036; 35°31′59.05"S, 138°50′5.42"E) and NL (Long Point logger A4261135; 35°41′44.38"S, 139° 9′42.41"E), both within 1 km of the sampling locations in each region. Surface water data were averaged across the sampling nights that coincided with fyke net deployments in each region and survey. Salinity in Practical Salinity Units (PSU) was calculated from the specific electrical conductivity (EC, mS cm^{-1} at 25 °C) using the equation developed for the Coorong (Mosley et al., 2023). Monthly barrage flow across the five barrages that enter the Coorong (GL $month^{-1}$) (Fig. 1) were obtained from the River Murray Calculated Barrage Flow Logger (A4261002) at WaterData SA (DEW, 2024).

While the primary objective of this study was to determine associations of fish with reef and non-reef habitats, there were unforeseen stressors confounding the fish community. Fish surveys coincided with environmental stressors of flood, heatwave and cyanobacteria bloom and biological stressor of invasive freshwater fish (hereafter ‘invasives’). All non-native freshwater fish found in this study are declared aquatic pest species in Australia including European carp (*Cyprinus carpio*), redfin perch (*Perca fluviatilis*), goldfish (*Carassius auratus*) and oriental weatherloach (*Misgurnus anguillicaudatus*) (PIRSA, 2025). Collectively, these non-natives were referred to as ‘invasives’, given that *C. carpio* dominated numerically and is defined as invasive in the MDB (widespread, causes environmental degradation and negatively impacts native fish species through competition and predation) (Cheshire et al., 2013). Above mentioned invasives are normally freshwater stragglers, occasionally found in the Murray Estuary and Coorong in low abundances, but the flood event washed large numbers of these species downstream into the estuary where they survived while floodwaters lowered salinities.

For a given survey, each stressor was categorised as none, moderate and extreme, based on criteria thresholds and available supplementary environmental data (Tables S2 and S3). Flood data were sourced from WaterData SA (https://water.data.sa.gov.au) from the River Murray Calculated Barrage Flow Logger (A4261002) and compared against the average annual flow to the Coorong from historical averages (none= <4723 GL $year^{-1}$, moderate= >4723 GL $year^{-1}$, extreme= >12,233 GL $year^{-1}$) (Ryan, 2018). Atmospheric air temperature was sourced from BOM (http://www.bom.gov.au/climate/data/) for the ME (Hindmarsh Island, SA Station 023894; 35.52°S, 138.87°E) and NL (Meningie, SA Station 024518; 35.69°S, 139.34°E) to classify heatwave events (none, moderate and high = ≥ 3 and ≥4 days, respectively, of abnormally high maximum and minimum atmospheric temperatures) (BOM, 2024). Cyanobacteria biovolume data were sourced from Mosley et al. (2023) for the ME (Murray Mouth) and NL (Long Point), and compared against Australian guidelines for green, amber and red alerts of cyanobacteria blooms in recreational water (none= <0.4 mm^3 L^{-1}, moderate = ≥ 0.4 mm^3 L^{-1}, extreme= > 4 mm^3 L^{-1} (toxic BGA dominant) or >10 mm^3 L^{-1} (toxic BGA non-dominant) (Australian Government, 2008). Invasive fish data were collected in this study and compared based on the percentage of invasives contributing to the total catch (none= <10 % of total catch, moderate= <75 % of total catch, extreme = ≥75 % of total catch).

2.4. *Data analysis*

Prior to the analysis of fish community data, the catches of invasive freshwater species were removed as their occurrence was flood related (Table S3) and would confound assessments of the fish community in reef and non-reef habitats. All other native species (hereafter ‘fish’) were grouped by estuarine use functional guild (EUFG) revised by Potter et al. (2015) and assigned by Bice et al. (2018a) based on expert knowledge of species from the Coorong, Lower Lakes and Murray Mouth region. The EUFG groups similar species mainly based on the environment in which spawning occurs (Potter et al., 2015), and in this study species found belonged to one of the four broad categories of freshwater, estuarine, marine and diadromous. The freshwater FG included freshwater species that (1) commonly use estuaries in large numbers (freshwater-estuarine opportunist and (2) occasionally enter estuaries in low numbers (freshwater stragglers) (Potter et al., 2015). The diadromous FG included species that (1) migrate downstream into the marine environment to spawn (catadromous) and (2) are generally catadromous, but spawning migrations cease in the estuary (semi-catadromous) (Potter et al., 2015). The estuarine FG included species that (1) only reproduce in estuarine habitats (solely estuarine) and (2) reproduce and form separate populations in both estuarine and marine environments (estuarine and marine) (Potter et al., 2015). The marine FG included marine species that (1) commonly enter estuaries in large numbers and as juveniles (marine-estuarine opportunist) and (2) occasionally enter estuaries in low numbers (marine straggler) (Potter et al., 2015).

For each fish species, the percentage of juvenile fish was calculated based on individuals measured, by dividing the number of individuals with a TL below the size of maturity by the total number measured and multiplied by 100. Fish species maturity size was obtained from previous studies conducted in the Coorong region (Lintermans, 2007; Bice, 2010; Cheshire et al., 2013). For missing data on species maturity size in the region (*Tasmanogobius lasti, Arenigobius bifrenatus, Gymnapistes marmoratus, Acanthaluteres spilomelanurus, Cristiceps australis, Hyporhamphus melanochir, Mitotichthys tuckeri, Nematalosa erebi, Retropinna semoni, Macquaria ambigua, Hypseleotris* spp, *Galaxias maculatus*), an estimate was calculated as two-third of species’ maximum length (e.g., Chong et al., 2021; Nagelkerken and Van der Velde, 2002) for maximum lengths obtained from Fishes of Australia.

Total fish catch in catch-per-unit-effort (CPUE) was defined as the individual number of fish per fyke net, set for approximately 15 h overnight (individuals net^{-1} $night^{-1}$). Traditional diversity metrics for fish catch were reported, including number of species (i.e., species richness) (S), Shannon Diversity index with natural logarithm (ln) and Pielou’s evenness index (Magurran and Anne, 2013).” Univariate data (total CPUE) were square-root transformed and analysed with Euclidean distance matrix but did not meet the assumptions for homoscedasticity and normality. PERMutational ANalysis Of VAriance (PERMANOVA) tests (Anderson, 2008) were used to test whether the total CPUE differed between reef and non-reef (habitats), and to elucidate spatial (regions) and temporal (season-year) patterns. PERMANOVA tests were used with 9999 permutations, based on a three fixed factor design of habitats (2 levels: reef and non-reef), regions (2 levels: ME and NL), and season-year (6 levels: spring 2022, summer 2022, autumn 2023, spring 2023, summer 2023 and autumn 2024). For factors or interactions (habitats x region x season-year) that were statistically significant, pairwise tests were used to identify specific surveys where reef and non-reef habitats differed significantly.

For multivariate analysis, data were pre-assessed with shade plots (Clarke et al., 2014). Dispersion weighting was applied to remove the dominant effects of large counts that were highly variable across replicates for schooling species (e.g., sandy sprat and smallmouth hardyhead) (Clarke et al., 2006, 2014). Data were then square-root transformed to down-weight consistently abundant species and apply more weight to rarer species in the community (Clarke et al., 2014). To test for significant differences in fish community structure between reef and non-reef habitats, a PERMANOVA test (9999 permutations) was applied based on Bray-Curtis similarity and the prior mentioned three fixed factor design. Pairwise tests were conducted for significant differences found for fixed factors or interactions (habitats x region x season-year). Canonical analysis of principal coordinated (CAP) plots were used to visualize the reef and non-reef fish communities of each region, excluding season-year data where there was no significant difference in fish community structure between habitats. Vector overlays on CAP plots showed the key species contributing to the community variation for multiple correlations >0.5. SIMilarity PERcentage breakdown (SIMPER) analysis (Clarke and Warwick, 2001) was carried out to further explore the main fish species which were accounting for >70 % of the dissimilarity between reef and non-reef habitats.

To investigate temporal variation in fish communities, a non-metric MultiDimensional Scaling (nMDS) plot with overlay trajectory was used to show averages of season-year surveys and statistically significant clustering based on group-average linking (CLUSTER) and a SIMilarity PROFiles (SIMPROF) test (Clarke et al., 2008). In addition, a shade plot of relative abundance grouped fish species by their functional guilds of either estuarine, marine, diadromous, and freshwater to visualize patterns in functional guilds across space and time (Potter et al., 2015).

To investigate the relationship between the fish community with the environmental conditions and stressors, a Distance based Linear Model (DistLM) analysis was carried out, using a step-wise selection and AIC (Akaike Information Criterion) model (Anderson, 2008). The fish community data were derived from both reef and non-reef habitats in each region (ME and NL) to capture greater spatial variation in the fish community and how it was influenced by environmental changes. The variables used in the analysis included measured water quality conditions and categorial variables of environmental or biological stressors. For each survey, stressors were categorised as either none, moderate or extreme, based on criteria thresholds defined for each category and available numerical data at the time of the survey (Tables S2 and S3). Each stressor and stressor category was given a score of 0 if absent, and a score of 1 if present. The categorial variables (stressors) were included in the DistLM analysis using their binary scores. Results from the DistLM were visualised on a distance-based Redundancy Analysis (dbRDA) plot. A BEST test was used to identify the best combination of variables that could explain the variation in the fish community. All statistical analyses on fish data were carried out in Primer 7 (Clarke and Gorley, 2015) and PERMANOVA+ (Anderson, 2008).

3. Results

3.1. Environmental conditions and stressors

The extreme flood event in 2022 resulted in very high barrage flows and lowered salinities throughout the Coorong estuary and lagoons (Fig. 2A). The onset of the flood, which coincided with the spring and summer (2022) fish surveys, was characterised by low salinities of 0.2–0.6 in the ME and 7–11 in the NL, in addition to turbid conditions, high-water levels and moderate stress from invasive fish (Fig. 2; Table S2–3). After the flood peak in January 2023, the monthly flows and water levels receded during February prior to the start of the autumn (2022) fish survey in March, when an extreme stress from invasive fish occurred in the ME (Fig. 2A). During the 2023 surveys after the flood, water levels dropped further, salinities increased, and water transparency improved (Fig. 2C–E). Salinities during the 2023 fish surveys ranged between 9 and 18 in the ME and 9–31 in the NL (Fig. 2B) and remained low in comparison to the long-term averages over the last two decades (24.8 ± 0.9 in the ME and 41.7 ± 1.4 in the NL) (Fig. S3). Water temperatures in spring, summer and autumn seasonal surveys varied between 15 and 20 °C in 2022 and 16–23 °C in 2023 (Fig. 2D). The lowest dissolved oxygen concentrations were during autumn surveys in the ME and were 8.63 mg L^{-1} in 2022 and 5.86 mg L^{-1} in 2023 (Fig. 2D). The other environmental stressor events in the 2023 flow year included a moderate blue-green algae bloom and invasives in the ME during the spring survey, and an extreme heatwave in the ME during the autumn survey (Fig. 2A; Table S3).

3.2. Catch summary in reef and non-reef habitats

The total number of fish caught was 22,755 individuals in reef habitats and 28,031 individuals in non-reef habitats. The fish comprised 22 species from 17 families and were represented by four functional guilds (freshwater, estuarine, marine and diadromous) (Table 1). The overall catch was dominated by small-bodied species (mature individuals <15 cm maximum TL) (91.9 % of total catch), but also included large-bodied species (mature individuals ≥15 cm maximum TL), mostly as juveniles (Table 1, Table S4). There was a significant interaction for total CPUE between habitats, regions and seasons, indicating inconsistent patterns in spatial and temporal variation (PERMANOVA $p = 0.03$; Table 2; Fig. 3).

In the ME, total CPUE was similar between reef and non-reef habitats in four out of the six surveys (PERMANOVA, $p < 0.05$; Fig. S4). The median of the total CPUE in summer 2022 was 93 and 353 individuals net^{-1} $night^{-1}$ (ranges 56–397 and 216–3394) in the reef and non-reef habitats, respectively. The median total CPUE in autumn 2022 was 11 and 89 individuals net^{-1} $night^{-1}$ (ranges 0–42 and 6–1489) in the reef and non-reef habitats, respectively. The small-bodied and schooling species sandy sprat (*Hyperlophus vittatus*) and congolli (*Pseudaphritis urvillii*) contributed to a greater total CPUE in the non-reef versus reef habitats in summer 2022 and autumn 2022 respectively (Figs. 3 and 4). In the NL, differences in total CPUE between reef and non-reef habitats were more common than in the ME. Total CPUE was significantly greater in the reef versus non-reef habitats for four out of six surveys (summer 2022, autumn 2022, summer 2023 and autumn 2023) (PERMANOVA, $p = 0.03$; Fig. 3.; Fig. S4). In summer, Tamar goby (*Afurcagobius tamarensis*), bridled goby (*Arenigobius bifrenatus)* and *P. urvillii* were the most abundant species of reef catch (Fig. 4). The highest seasonal catch in the NL occurred in autumn of both flow years, with significantly greater CPUE in the reef habitat (PERMANOVA, $p < 0.05$, Fig. S4; Fig. 3). In autumn 2022, the total CPUE had a median of 297 individuals net^{-1} $night^{-1}$ (range 30–2695) in the reef habitat, and a median of 82 individuals net^{-1} $night^{-1}$ (range 12–156) in the non-reef habitat (Fig. 3). The same pattern of highest catches occurring in the reef versus non-reef habitat was also observed in autumn 2023 when the median total CPUE was 338 individuals net^{-1} $night^{-1}$ (range 257–1460) and 59 individuals net^{-1} $night^{-1}$ (range 4–265) for each habitat type, respectively (Fig. 3). The higher reef catches in the NL during autumn surveys were due to a dominance of smallmouth hardyhead (*Atherinosoma microstoma*) (Fig. 4).

A total of 20 fish species were recorded in the reef habitat and 19

Table 1

The percentage (%) of juvenile fish for each species sampled at the reef and non-reef habitats in each the Murray Estuary (ME) and North Lagoon (NL) across seasons spring (Sp), summer (Su) and autumn (Au) for surveys pooled over two consecutive flow years (2022 and 2023). Fish species are listed by functional guild (Potter et al., 2015) and ticks are given for small bodied species (SB, <15 cm TL at size of maturity). For each species, the range in total length (TL, minimum–maximum) for individuals caught and the TL of size of maturity is included (estimated sizes of maturity are indicated by an *).

Species by functional guild	SB	TL (min–max in cm)	TL of maturity (cm)	ME Reef			ME Non-reef			NL Reef			NL Non-reef		
				Au	Sp	Su	Au	Sp	Su	Au	Sp	Su	Au	Sp	Su
Freshwater Category															
Freshwater-estuarine Opportunist															
Philypnodon grandiceps	✓	2.2–7.6	4.2	–	17	13	100	41	10	100	100	9	–	100	100
Nematalosa erebi		11.0	10*	–	–	0	–	–	–	–	–	–	–	–	–
Freshwater Straggler															
Retropinna semoni	✓	2.1–8.1	6.7*	–	100	100	–	100	100	100	–	100	100	–	–
Macquaria ambigua		7.2–19.7	50.7*	100	100	100	–	–	100	–	–	–	–	–	–
Hypseleotris spp.	✓	2.3–4.6	4.7*	–	–	–	100	–	100	100	–	–	–	–	100
Diadromous Category															
Catadromous															
Pseudaphritis urvillii		1.0–20.0	16.5	98	100	99	99	98	98	97	99	100	99	97	100
Semi-catadromous															
Galaxias maculatus	✓	1.8–13.5	5.0*	76	25	33	3	27	21	0	–	45	–	0	50
Estuarine Category															
Solely Estuarine															
Acanthopagrus butcheri		1.7–36.0	28.9	–	100	100	50	–	100	100	–	–	–	–	–
Afurcagobius tamarensis	✓	0.9–13.1	5.3	91	5	26	94	11	22	7	6	2	100	3	0
Atherinosoma microstoma	✓	0.9–10.8	4.5	28	3	12	73	5	1	52	14	50	85	48	54
Pseudogobius olorum	✓	1.5–7.0	3.6	100	17	0	–	0	0	76	40	3	82	15	15
Tasmanogobius lasti	✓	0.3–6.5	2.7*	50	52	82	100	40	69	95	–	50	100	–	100
Estuarine and Marine															
Arenigobius bifrenatus	✓	2.5–15.5	12.0*	100	100	–	100	100	–	100	100	64	100	59	73
Gymnapistes marmoratus		12.5–13.5	15.3*	–	–	–	–	–	100	100	–	–	–	–	–
Marine Category															
Marine-estuarine Opportunist															
Aldrichetta forsteri		2.5–37.5	25.6	100	96	93	81	100	50	–	42	100	100	100	100
Arripis truttaceus		4.0–13.6	55.0	–	–	100	100	–	100	–	100	100	–	100	–
Hyperlophus vittatus	✓	1.6–6.4	5.8	100	100	100	100	86	99	–	100	100	–	100	50
Rhombosolea tapirina		1.3–23.8	20.3	100	100	100	100	94	100	–	96	100	–	100	–
Marine Straggler															
Acanthaluteres spilomelanurus		5.9	9.3*	100	–	–	–	–	–	–	–	–	–	–	–
Cristiceps australis		9.0	20.0*	–	–	–	100	–	–	–	–	–	–	–	–
Hyporhamphus melanochir		10.4	34.0*	–	–	–	–	–	–	100	–	–	–	–	–
Mitotichthys tuckeri		9.2	12.7*	–	–	100	–	–	–	–	–	–	–		

Table 2

Univariate PERMutational ANalysis Of VAriance (PERMANOVA) on **a)** CPUE (individuals net^{-1} night^{-1}), **b)** species richness (S) **c)** Shannon Diversity (H′) and **d)** Pielou's Evenness (J′) of native fish to test for differences between Habitats (reef and non-reef), Regions (Murray Estuary and North Lagoon) and Seasons (spring, summer and autumn in flow years 2022 and 2023). Significant values ($p < 0.05$) are indicated in bold.

Source	df	MS	Pseudo-F	*p*	df	MS	Pseudo-F	*p*
	a. Total CPUE (individuals net^{-1} night^{-1})				**b. Species Richness (S net^{-1} night^{-1})**			
Habitat (Ha)	1	6.997	0.072	0.789	1	14.083	6.873	**0.009**
Region (Re)	1	773.290	7.963	**0.005**	1	42.188	20.588	**0.000**
Season (Se)	5	1048.100	10.792	**0.000**	5	38.375	18.728	**0.000**
Ha x Re	1	1349.300	13.894	**0.000**	1	7.521	3.670	0.058
Ha x Se	5	102.690	1.058	0.384	5	2.608	1.273	0.279
Re x Se	5	524.900	5.405	**0.000**	5	38.163	18.624	**0.000**
Ha x Re x Se	5	232.530	2.395	**0.034**	5	7.646	3.731	**0.003**
Res	168	97.112			168	2.049		
Total	191				191			
	c. Shannon Diversity (H′)				**d. Pielou's Evenness (J′)**			
Habitat (Ha)	1	1.205	9.269	**0.003**	1	0.084	2.219	0.143
Region (Re)	1	0.298	2.292	0.134	1	0.025	0.649	0.421
Season (Se)	5	2.544	19.570	**0.000**	5	0.572	15.049	**0.000**
Ha x Re	1	0.340	2.614	0.101	1	0.393	10.339	**0.002**
Ha x Se	5	0.273	2.101	0.067	5	0.049	1.300	0.271
Re x Se	5	0.257	1.980	0.083	5	0.306	8.068	**0.000**
Ha x Re x Se	5	0.947	7.282	**0.000**	5	0.138	3.642	**0.005**
Res	168	0.130			168	0.038		
Total	191				191			

species in the non-reef habitat across all surveys. The species richness between habitats were statistically different (PERMANOVA, $p < 0.01$, Table 2). The species richness varied between season and regions (Table 2). The species richness was highest in the ME during summer 2022 when there was strong representation of all four functional guilds, and a total of 13 species in each of the reef and non-reef habitats (Fig. 5A). In contrast, the lowest species richness was six species in the NL habitats during spring 2022 when the marine functional guild was absent (Fig. 5B).

The diversity and evenness indices (H′) and (J′) varied between

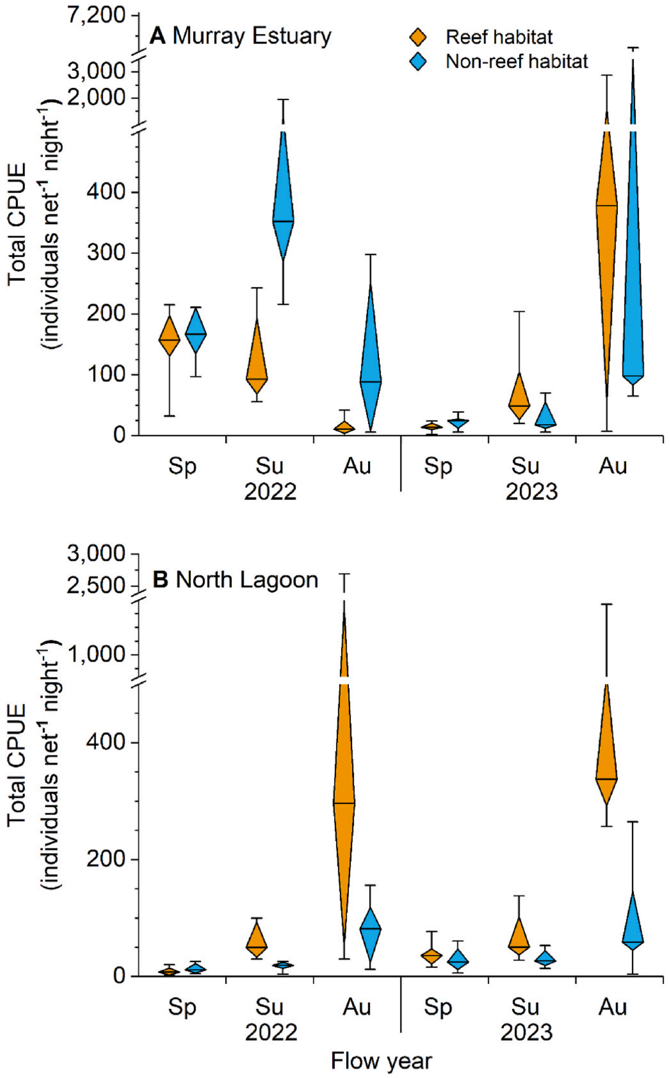

Fig. 3. Box plots of total native fish catch per unit effort (CPUE) (individuals net^{-1} night^{-1}) between reef and non-reef habitats in **A)** Murray Estuary and **B)** North Lagoon during spring (Sp), summer (Su) and autumn (Au) surveys in flow years 2022 and 2023.

habitats, regions and surveys (Table 2; Fig. 5C–F). In the ME, H′ and J′ were significantly greater in the reef versus non-reef habitat during spring, summer and autumn 2022 surveys (PERMANOVA $p < 0.05$; Fig. S2). However, in the ME during 2023 surveys, H′ and J′ were similar between habitats and declined from spring over summer to autumn (Fig. 5C and E). In the NL, H′ and J' were higher in reef than non-reef habitat in spring 2022, but significantly higher in the reef versus non-reef habitat during spring 2023 (PERMANOVA $p < 0.05$, Fig. S2, Fig. 5D and F). Both indices declined from summer to autumn 2022 but were similar in summer and autumn 2023 (Fig. 5D and F).

3.3. *Fish community structure of reef and non-reef habitats*

There was spatial and temporal variation in the fish community association with habitats, indicated by a significant interaction between habitats, regions and seasons (PERMANOVA $p < 0.0001$; Table 3a; Fig. 4). Pairwise comparisons showed that the community structure differed between reef and non-reef habitats for three and five seasons out of a total of six seasons respectively for the ME and NL regions (Table 3b; Fig. 6).

In the ME, community structure differed between habitats only in spring and summer 2022 and spring 2023 (Table 3b). SIMPER analysis identified that reef and non-reef communities in the ME were most dissimilar in spring 2023 (66.5 % dissimilarity), which was driven by a greater presence of lagoon goby (*Tasmanogobius lasti*) in the reef community (Fig. 6A; Table S5). Yellow-eye mullet (*Aldrichetta forsteri*) and *P. urvillii* were other key species that contributed to the reef community in spring and summer 2022 (Fig. 6A). In contrast, the non-reef community in spring and summer 2022, and spring 2023 were characterised mostly by common galaxias (*Galaxias maculatus*), flatheaded gudgeon (*Philypnodon grandiceps*) and greenback flounder (*Rhombosolea tapirina*) (Fig. 6A).

In the NL, reef and non-reef communities differed in structure in all seasons except from autumn 2022 (Table 3b). In summer 2022, reef and non-reef communities showed the highest dissimilarity of 54.5 %. Key species that contributed to the NL reef community, especially during summer 2022 were *A. tamarensis*, *A. bifrenatus* and bluespot goby (*Pseudogobius olorum*) (Fig. 6B; Table S6). Temporal variation in the NL reef community was reflected by the presence of *R. tapirina* and juvenile Western Australian salmon (*Arripis truttaceus*) during spring 2023, and *A. microstoma* and juvenile black bream (*Acanthopagrus butcheri*) during autumn 2023 (Fig. 6B.; Table 1). Instead, the NL non-reef community variation was mostly characterised by *P. urvillii* in 2023.

3.4. *Temporal changes in fish community structure*

Temporal changes occurred in the fish community structure in both the ME and NL (Fig. 4; Fig. 7).In the ME, three statistically significant clusters of communities were identified (onset of flood, after the flood, and autumn 2023), with each cluster comprised of closely similar fish species in both reef and non-reef habitats (Fig. 7A). During the onset of flood conditions in spring and summer 2022, ME fish communities in both reef and non-reef habitats were characterised by a high abundance and diversity of freshwater and diadromous fish (Figs. 4 and 7A). After the flood in the ME there were fewer diadromous and freshwater species and overall lower abundances (Figs. 4 and 7A). This community cluster included surveys in the ME from autumn 2022, spring 2023 and summer 2023 (Fig. 7A). In autumn 2023, fish communities in reef and non-reef habitats were characterised by a greater diversity of marine species and increased abundances of the marine species *H. vittatus*, and estuarine species *A. tamarensis* (Figs. 4 and 7A). In the NL, there were no statistically different clusters of communities from SIMPROF tests, but temporal changes still occurred (Fig. 7B). In the NL during 2022, the estuarine species *P. olorum* dominated in the community, whereas in 2023, diadromous species *P. urvillii* was the most dominant species in the community (Fig. 4). In both the ME and NL, there were temporal seriation of reef and non-reef habitats (Fig. 7A and B).

3.5. *The effects of environmental conditions and stressors on fish community*

All environmental conditions and stressors included in the DISTLM analysis (five water quality variables and four stressors), accounted for 32.9 % of the total variation in the fish community (Fig. 8) and explained 67.3 % of the fitted variation on the first two dbRDA axes. BEST test analysis identified a combination of three water quality variables (water transparency, temperature and total monthly flow) and four stressors (moderate flood, moderate blue-green algae bloom, moderate invasives and extreme heatwave) which could most strongly predict the spatial and temporal variation in the fish community (AIC = 319.09, $R^2 = 0.489$; Table 4). Water transparency had the greatest correlation with the first dbRDA axis, while total monthly flow had the greatest correlation with the second dbRDA axis (Fig. 8, Table 4). The fish community in 2022 were positively correlated with total monthly flow and was influenced by stressors of the extreme flood, moderate blue-green algae bloom and moderate levels of invasive catch. The fish community in 2023 was mostly influenced by a moderate flood (Fig. 8).

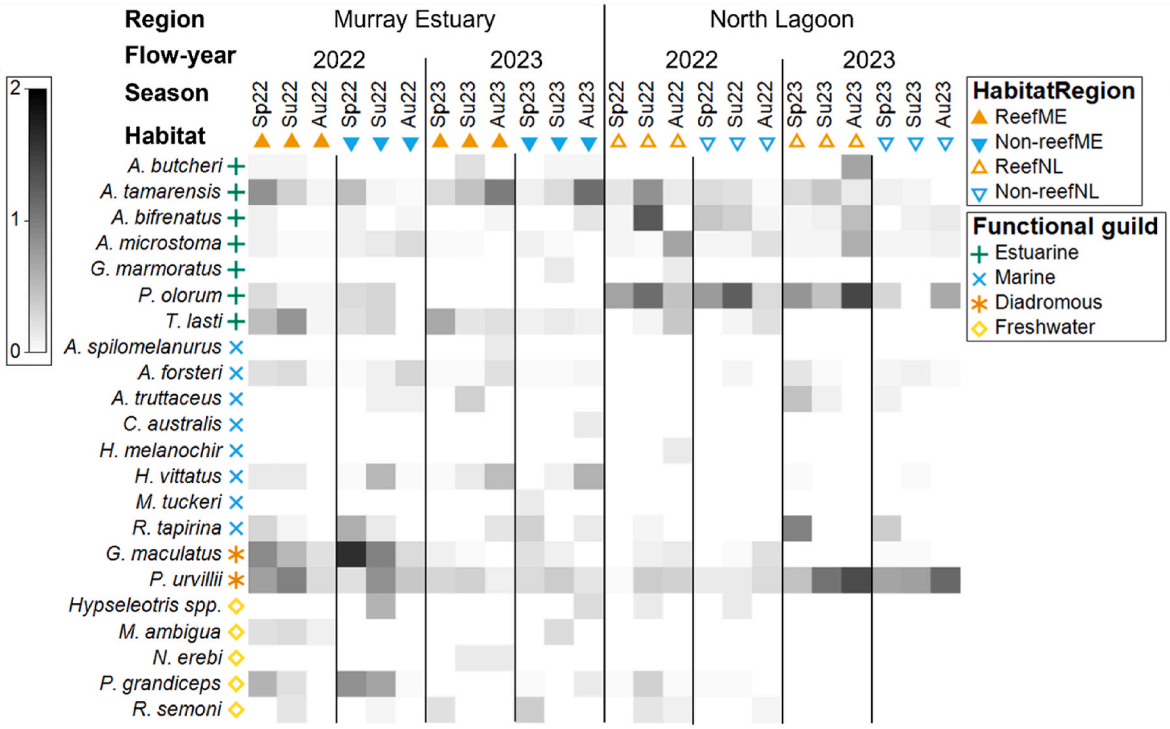

Fig. 4. Shade plot of the average dispersion-weighted and square-root transformed abundance of fish in each habitat, season, flow-year and region. Species are grouped by functional guilds of estuarine, marine, diadromous and freshwater.

In autumn 2023, the stressor of an extreme heatwave, and water temperature influenced the fish community (Fig. 8).

4. Discussion

Polychaete reefs provide a three-dimensional structured habitat, and this study was the first to investigate the association between estuarine fish communities and the reef building polychaete, *F. enigmaticus*. The study revealed that estuarine fish communities are influenced by *F. enigmaticus* reefs, despite the flow regime which is driving the spatial and temporal patterns in estuarine habitats. The Coorong estuary and lagoons in Southern Australia was used as a case study, with results that partially supported the hypothesis (1) a higher total abundance and diversity of fish in reef versus non-reef habitats, and supported the hypotheses (2) fish community structure differs between reef and non-reef habitats and (3) spatial and temporal patterns in fish community are influenced by the flood event and environmental stressors.

4.1. Catch summary in reef versus non-reef habitats

F. enigmaticus reef habitats in the Coorong influenced the total abundance but not the species diversity of fish. However, the differences in total abundance of fish between reef and non-reef habitats were more pronounced in the NL region of the Coorong. A greater total abundance of fish occurred in the NL reef versus non-reef habitat in summer and autumn for two consecutive flow years. In summer, *A. tamarensis* was a key species that contributed to a higher total abundance in the reef habitat. *Afurcagobius tamarensis* is a demersal species known to seek refuge in burrows or physical structure (e.g. rocks, logs) (Lintermans, 2007) and could use reef habitat to shelter such as inside reef crevices or amongst macroalgae attached on the reef. In general, gobies spawn demersal and adhesive eggs (Houde et al., 2022). The reefs could offer a hard substrate for gobies to attach their eggs during the breeding season, which occurs in spring to summer for *A. tamarensis* in the Coorong (Bice, 2010; Cheshire et al., 2013). During autumn the schooling species *A. microstoma*, contributed to a greater total abundance in the NL reef habitat. *Atherinosoma microstoma* is a solely estuarine species (Potter et al., 2015), lives for approximately one year, and spawns over multiple months from spring to summer before perishing (Molsher et al., 1994; Ye et al., 2021). A high proportion of juveniles of *A. microstoma* present in the autumn survey provides evidence for recruitment events and may suggest that reef habitats are used for shelter by this species during the juvenile life stage. Overall, the difference in total fish abundance between reef and non-reef habitats was greater in the NL than in the ME, likely reflecting reef habitat complexities and the environmental context of each region.

4.2. Fish community structure in reef versus non-reef habitats

The fish community was influenced by the reef habitats provided by *F. enigmaticus* within the ME and NL of the Coorong. The NL reef community was characterised by greater abundances of the three goby species of *A. tamarensis*, *A. bifrenatus* and *P. olorum*. Gobies are bottom dwellers and the reef could offer more sheltering opportunities to avoid predation by large-bodied piscivorous predators. The co-occurrence of all three gobiids in the reef habitat may indicate they are using different resources from the reef. *Arenigobius bifrenatus* shelter and hide underneath the reef edges close to the bottom and are occasionally coming out to forage (Pers obs.; Figs. S5 and S6). In comparison, *A. tamarensis* and *P. olorum* forages on the reef in bursts in-between taking shelter and hiding in crevices (Pers obs.; Fig. S5). Alternatively, dietary preferences may be important for the coexistence of gobiids in overlapping habitats in the Coorong (Hossain et al., 2017b; Giatas et al., 2022).

The pattern of association between gobies and polychaete reefs has previously been observed and both non-trophic and trophic interactions have been recorded (Bianchi and Morri, 1996; Poloczanska et al., 2004; Charles et al., 2018). Resident gobies hide underneath polychaete reef edges, such as for *Vermiliopsis pygidialis* reefs in the Gulf of Eliat (Por and Dor, 1975). *Serpula vermicularis* reefs in Scotland offer shelter for gobies (*Pomatoschistus* sp.) which also prey upon the feeding crowns of the

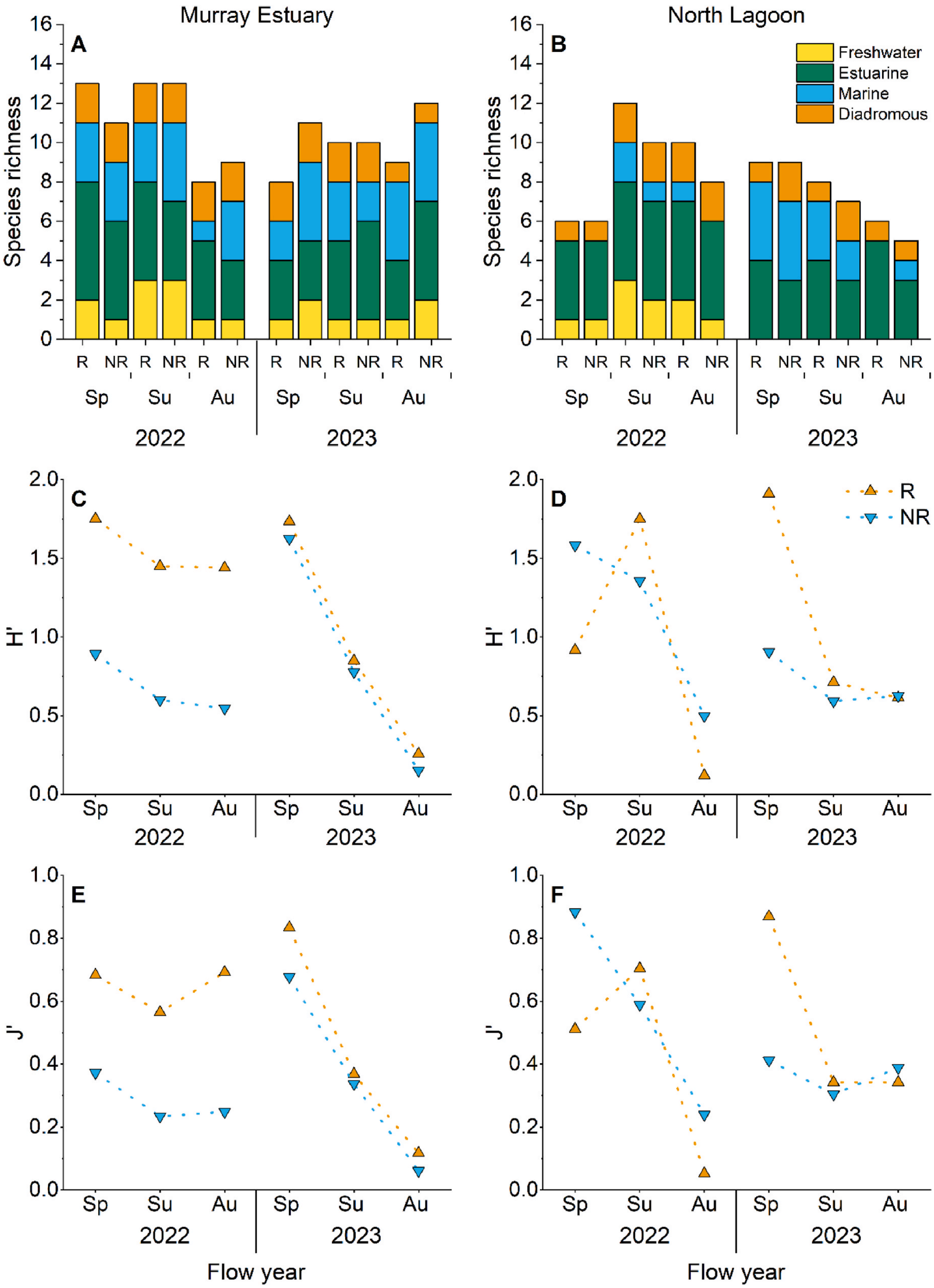

Fig. 5. **A–B)** Stacked bar graph of fish species richness (S) by functional guilds of freshwater (freshwater straggler, freshwater-estuarine opportunist), estuarine (solely estuarine, estuarine and marine), marine (marine-estuarine opportunist, marine straggler) and diadromous (catadromous, semi-catadromous) (Potter et al., 2015), **C–D)** Shannon diversity index (H′) and **E–F)** Pielou's evenness index (J′) in the Murray Estuary (left) and North Lagoon (right) for surveys in the reef (R) and non-reef (NR) habitats during spring (Sp), summer (Su) and autumn (Au) surveys in flow years 2022 and 2023.

Table 3
Multivariate PERMmutational ANalysis Of VAriance (PERMANOVA) **a)** main test results and **b)** pairwise test results on differences in the native fish community structure between Habitats (reef and non-reef), Regions (Murray Estuary and North Lagoon) and seasons (spring, summer and autumn in flow years 2022 and 2023). Significant values ($p < 0.05$) are indicated in bold.

a. Fish community	df	MS	Pseudo-F	*p*
Habitat (Ha)	1	6114	9.64	**0.0001**
Region (Re)	1	41942	66.10	**0.0001**
Season (Se)	5	13030	20.54	**0.0001**
Ha x Re	1	4574	8.28	**0.0001**
Ha x Se	5	8036	2.91	**0.0001**
Re x Se	5	54390	19.69	**0.0001**
Ha x Re x Se	5	2426	3.82	**0.0001**
Res	168	635		
Total	191			

b. Pairwise test	Murray Estuary (Reef vs non-reef)		North Lagoon (Reef vs non-reef)	
Season	t	*p*	t	*p*
Spring 2022	2.89	**0.0003**	1.79	**0.0400**
Summer 2022	3.02	**0.0002**	3.29	**0.0001**
Autumn 2022	1.35	0.0920	1.52	0.0810
Spring 2023	2.04	**0.0011**	2.53	**0.0079**
Summer 2023	1.36	0.0840	2.83	**0.0016**
Autumn 2023	0.95	0.4800	3.19	**0.0003**

tubeworm *S. vermicularis* (Poloczanska et al., 2004). Similarly, gobies making high speed lunges at the feeding crowns of the tubeworms in the reef were recorded for *Austrogobius parri* and *Gobius niger* with *F. enigmaticus* reefs in Mar Chiquita lagoon (Argentina) (Olivier et al., 1972; Bianchi and Morri, 1996). Alternatively, gobies could also prey upon amphipods, mysids and other polychaetes in the reef, as high infauna densities, especially amphipods, occur in *F. enigmaticus* reefs (Bazterrica et al., 2020). Previous studies indicate gobies have a strong preference for fine sediment to construct their burrows (Theobald, 2007; Chargulaf et al., 2013). The reef association of gobies could instead be due to increased fine sediments trapped in the vicinity of *F. enigmaticus* reefs (e.g. Schwindt et al., 2004).

In the NL, other species-specific responses were driving variation in the community of the reef habitat across seasons. In spring, juveniles of large-bodied species such as *R. tapirina* and *A. truttaceus* were key species associated with the sediments adjacent to *F. enigmaticus* reefs, and using the reefs as shelter, respectively. *Rhombosolea tapirina* is a flatfish and marine-estuarine opportunist species, with juveniles often entering in large numbers to the Coorong during spring to early summer, residing and using the system as a nursery ground (Ye et al., 2013; Earl et al., 2017). For a different species of flatfish, *Pleuronectes platessa*, polychaete reefs of *Lanice conchilega* provide structural complexity that serves as an important refuge and feeding ground (Rabaut et al., 2010, 2013; De Smet et al., 2015). Similarly, *F. enigmaticus* reefs increase habitat complexity and juvenile *R. tapirina* may show a preference for soft sediments in the vicinity of *F. enigmaticus* reefs in shallow areas of the NL. Western *Arripis truttaceus* is also a marine-estuarine opportunist species that uses the Coorong as a nursery area (Giatas and Ye, 2015). *Arripis truttaceus* individuals are highly mobile, often schooling, and may be opportunistically using *F. enigmaticus* reefs in the NL. Juveniles of *A. truttaceus* prey upon both teleosts such as atherinids and gobies, and crustaceans such as amphipods and mysid shrimps (Giatas and Ye, 2015) which are highly abundant in *F. enigmaticus* reefs (Bazterrica et al., 2020) and could explain their preference of reef habitat in the NL.

Other species driving temporal variation in the NL reef community included the solely estuarine species of *A. microstoma* and *A. butcheri* during autumn. As previously mentioned, *A. microstoma* juveniles may prefer to shelter amongst *F. enigmaticus* reefs which offer more complexity compared to non-reef habitats to avoid predation in the shallows. The only occurrence of juvenile *A. butcheri* in the NL was exclusive to the *F. enigmaticus* reef habitat. This pattern highlights that reef habitat is essential to provide shelter for black bream during the juvenile life stages, likely providing protection from predators. *Acanthopagrus butcheri* abundance has been positively correlated with benthic habitat structure such as macroalgae and seagrass (Woodland et al., 2019). The species-specific responses to *F. enigmaticus* reef habitat seen in the NL, were also apparent for the ME region.

In the ME, *T. lasti* was strongly associated with *F. enigmaticus* reef habitat compared to non-reef habitat. *Tasmanogobius lasti* is an estuarine resident and benthic associated species, feeding mainly on amphipods in the Coorong (Giatas et al., 2022). Both shelter and food availability in the reef habitat, may explain the greater presence of *T. lasti*, especially given that their key prey item of amphipods are known to inhabit *F. enigmaticus* reefs in large densities (e.g., Bruschetti et al., 2009; Heiman and Micheli, 2010). In the ME during spring and summer, juveniles of large-bodied species *A. forsteri* and *P. urvillii* were abundant in the reef habitat. The association between mullet and polychaete reefs has previously been recorded (Bailey-Brock, 1984; Bianchi and Morri, 1996). Fish behaviours such as grazing and biting upon tube edges were observed for the grey mullet, *Liza saliens*, with *F. enigmaticus* (Bianchi and Morri, 1996). In the ME, *A. forsteri,* a marine-estuarine opportunist species, may prefer *F. enigmaticus* habitats to forage upon macroalgae found attached to reefs. *Pseudaphritis urvillii* is a catadromous species and females migrate from freshwater environments to the open sea during winter to spawn, with juveniles entering the Coorong in spring to summer (Bice et al., 2018b). The diet of juvenile *P. urvillii* consists of small gammaridean amphipods, nereid polychaetes and copepods (Giatas and Ye, 2015). In the ME, reef habitats may have a higher availability of food and shelter resources to support *P. urvillii* during the juvenile life stage, which could explain their prevalence in the fish community of the reef versus non-reef habitat. These examples highlight species-specific responses of fish in *F. enigmaticus* reef habitats, but these associations can also vary with the prevailing environmental conditions in the estuary.

4.3. Temporal changes in fish community structure

Flow regime is a key driver of fish communities in estuaries and plays a critical role in the life history processes of fish such as spawning, migration and recruitment (Potter et al., 2015). In the Coorong, freshwater flows through a complex of barrages maintain the connectivity and estuarine habitats for fish (Ferguson et al., 2013; Ye et al., 2020; Brookes et al., 2022). The overall dynamics of the fish community across space and time in this study, were also reflective of the flow regime. In a two-year period (flow years 2022 and 2023) characterised by the third highest flood event in the River Murray that reached the Coorong, freshwater to brackish salinities prevailed, and freshwater and estuarine fish were numerically dominant in the community. There was strong recruitment of small-bodied species, which included marine-estuarine opportunist species *H. vittatus* in the ME, and estuarine species *A. microstoma* and *A. tamarensis* in the NL. This conforms with previous monitoring in the Coorong estuary during times of freshwater inflows, where lowered salinities and increased primary productivity supports the recruitment of small-bodied species (Zampatti et al., 2010; Ye et al., 2016). Similarly, for another temperate estuary, the Kariega Estuary in South Africa, an extreme flood event reset the system back to normal estuarine conditions, increasing the recruitment of marine-estuarine opportunists (Nodo et al., 2018).

There was temporal change in the fish community in both the ME and NL. In the ME, fish communities were distinct between the onset of the flood, immediately after the flood and one year after the flood. This pattern may indicate that the fish communities in the ME encountered an immediate disturbance due to the flood event. Freshwater straggler species were mainly part of the ME community during the onset of the flood, and marine straggler species were absent, likely reflective of the freshwater salinities. For other temperate estuaries, this pattern of a decrease in marine stragglers in the lower reaches during extreme

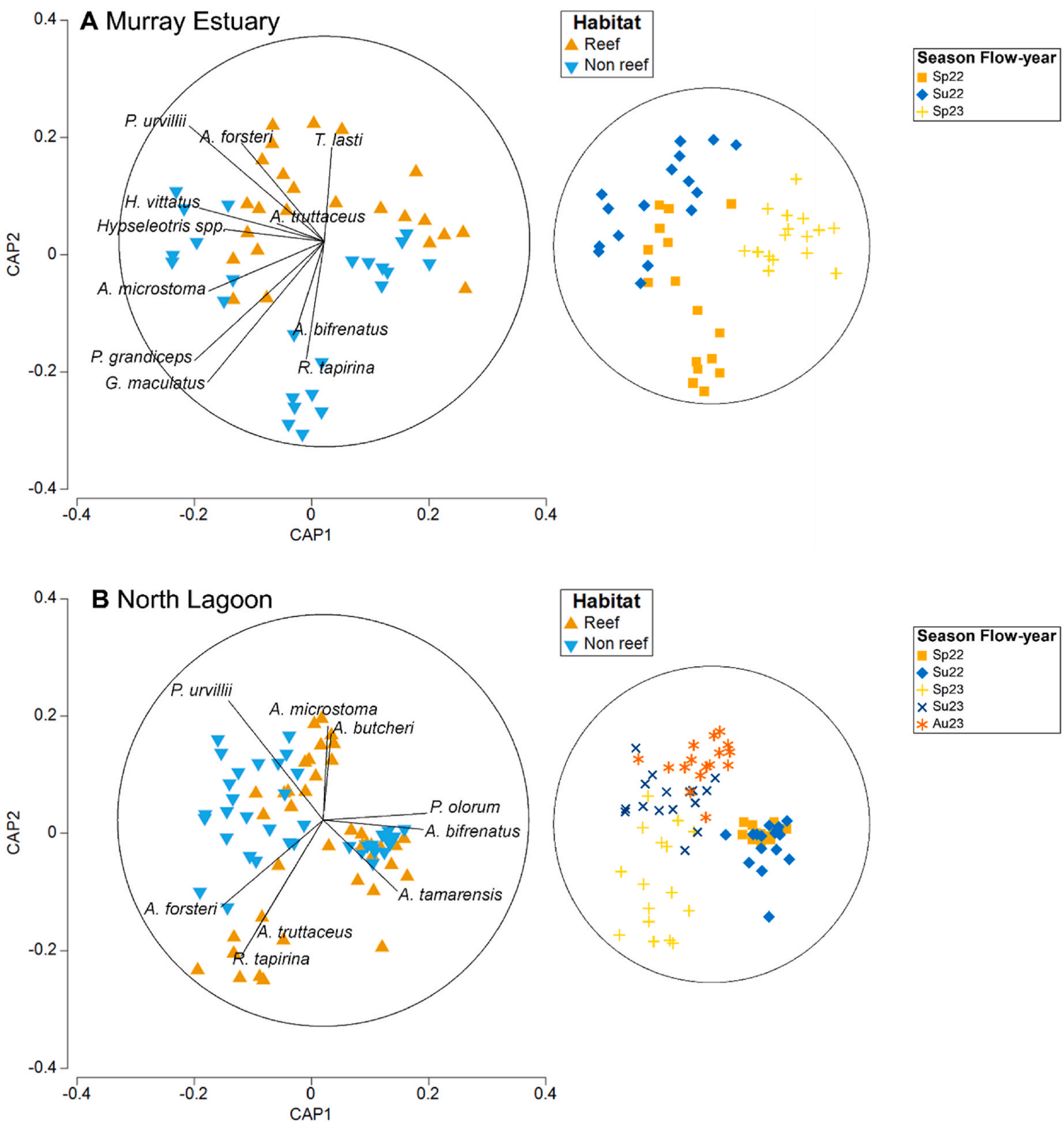

Fig. 6. Canonical analysis of principal coordinates (CAP) plots of native fish communities in reef versus non-reef habitats from **A)** the Murray Estuary and **B)** the North Lagoon. Seasonal surveys were only included if there were statistical differences in community structure between reef and non-reef habitats, based on pairwise test results. Seasonal variability is shown as the inset plot. The vector overlay of species show Pearson rank correlations ≥0.4 with the CAP1 and CAP2 axis.

flooding is commonly observed (Nodo et al., 2018). In this study, in the ME after the flood, there were few freshwater stragglers coinciding with the still low occurrences of marine species, which was likely a result of the persisting low salinities (approximately 8–20 ppt). One year after the flood peak, the ME community further changed and included increased abundances of marine species and estuarine species, likely reflecting a reset of 'normal' estuarine conditions (approximately 20–30 ppt, Fig. S3) and a recovery from the disturbance caused by very high flows during the flood event. In the NL fish communities were less distinct at the onset of the flood, but showed some differences between the flow years, with less freshwater stragglers and more marine species one year after the flood peak.

4.4. *Effects of environmental conditions and stressors on fish community*

Both the reef and non-reef fish communities in the ME and NL of the Coorong during the 2022 and 2023 flow years were significantly correlated with the environmental conditions of total monthly flow, water transparency and temperature (Table 4). There were additional multiple stressors which coincided with the fish surveys. Temporal change in the community before and after the flood in both regions of the Coorong could be explained by the total monthly flow. The timing, duration and volume of freshwater flows is important for estuarine fish communities, as they facilitate species in different ways to complete key life history processes (Bice et al., 2018a; Ye et al., 2021; Whitfield et al., 2023).

In addition to the total monthly flow, water temperature explained seasonal variation in the fish community. Water temperature can affect key life history processes for estuarine fish such as cues for spawning and migration, recruitment and fish physiology such as growth rates (Potter et al., 2015; Guerreiro et al., 2021; Lourenço et al., 2023). Seasonal variability in estuarine fish driven by water temperature is supported by

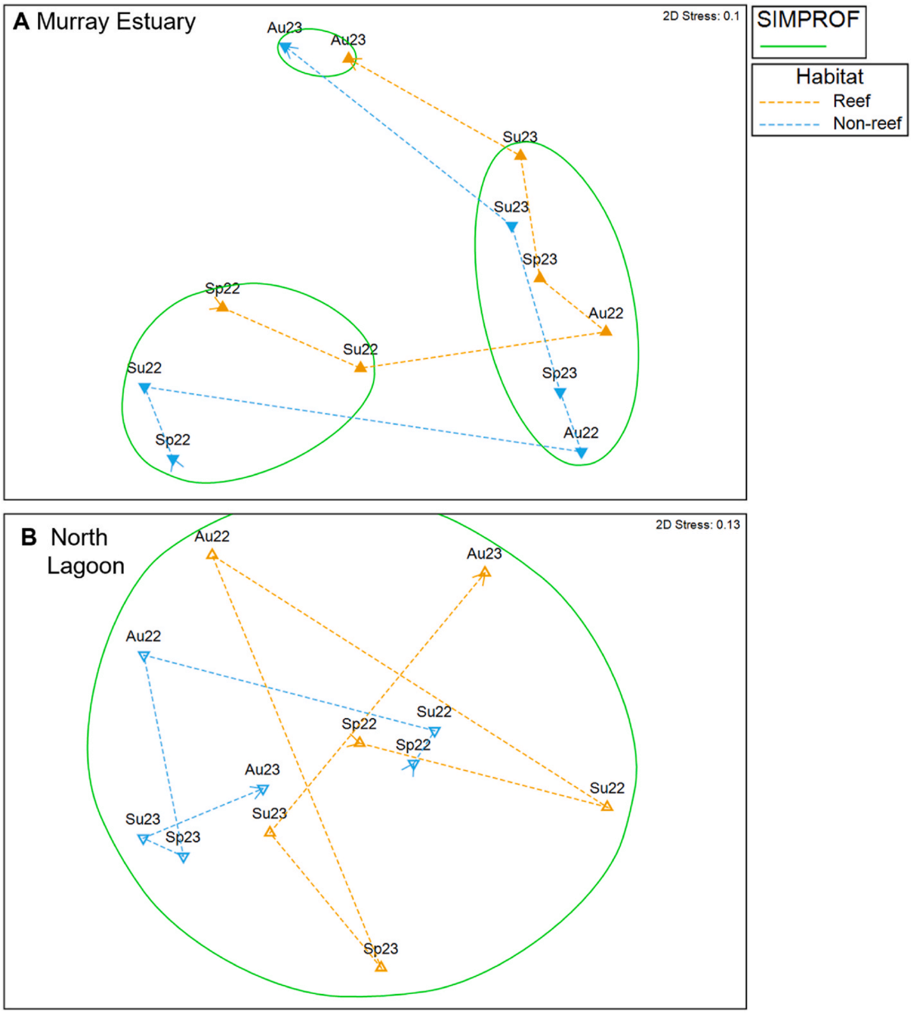

Fig. 7. Non-metric multidimensional scaling (nMDS) plots overlaid with contours of significant groups identified from cluster analysis (SIMPFROF tests) in **A)** Murray Estuary and **B)** North Lagoon regions of the Coorong. The trajectory shows temporal change of reef and non-reef fish communities across seasons spring (Sp), summer (Su) and autumn (Au) in flow years 2022 (22) and 2023 (23).

previous studies (Wu et al., 2019; Guerreiro et al., 2021; Tweedley et al., 2024), including for the Coorong estuary where estuarine species typically spawn during spring and summer, and recruit during autumn (Ye et al., 2021).

Water transparency was one of the strongest environmental conditions explaining spatial separation of the fish community between the ME and NL. The water transparency was likely flood-related, where turbulent freshwater flows from the flood caused high turbidity in the ME. Turbid conditions can influence fish behaviour including predator-prey relationships (González-Ortegón et al., 2010; Zanghi and Ioannou, 2024), visual feeding (Utne-Palm, 2002) or fish physiology (e.g., Fortin-Hamel and Chapman, 2024). For example, the dominance of pelagic sandy sprat in the ME during this study may be a result of both the closer proximity of the ME than the NL to the Murray Mouth and sea, and the higher turbidity in the ME than the NL protecting them from predation by piscivorous birds.

The main environmental stressor that influenced the fish community in both the ME and NL of the Coorong was the flood. However, the results suggest that the ME fish community was also influenced by multiple additional stressors (heatwave, invasives and BGA bloom), particularly the extreme heatwave in autumn 2023 and the moderate abundance of invasives in summer 2022. *Afurcagobius tamarensis* were greater in abundance in the ME community during autumn in 2023 compared to autumn in 2022, and these conditions were at the upper limit of the species temperature tolerance (23 °C) (Gee and Gee, 1991; Bice, 2010).

A moderate abundance of invasives influenced the fish community, and mostly during summer 2022 in the ME. Invasives such as *C. carpio* and *P. fluviatilis* can have negative impacts on the fish community through competition and predation (e.g., Ilarri et al., 2022). After the flood peak there was an overall decrease in abundance and diversity of fish, a common phenomenon observed in other estuaries after an extreme flood event (e.g., Nodo et al., 2018; Henderson et al., 2024). The examples from this study highlighted that the ME was most susceptible to change in the fish community from multiple stressors. Cumulative stressors on fish communities are increasing due to anthropogenic causes, however, are difficult to untangle as shown for fish communities in temperate estuaries from Southern Australia (Whitmarsh et al., 2020).

In the Coorong, *F. enigmaticus* reefs are widespread biogenic structures in the estuary and lagoon. They are integral to the functioning of the ecosystem due to their provision of shelter for juveniles and estuarine fish species. Macroalgae and macrophytes often attach to reefs, which could increase the value of reefs as nursery sites for fish and should be explored further. Across many regions of the world, *F. enigmaticus* can be highly invasive, fouling on infrastructure or other animals (e.g., turtles), causing irreversible abiotic and biotic changes in the environment, facilitating the establishment of other non-native

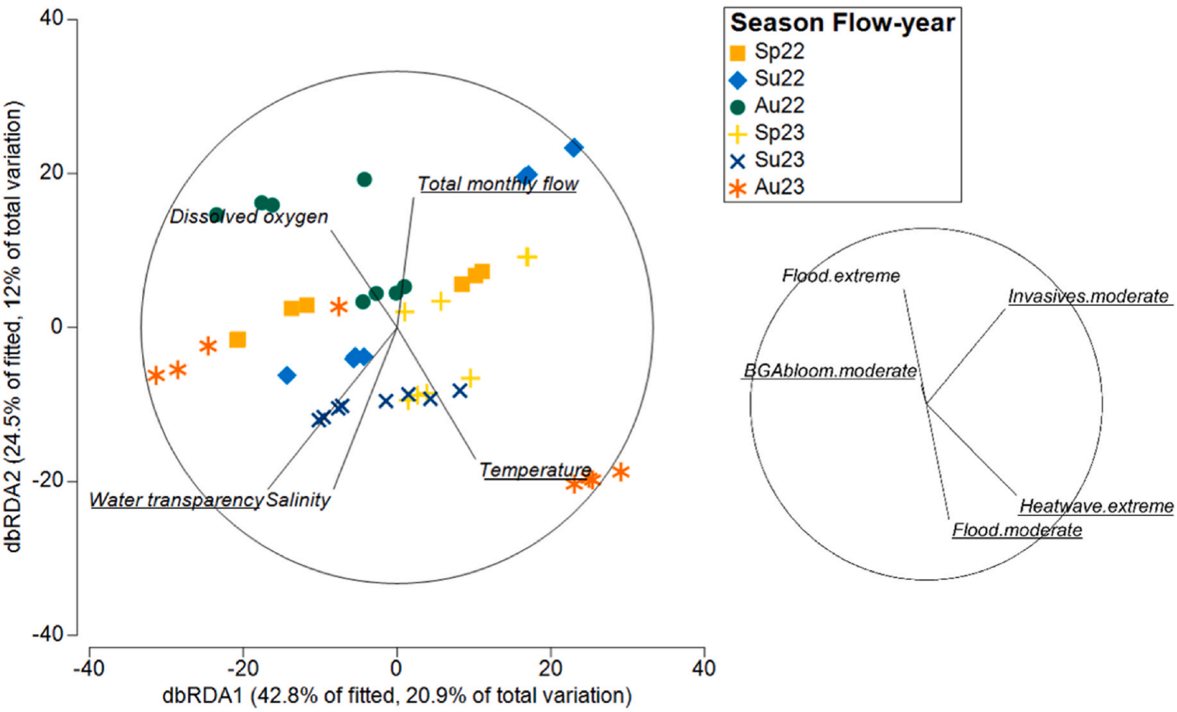

Fig. 8. Distance based redundancy analysis (dbRDA) constrained ordination plot which visualizes the results from a DistLM on multivariate regressions between fish community data (reef and non-reef habitats in each ME and NL) with environmental conditions and stressors combined in the single model. The vector overlay shows variables that have a Pearson's correlation of >0.4, and those underlined were identified in the BEST test analysis as variables that were part of the best model and significantly explained variation in the fish community. The second circle (right) shows vector overlays of the multiple unforeseen stressors that occurred during the study period and were correlated with the fish community and were combined in the same single DistLM model.

Table 4
BEST (best possible rank order match) test results for the combination of environmental conditions and stressors which BEST explained spatial and temporal variation in the native fish community, and their Pearson correlation values with the first two dbRDA axes, with the strongest correlation with each axis shown in bold.

Variable	Pseudo-F	*p*	Cumul.	Residual df	dbRDA1	dbRDA2
Water transparency	5.797	**0.000**	0.112	46	**−0.598**	−0.387
Flood (moderate)	6.175	**0.000**	0.219	45	0.436	−0.473
Temperature	5.183	**0.000**	0.301	44	0.454	−0.039
Blue-green algae bloom (moderate)	4.594	**0.000**	0.369	43	−0.075	−0.012
Invasives (moderate)	3.812	**0.001**	0.421	42	0.284	0.443
Heatwave (extreme)	2.236	**0.025**	0.451	41	0.395	−0.418
Total monthly flow	2.953	**0.005**	0.489	40	0.062	**0.504**

species, and outcompeting native species (Alvarez-Aguilar et al., 2022). In this study, the recognition of the multiple ecological functions of *F. enigmaticus* reefs, such as shelter provision and nursery sites for juvenile fish, implies that reefs have a conservation value in the Coorong. Currently, reef distributions do not cause problems by fouling, nor negative impacts to native species or facilitating other non-native species. However, anthropogenic impacts in the Coorong need to be reduced (e.g., eutrophication) to minimise the risk of reef proliferation as this could potentially restrict water movement and connectivity between the North and South Lagoon in the Coorong.

The influence of environmental stressors on fish and their biogenic reef habitats may have implications for ecosystem functions and services (Martínez-Baena et al., 2022; Wernberg et al., 2024). For reef building polychaetes, their calcareous reefs are susceptible to impacts of climate change, for example ocean acidification effects and storm surges from sea level rises (Smith et al., 2013; Wernberg et al., 2024). Naturally structured habitats are a key component of maintaining a functional estuary (Henderson et al., 2024). This study provided new evidence that reefs built by the polychaete *F. enigmaticus* deliver ecosystem functions, such as shelter for fish communities, and merit conservation.

5. Conclusion

Flow regime is a key driver of estuarine fish communities, nonetheless, this study provided evidence for fish associations with polychaetes reefs in a large temperate estuary and lagoon. Overall, the fish species composition was similar between reef and non-reef habitats, although there were species-specific responses to reef habitat that were complex in nature and driving differences in the fish community structure. Demersal gobies were often higher in abundance in polychaete reef habitats which could reflect that they are using reefs for shelter or food. Polychaete reef habitats were also important for other juveniles of estuarine species such as *A. microstoma* and *A. butcheri*. The extreme flood event, one of the highest recorded, lowered salinities throughout the Coorong, subsequently influencing spatial and temporal variation in the fish community in response to the environmental conditions and stressors present. Reefs built by the polychaete *F. enigmaticus* deliver ecosystem functions that benefit fish communities and merit conservation.

CRediT authorship contribution statement

Laura Schroder: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Orlando Lam-Gordillo:** Writing – review & editing, Visualization, Supervision, Methodology, Conceptualization. **Qifeng Ye:** Writing – review & editing, Visualization, Supervision, Resources, Methodology, Investigation, Conceptualization. **Sabine Dittmann:** Writing – review & editing, Visualization, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

Data availability statement

All the data used are presented in the article and supplementary materials.

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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.marenvres.2025.107212.

Data availability

Data will be made available on request.

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Chapter 5. Demersal and benthic macroinvertebrate associations with polychaete reefs

Burrow excavation underneath a polychaete reef. Photo credit: Laura Schroder.

Abstract

Reef-building polychaetes are important ecosystem engineers which can structure biotic communities. In this study, benthic and demersal macroinvertebrates associated with *Ficopomatus enigmaticus* reefs were investigated based on different reef types (i.e., size and density) as a main objective, across a large temperate estuary in southern Australia. The estuary was dominated by small and dense reefs whereas the lagoon had fewer but larger reefs, which provided an opportunity to test the generality of the pattern of macroinvertebrate associations across different reef types. Benthic macroinvertebrates were sampled from three substrates from the reef (reef matrix), soft sediment next to reefs (1 m apart), and non-reef sediments. In the same reef and non-reef locations, demersal macroinvertebrates were collected from overnight fyke-net deployments. It was hypothesised that reefs would influence both demersal and benthic macroinvertebrates with (1) higher abundance, diversity and different community structure found in reefs, (2) reef associations would be similar in the estuary and lagoon (3) seasonal variation or flood related changes. The results showed complex patterns where macroinvertebrate communities in reef and non-reef habitats varied with the environmental setting (i.e., across regions within the Coorong). The mean total abundance of benthic macroinvertebrates was highest in the reef matrix, intermediate in the reef sediment and lowest in the non-reef sediment. There was a dominance of crustaceans, mostly amphipods, in the reef matrix, followed by higher abundances of crustaceans, annelids and bivalves in the reef sediments compared to non-reef sediments. Sediments in reefs differed on occasions from non-reef sediments due to sediment characteristics such as well sorted, small median grain sized, and high organic matter sediments, which were driving patterns in the benthic community. Demersal macroinvertebrate communities were dynamic and influenced by other environmental conditions (e.g., salinity and freshwater flow) and seasonal variation. Estuarine soft sediment communities benefit from the habitat heterogeneity provided by *F. enigmaticus* reefs more than demersal communities, and this study further demonstrated for the first time that the pattern of benthic macroinvertebrate associations with polychaete reefs occurs regardless of reef type.

5.1 Introduction

Reef-building polychaetes are important ecosystem engineers in shallow water environments and can have a profound role in structuring biotic communities (Bruschetti, 2019; Montefalcone et al., 2022). Polychaete reefs modify the environment by reducing current flow speeds (Borsje et al., 2014; Schwindt et al., 2004a), increasing the sediment accumulation in the vicinity of reefs (Bruschetti et al., 2011; Schwindt et al., 2004a), and improving water quality and nutrient cycling by filter feeding (Bruschetti et al., 2018; Davies et al., 1989; Pan & Marcoval, 2014; Piccardo et al., 2024; Tait et al., 2023). As ecosystem engineers, polychaete reefs modulate resources for other biota (biotic or abiotic) through changes in the environment (Jones et al., 1994; Bruschetti, 2019; Tait et al., 2023). For example, reefs provide a substrate for sessile organisms and attachment for macroalgae, while spaces in-between or inside tubes or amongst macroalgae can be refuges for meiofauna and macrofauna (Bazterrica et al., 2021; Martinez et al., 2020: McQuaid & Griffiths, 2014; Palmer et al., 2021). However, reefs can outcompete other filter feeding species (Heiman & Micheli, 2010) and displace soft-sediment dependent macrofauna directly or indirectly, including those in surrounding sediments through trophic relationships (e.g., predation by crab fauna) (Schwindt et al., 2001). To better understand the ecological functioning of polychaete reefs, it is necessary to investigate their interactions and biotic associations with the water column, sediments, or reef structure itself (e.g., De Smet et al., 2015). Polychaete reefs built by sabellids influence multiple components of the reef associated biota (i.e., benthic, epi- and hyperfauna) (De Smet et al., 2015), but less is known for the biotic associations with the large calcareous reefs constructed by serpulids.

Ficopomatus enigmaticus (Fauvel, 1923) (Polychaeta, Serpulidae) is one of the most prominent providers of polychaete reefs in brackish and sheltered waters such as bays, estuaries and lagoons (Styan et al., 2017). This species has been introduced to many parts of the world via shipping or migratory shore birds and is considered a marine invasive species in some areas (Allen, 1953; Bruschetti et al., 2009; Alvarez-Aguilar et al., 2022). The putative native range of *F. enigmaticus* includes the temperate regions of the Indian Ocean and Australia (Dew, 1959), but the true origin of the species remains unresolved (Kupriyanova et al., 2023; Styan et al., 2017; Tovar-Hernández et al., 2022). Previous studies of *F. enigmaticus* in its non-native range have shown positive effects on the overall diversity and abundance of associated macrofauna in the reef matrix (Heiman & Micheli, 2010; Martinez et al., 2020; McQuaid & Griffiths, 2014). The reef matrix provided by *F. enigmaticus* provides a hard settlement substrate for other species such as bryozoans, ascidians, barnacles and mussels. In addition, juvenile polychaetes, gastropods, crabs, amphipods and tanaids seek shelter amongst the reef matrix or attached macrophytes (Bruschetti et al., 2009; Heiman et al., 2008; Heiman & Micheli, 2010; Schwindt & Iribarne, 1998). The habitat complexity provided by *F. enigmaticus* extends beyond the reef matrix and includes the surrounding soft sediment environments (Brundu & Magni 2021; Schwindt et al., 2001; Martinez et al., 2020). At the interface of the soft-sediments and reef (i.e., reef edges), the overhanging reef framework provides an enhanced level of protection for burrowing crabs (Schwindt et al., 2001). Apart from crab fauna (Schwindt et al., 2001), other demersal (i.e., hyperbenthos) macroinvertebrates that migrate to and utilise *F. enigmaticus* reefs have not been previously investigated from a community perspective.

Individual reefs of *F. enigmaticus* vary in their structural complexity such as irregular, circular, halo and platform types ranging from 0.2–30 m^2 in surface cover (Schwindt et al., 2004b; Fornós et al., 1997; Schroder et al., 2024). The gregarious nature of *F. enigmaticus* leads to expansive reef formations in low flow and eutrophic conditions, and large densities of several hundred reefs per hectare have been described (Schroder et al., 2024). Recently, different levels of complexity have been investigated, including at different distances from reef locations (e.g., Brundu & Magni, 2021) and substrate areas without reefs (Martinez et al., 2020). Brundu and Magni (2021) found a context dependent pattern in the benthic community between near and far distances from reefs for two of three lagoons with varying reef characteristics. However, Brundu and Magni (2021) did not sample the reefs directly. Martinez et al. (2020) found a distinct benthic community in the reefs and sediments near reefs compared to reef-free sediments, but did not explore the pattern across reef types. Reef habitats that differ in morphology, size and density and their local environmental settings could be inhabited by specific faunal associations. Yet, the effect of habitat complexity on macroinvertebrates has not been studied, and further investigations were needed to explore the generality of benthic community patterns in polychaete reefs.

Macroinvertebrate communities in estuaries are primarily influenced by freshwater flows and connectivity with the marine environment. In estuaries, continuous and intermediate freshwater flows can help to improve the resilience of estuarine macroinvertebrate communities to large scale disturbance events (i.e., drought or flood) (Dittmann et al., 2015). Extreme floods can impact macroinvertebrates if smothered by fine sediment deposited on mudflats, prolonged inundation of mudflats, lowered salinities and events with low dissolved oxygen (Nishijima et al., 2013; Norkko et al., 2006; Mayjor et al., 2023). Finer scale spatial and temporal patterns in macroinvertebrate communities can be driven by local environmental conditions such as the salinity gradient, organic matter and nutrients in the sediments, sediment particle size, water temperature and dissolved oxygen (Chariton et al., 2010; Lam-Gordillo et al., 2022; Tait et al., 2023; Lam-Gordillo et al., 2024).

The main aim of this study was to investigate the abundance and diversity of demersal (mobile epifauna) and benthic macroinvertebrates with *Ficopomatus enigmaticus* reefs. A second aim was to investigate the community composition of demersal and benthic macroinvertebrates in reef versus non-reef habitats and substrates. A third aim was to detect whether the environmental setting (i.e., estuarine or lagoon region) influenced community composition, and a fourth aim was to detect any seasonal changes. The last study aim was to assess whether the reef habitat had a stronger effect on the benthic than the demersal macroinvertebrate community. The field investigations for this study were carried out in a large temperate estuary in southern Australia.

It was hypothesised that both demersal and benthic macroinvertebrates occur with higher abundance and diversity in reef compared to non-reef habitats and substrates. Secondly, it was hypothesised that the community composition of demersal and benthic macroinvertebrates differs in reef compared to non-reef habitats and substrates. Thirdly, it was hypothesised that a similar community composition of demersal and benthic macroinvertebrates occurs between the estuarine and lagoon regions. Hypothesis four was that demersal and benthic macroinvertebrate community composition vary across seasons. Lastly, it was hypothesised that the reef habitat has a greater magnitude of effect on the benthic macroinvertebrate community than the demersal macroinvertebrate community.

5.2 Methods

5.2.1 Study Area

The polychaete reefs were studied in the Coorong, a large temperate estuary in southern Australia, located at the terminus of the Murray-Darling River system (Figure 5.1). Freshwater from the Murray River enters Lakes Alexandrina and Albert and flows through constructed barrages to the Coorong and open sea. The area (approximately 20 km^2) in the vicinity of the opening is referred to as the ‘Murray estuary’ (ME) and is a narrow channel (~500 m width and 6 m average depth). The tides in the ME are semi-diurnal with a moderate diurnal inequality and range from ~ 0.4 to ~1.2 m during neap and spring tides, respectively (Webster, 2010). Adjacent to the ME, the North Lagoon (NL) is a connected water body (85 km^2) with an average channel width of 1.5 km and average depth of 1.2 m, which can vary with wind seiches (Webster, 2010). There is a strong salinity gradient in the Coorong from an average of 20 PSU in the ME to 30–80 PSU on average in the NL (Mosley et al., 2023).

5.2.2 Reef and non-reef habitats

Polychaete reefs in the Coorong are built by *Ficopomatus enigmaticus* (hereafter ‘reefs’) and are distributed throughout the ME and NL (Chapter 2; Schroder et al., 2024). Reef habitat in the ME was characterised by small sized reefs (0.8 m average diameter, 0.2 m average height) that were irregular, halo, or platform types and occurred in high densities (525 reefs ha^{-1}, Chapter 4 Fig. 1). In contrast, NL reef habitat included large (1.5 m average diameter, 0.5 m average height) and mostly circular or platform type reefs occurring in lower densities (139 reefs ha^{-1}, Chapter 4 Fig 1). The polychaete reefs in the ME and NL were occasionally covered by filamentous algae and not all tubes were inhabited by living *F. enigmaticus*. In contrast, ‘non-reef habitats’, included unstructured soft sediments of predominantly fine to medium sand (57–80%) located at least 0.5 km away from high density reef areas.

5.2.3 Survey design

Surveys were carried out for demersal and benthic macroinvertebrates at reef and non-reef habitats in both the ME and NL regions (Figure 5.1). The demersal macroinvertebrate surveys included a comparison between two habitats (1) reef (>100 reefs ha^{-1}) and (2) non-reef (<1 reef ha^{-1}) (Figure 5.1A and B). The benthic macroinvertebrate surveys included a comparison between three substrates (1) reef matrix from high density reef areas (>100 reefs ha^{-1}) (herein ‘reef matrix’) (2) soft sediments in high density reef areas (>100 reefs ha^{-1}) (herein ‘reef habitat’), and (3) soft sediments in non-reef areas (<1 reef ha^{-1}) (Figure 5.1A and B).

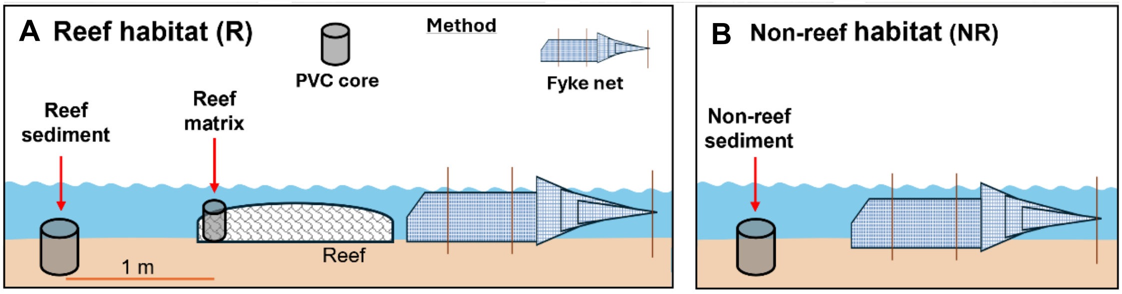

Figure 5.1. A) Benthic macroinvertebrates were sampled with a PVC corer and demersal macroinvertebrates with a fyke net in **A)** R=reef habitat and **B)** NR=non-reef habitats in both the ME and NL. Refer to Chapter 4 for reef and non-reef habitats sampled in the Murray Estuary and North Lagoon of the Coorong.

In the flow year 2022 (i.e., July 2022 to June 2023, herein ‘2022’), high rainfall in the Murray-Darling River system caused the third highest flood ever recorded, and the highest flow rates to reach the Lower Lakes and Coorong since 1956 (Mosley et al., 2024). The start of the demersal macroinvertebrate surveys occurred in the Austral spring (October) and Austral summer (late November to December) during the onset of the very high flows reaching the Coorong (Figure 5.2; Appendix D Table S1), and were repeated in the Austral spring, summer and autumn for a second flow year in 2023 (i.e., July 2023 to June 2024, herein ‘2023’) (Figure 5.2; Appendix D Table S1). Benthic macroinvertebrate surveys were conducted for two seasons only during the Austral spring and summer in 2023 (after the flood peak).

5.2.4 Field surveys

5.2.4.1 Environmental data

Environmental conditions were collected to correlate the macroinvertebrate data with changes in estuarine habitat in the Coorong. Surface water data including salinity and temperature (°C) were obtained from WaterData SA (https://water.data.sa.gov.au), for the ME (Goolwa Channel logger A4261036; 35°31'59.05"S, 138°50'5.42"E) and NL (Long Point logger A4261135; 35°41'44.38"S, 139° 9'42.41"E). Surface water data were averaged across each field survey. Salinity in ppt was calculated from the specific electrical conductivity (EC, mS cm^{-1} at 25 °C) using the equation developed for the Coorong (Mosley et al., 2023). Flow over all barrages that enter the Coorong (GL month^{-1}, hereafter ‘monthly barrage flow’) were obtained from the River Murray Calculated Barrage Flow Logger (A4261002) at WaterData SA (DEW, 2025). In the field, dissolved oxygen (DO, mg L^{-1}) was measured at approximately 20 cm depth below the water surface using a Hanna DO meter (model HI9146) and YSI DO meter (model 55), taking six replicate measurements per region during a given survey.

Samples were taken for sediment characteristics in reef and non-reef sediment substrates (three replicates per parameter per substrate, region, and season), to later correlate with the benthic macroinvertebrate data. Sediment samples for organic matter were collected using a 10 mL cut-off syringe (1.8 cm^2) and for grain size using a 60 mL cut-off syringe (6.6 cm^2). All sediment samples were frozen (-20°C) until processed.

5.2.4.2 Demersal macroinvertebrates

Demersal macroinvertebrates were sampled using single wing fyke nets (5.6 m long with circular hoops of 0.6 m funnel, 3 m single wing and 8 mm mesh), which were set whilst undertaking a fish survey (Chapter 3). In each region of the ME and NL, eight overnight replicate deployments were made over two consecutive nights, per reef and non-reef habitat. Nets were set for a duration of approximately 15 hours. In the reef habitat, nets were deployed by wrapping net wings around the polychaete reefs. Catch from each replicate net were retrieved the following morning and all taxa were identified in the field to the lowest taxonomic level possible (Gowlett-Holmes, 2008; Wade et al., 2004). Carapace width was measured for crabs to the nearest 1 mm.

5.2.4.3 Benthic macroinvertebrates

In each region of the ME and NL, reef sediment and non-reef sediment samples for benthic macrofauna were taken with a cylindrical PVC corer (diameter= 10.3 cm, surface area=83.32 cm^2) to 15 cm depth, which included 8 replicate samples randomly taken within an area of 20 m^2 per reef and non-reef habitat. In the reef habitat, replicates were taken at 1 m distance from the edge of a reef (e.g. Martinez et al., 2020). Samples were sieved through a 500 µm mesh in the field and frozen at -20°C until further processing. Reef matrix samples were collected using a cylindrical PVC corer (diameter= 5.0 cm, surface area=19.63 cm^2) to core into the top of a reef to 15 cm depth. Sediment underneath the reef matrix was not included, due to anoxic conditions devoid of macrofauna. Reef matrix samples were collected from living edges of the reef (Schwindt et al., 2004b). Replicates were collected from different individual reefs, that were haphazardly chosen and a minimum distance of 5 m apart. Reef matrix, reef sediment and non-reef sediment samples were frozen intact at -20°C until further processing.

5.2.5 Laboratory analysis

Sediment organic matter was determined by Loss on Ignition (LOI) (Heiri et al., 2001; Kenny and Sotheran, 2013). Samples were oven dried at 80 °C until a constant weight was reached, then placed into a muffle furnace at 450 °C for 5 hours. Burnt sediment samples were allowed to cool in a desiccator to record the ash mass, then ash free dry mass (AFDM) was calculated by subtracting the ash mass from the dry mass. All samples were weighed to an accuracy of ± 0.0001 g on an A&D Company Ltd. GR-200 balance. Grain size samples were analysed by laser diffraction using a Malvern Mastersizer (Model 3000). Median grain size (D_{50}) and sorting coefficient using the Folk and Ward method were calculated from the Gradistat program v8 (Blott and Pye, 2012).

The benthic macroinvertebrate samples were thawed, and the reef matrix samples were rinsed and sieved through a 500 µm mesh. Benthic macrofauna in reef and non-reef sediment samples, and those retained in the sieve from the reef matrix samples were sorted and identified to the lowest possible taxonomic level and counted. To compare the size of crabs to those in the demersal catch, the carapace width of individuals was measured using digital callipers (to the nearest 0.1 mm). For each replicate sample, individuals from each taxon were pooled, blotted on Kimwipes® before taking wet mass (WM), and oven dried at 60 °C until constant weight was reached (Nitschke et al., 2024). For small bivalves (<5 mm) biomass was determined with shell, and for large bivalves (>5 mm) shells were removed for WM and DM. Dried samples were combusted in a muffle furnace at 450°C for 5h, then allowed to cool in a desiccator to record the ash mass. Ash free dry mass (AFDM) was calculated from taking the DM and subtracting the ash mass. All samples were weighed to an accuracy of ± 0.0001 g on an A&D Company Ltd. GR-200 balance. *Ficopomatus enigmaticus* was not counted or included in the biomass analysis.

Macroalgae present in the benthic macrofauna samples were retained to investigate potential correlations with amphipod abundances. The displacement volume (mL) of macroalgae was pooled from each sample and then oven dried at 40 °C until constant weight was reached.

5.2.6 Data analysis

Total demersal macroinvertebrate catch was standardised to catch-per-unit-effort (CPUE), which was the total individual number of macroinvertebrates per fyke net set for approximately 15 hours overnight (individuals net^{-1} night^{-1}). Traditional diversity metrics of species richness (S), Shannon Diversity (H') and Pielou's evenness (J') were calculated for demersal macroinvertebrates. Univariate data were square-root transformed prior to analysis as an Euclidean distance matrix. A three-way fixed factor PERMutational ANalysis Of VAriance (PERMANOVA) design was used to test for differences in demersal macroinvertebrate total CPUE, S, H' and J' between habitats (2 levels: reef and non-reef), regions (2 levels: ME and NL), and season-year (6 levels: spring 2022, summer 2022, autumn 2022, spring 2023, summer 2023 and autumn 2024). PERMANOVA tests were set to 9,999 permutations (Anderson, 2008). Pairwise tests were investigated for a significant interaction effect (Habitat × Region × Season-year) to identify specific differences between season-year surveys or regions for which the reef and non-reef habitat was significantly different. Preliminary testing indicated that there was no significant differences were found between consecutive sampling nights (Appendix D Table S2).

To test for significant differences in the demersal macroinvertebrate community between habitats, regions and season-year surveys, the prior mentioned three-way fixed factor PERMANOVA design was applied to a Bray Curtis similarity matrix of fourth root transformed data. Pairwise tests were carried out for significant interactions (Habitat × Season-year). Canonical analysis of principal coordinates (CAP) plots were used to emphasize the significant differences found between habitats, regions and seasons. CAP also generated a p-value using the trace statistic, represented by the matrix ($Q_m^0{}'HQ_m^0$), to test for differences among groups (within habitats, regions and seasons) in multidimensional space (Anderson, 2008). SIMilarity PERcentage (SIMPER) analysis (Clarke and Warwick, 2001) was used to identify the group of main taxa that collectively contribute to the >70% dissimilarity between reef and non-reef habitats. A shade-plot of average abundance of demersal macroinvertebrates (CPUE, square root transformed) grouped by habitat, region and season-year was used to visualize spatial-temporal trends. The Whittaker index of association was used to group species, and clustering based on group average linking (CLUSTER) tests on average data were used to group samples, listing taxa separately (Clarke et al., 2008).

All benthic macroinvertebrate abundance data were standardised to the surface area of the large corer (83.32 cm^{-2}). This reflected a more reasonable surface area as reef sizes sampled in the ME were <1 m^{-2}., Total abundance and abundances of the main taxa groups (Crustacea, Insecta, Annelida, Gastropoda and Bivalvia) were calculated for benthic macroinvertebrates. Traditional diversity metrices (S, H' and J') were calculated based on the raw data from each type of corer used. Univariate data were square root transformed, and a matrix was made based on Euclidean distances. A three-way fixed factor PERMANOVA design was used to test for differences in benthic macroinvertebrate total abundance, abundance of main taxa groups, S, H' and J' between substrates (3 levels: reef matrix, reef sediment and non-reef sediment), regions (2 levels: ME and NL), and seasons (2 levels: spring and summer 2023). PERMANOVA tests were used with 9,999 permutations, and pairwise tests were used if there was an interaction effect (Substrate × Region × Season).

To test for multivariate differences in the benthic macroinvertebrate community between substrates, regions and seasons, a PERMANOVA test was carried out on the same three-way fixed factor design, based on a Bray Curtis similarity matrix of fourth root transformed data. The main group of taxa driving >70% of the dissimilarity between substrate types for specific seasons or regions were identified using a SIMPER analysis. A non-metric Multidimensional Scaling plot (nMDS) was used to show variation in the benthic community (Clarke et al., 2008). A shade-plot of average densities of benthic macroinvertebrates (individuals 83.32 cm^{-2}, fourth root transformed) grouped by substrate, region and season was used to visualize spatial-temporal patterns. The Whittaker index of association was used to group species, and clustering based on group average linking (CLUSTER) tests on average data were used to group samples, listing taxa separately (Clarke et al., 2008).

Biomass of benthic macroinvertebrates was standardised as ash free dry weight (AFDW) in g 83.32 cm^{-2}. Total biomass data were square-root transformed and analysed with Euclidean distance. A PERMANOVA test set to 9,999 permutations (Anderson, 2008) was used to determine significant differences in the total biomass between substrates, regions and seasons. Pairwise tests were used to explore the interaction effect (Region × Season).

To investigate if amphipod abundances recorded in the reef matrix were affected by the amount of macroalgae present, Spearman rank correlation was used to test for a significant relationship between amphipod density (individual count) and macroalgae biomass (dry weight) in OriginPro 2021b (V 9.8.5.201). To investigate differences in feeding modes across seasons, regions, and substrates, functional trait information were obtained from the South Australian Macroinvertebrate trait database (SAMT) (Lam-Gordillo et al., 2020) for 100% of the assigned taxa and community weighted mean (CWM) values were calculated using the package “FD” (Laliberte et al., 2014) in R software (R development Core Team, 2018).

A Distance based Linear Model (DistLM) analysis using a step-wise selection and AIC (Akaike Information Criterion) model (Anderson, 2008) was used to investigate the relationship between the macroinvertebrate community and environmental conditions. A DistLM analysis on demersal macroinvertebrate community included a set of five environmental variables (salinity, temperature, dissolved oxygen, water transparency and total monthly flow). A DistLM analysis on benthic macroinvertebrate community were only conducted for the reef and non-reef sediments and included a set of four environmental variables (salinity, temperature, dissolved oxygen and water transparency) and three sediment condition variables (Organic matter content, median grain size, and sorting coefficient). The best solution of variables predicting variation in the community that were identified in the DistLM analysis were visualized on a distance-based Redundancy Analysis (dbRDA) plot.

To compare the magnitude of the reef habitat effect on demersal versus benthic macroinvertebrate communities, datasets were individually analysed with a 3-way ANOSIM for factors Habitat, Region and Season. The datasets included the fourth root transformed data, Bray-Curtis similarity matrices (no dummy value) for each the demersal and benthic macroinvertebrates. For a similar comparison, the benthic macroinvertebrates matrix included data for only the sediments in reef and non-reef habitats (i.e., excluded substrate ‘reef matrix’). For each dataset, 3-way ANOSIM was used to test for differences in community composition between groups for each factor (Habitat, Region, Season). The global R values were then compared between the demersal and benthic communities. All statistical analyses were carried out in Primer 7 (Clarke and Gorley, 2015) and PERMANOVA+ (Anderson, 2008), with statistical significance of $p<0.05$. Box and whisker plots were used to show the median total CPUE, abundances and AFDW, the 25th and 75th percentiles in the diamond, and the 1.5 IQR (interquartile range) in the error bars.

5.3 Results

5.3.1 Environmental conditions and sediment characteristics

The extreme flood event in 2022/23, resulted in high barrage flows and lowered salinities in the Murray Estuary (ME) and North Lagoon (NL) of the Coorong. Spring and summer (2022) surveys for demersal macroinvertebrates coincided with the onset of the extreme flood and were characterised by a salinity of 0.2–0.6 in the ME and 7–11 in the NL (Figure 5.2A). After the flood peak at the time of the autumn (2022) survey, monthly barrage flows had receded, but salinities remained fresh in the ME and brackish in the NL. In winter 2023 a second small peak in barrage flow occurred prior to the commencement of spring, summer and autumn 2023 surveys (Figure 5.2A). Salinities during the 2023 demersal and benthic macroinvertebrate surveys ranged between 9–18 in the ME and 9–31 in the NL (Figure 5.2B). Water temperatures in spring, summer and autumn seasonal surveys varied between 15–20 °C in 2022 and 16–23 °C in 2023 (Figure 5.2C). The lowest dissolved oxygen concentrations were recorded during autumn surveys in the ME (8.63 mg L^{-1} in 2022 and 5.86 mg L^{-1} in 2023) (Figure 5.2C).

Sediments were similar in organic matter content between the reef and non-reef habitats (PERMANOVA $p>0.05$, Figure 5.2D). Organic matter was higher in the Murray Estuary versus North Lagoon sediments (PERMANOVA $p<0.05$, Figure 5.2D). In the ME, organic matter in the sediments was significantly higher in spring than summer (PERMANOVA $p<0.05$). In the ME during spring, 2023, sediments had an organic matter content of 1.32 % ± 0.22 in the reef and 1.92 % ± 0.43 in the non-reef habitats (Figure 5.2D).

Sediment grain size was predominantly characterised by fine to medium sand (Figure 5.2E). Grain size composition varied between reef and non-reef sediments. The fractions of very coarse sand, coarse sand and medium sand were significantly different between habitats (PERMANOVA $p<0.05$). The proportion of very coarse sand in the NL non-reef habitat decreased from spring to summer in 2023. The NL non-reef habitat had a low proportion of mud content during both surveys in 2023. Very fine sand was almost absent from the NL reef habitat during both surveys.

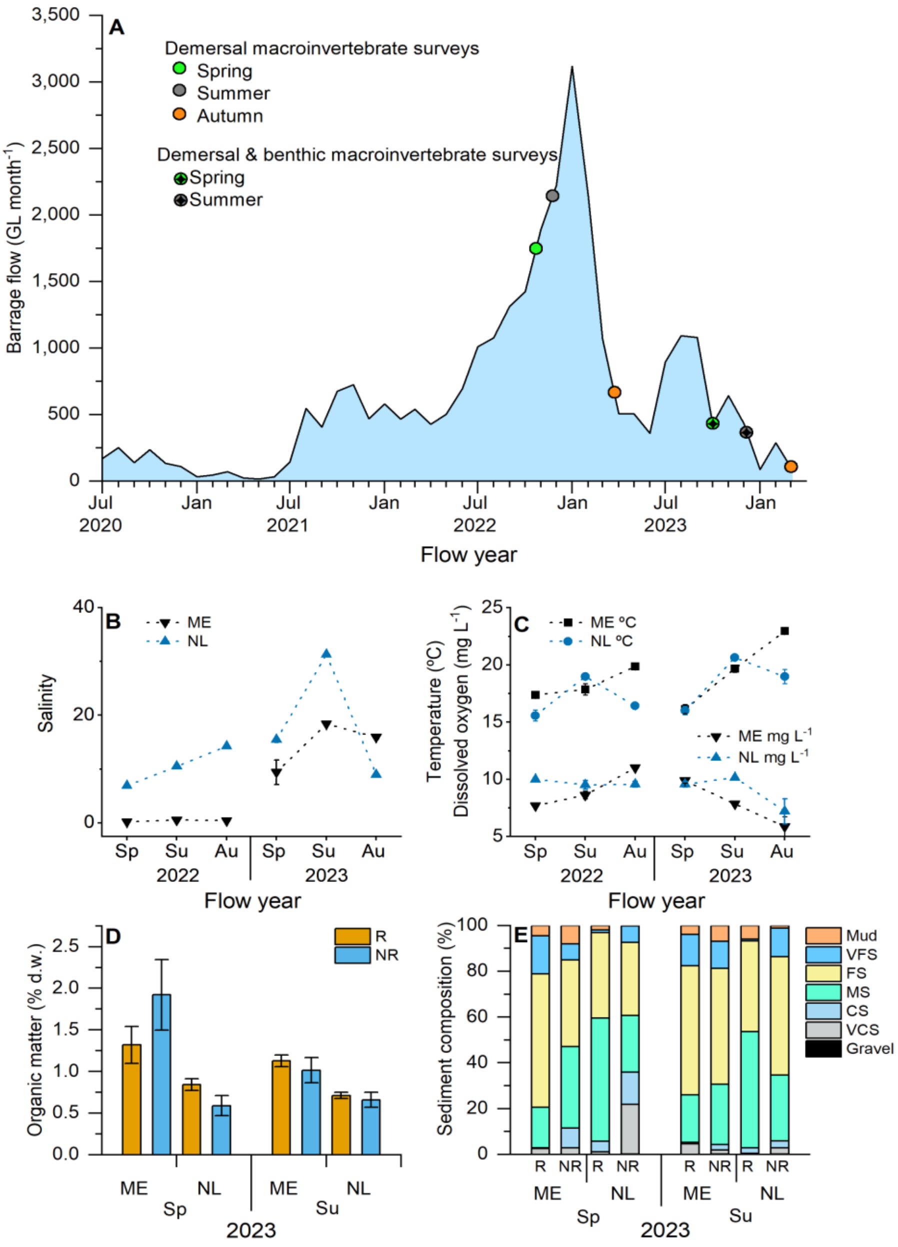

Figure 5.2. **A)** Barrage flow (GL month^{-1}) of freshwater entering the Coorong across all barrages for flow years from 2020 to 2023. Mobile and benthic macroinvertebrate survey start dates are indicated by dots and show seasonal surveys conducted in spring, summer, and autumn in flow years 2022 and 2023. The mean ± s.e. of other environmental conditions during the Murray Estuary (ME) and North Lagoon (NL) surveys shown are **B)** salinity, **C)** temperature (°C) and dissolved oxygen (mg L^{-1}). Data presented from **A–C)** were derived from WaterData SA (DEW, 2025) and field data. Sediment characteristics during benthic macroinvertebrate surveys are shown for **D)** Organic matter (mean ± s.e. of % ash free fry weight) and **E)** sediment grain size composition (%) across reef (R) and non-reef (NR) habitats in the ME and NL during spring and summer 2023.

5.3.2 Demersal macroinvertebrates

5.3.2.1 Catch summary

A total of 8 demersal macroinvertebrate species were found across reef and non-reef habitats (Tables 5.1 and 5.2). Demersal macroinvertebrates sampled were freshwater species *Amarinus laevis, Cherax destructor, Paratya* cf *australiensis,* and marine species *Paragrapsus gaimardii, Halicarcinus ovatus, Helograpsus haswellianus*, *Palaemon serenus,* and Mysida indet. In the ME, *A. laevis* and Mysida indet. were the most abundant demersal taxa in 2022 and 2023 respectively (Tables 5.1 and 5.2). In the NL, *P. serenus* was the most abundant demersal taxa in both 2022 and 2023 (Tables 5.1 and 5.2). Average demersal abundance of taxa was similar between reef versus non-reef habitat, but occasionally varied. For example, in the ME, a higher average abundance of Mysida indet. was recorded in the reef habitat during spring 2023 (Table 5.2). In the NL, higher average abundance of *P. serenus* occurred in spring, summer and autumn in 2023 (Table 5.2).

Crabs, *A. laevis* and *P. gaimardii,* were more often found in the demersal catch from the ME than the NL. The sizes of *A. laevis* in the ME reef and non-reef habitat were similar, with an average carapace width of 11.6 ± 0.2 mm and 12.3 ± 0.3 mm respectively (Appendix D Table S3). The average carapace width of *P. gaimardii* was smaller in reefs (18.7 ± 0.9 mm) than non-reef habitats (21.2 ± 0.9 mm) in the ME (Appendix D Table S3).

Table 5.1. Average CPUE (individuals net^{-1} night^{-1}) (± s.e.) of demersal macroinvertebrates in reef and non-reef habitats, in the Murray Estuary (ME) and North Lagoon (NL) of the Coorong sampled in 2022.

Demersal taxa	**ME Reef**			**ME Non-reef**			**NL Reef**			**NL Non-reef**		
	Au	**Sp**	**Su**	**Au**	**Sp**	**Su**	**Au**	**Sp**	**Su**	**Au**	**Sp**	**Su**
Amarinus laevis	1.9 ± 0.7	20.5 ± 4.6	17.8 ± 3.0	1.3 ± 0.3	5.9 ± 1.3	44.3 ± 6.3	0.1 ± 0.1	0.9 ± 0.4	1.8 ± 0.6	0.4 ± 0.2	0.3 ± 0.2	1.4 ± 0.5
Cherax destructor	0.0	0.0	0.0	0.0	0.0	0.4 ± 0.3	0.0	0.0	0.0	0.0	0.0	0.0
Halicarcinus ovatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Helograpsus haswellianus	0.0	0.0	0.0	0.0	0.4 ± 0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Palaemon serenus	0.0	0.0	3.0 ± 0.6	0.3 ± 0.2	0.6 ± 0.6	7.0 ± 4.0	8.4 ± 3.2	7.0 ± 1.5	6.4 ± 2	3.1 ± 0.9	13.8 ± 3.8	5.5 ± 1.7
Paragrapsus gaimardii	0.3 ± 0.2	4.9 ± 1.5	0.6 ± 0.4	1.3 ± 0.4	3.5 ± 1.2	2.9 ± 0.6	0.0	0.0	0.1 ± 0.1	0.0	0.0	0.0
Paratya cf *australinenis*	0.0	0.0	0.0	1.3 ± 0.4	0.0	0.3 ± 0.3	0.0	0.0	0.0	0.0	0.0	0.1 ± 0.1
Mysida indet.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0 ± 1.0	0.0	0.0	0.0	0.1 ± 0.1

Table 5.2. Average CPUE (individuals net^{-1} night^{-1}) (± s.e.) of demersal macroinvertebrates in reef and non-reef habitats, in the Murray Estuary (ME) and North Lagoon (NL) of the Coorong sampled in 2023.

Demersal taxa	**ME Reef**			**ME Non-reef**			**NL Reef**			**NL Non-reef**		
	Au	**Sp**	**Su**	**Au**	**Sp**	**Su**	**Au**	**Sp**	**Su**	**Au**	**Sp**	**Su**
Amarinus laevis	0.3 ± 0.3	1.0 ± 0.5	0.1 ± 0.1	0.0	1.0 ± 0.5	0.1 ± 0.1	0.6 ± 0.2	1.5 ± 0.5	0.9 ± 0.3	0.6 ± 0.2	0.9 ± 0.3	0.1 ± 0.1
Cherax destructor	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halicarcinus ovatus	1.6 ± 0.5	1.6 ± 1.2	0.3 ± 0.3	0.3 ± 0.2	0.0	0.0	0.0	0.1 ± 0.1	0.0	0.0	0.0	0.0
Helograpsus haswellianus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Palaemon serenus	5.5 ± 1.8	0.5 ± 0.3	0.9 ± 0.2	9.0 ± 3.0	3.0 ± 1.0	0.4 ± 0.2	32.3 ± 11.1	24.9 ± 9.3	38.9 ± 11.6	6.3 ± 2.8	5.3 ± 1.4	0.9 ± 0.4
Paragrapsus gaimardii	2.3 ± 1.0	1.0 ± 0.4	0.3 ± 0.2	0.5 ± 0.3	2.0 ± 0.8	0.3 ± 0.2	1.1 ± 0.4	0.0	0.3 ± 0.2	0.8 ± 0.3	0.0	0.0
Paratya cf *australinenis*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1 ± 0.1	0.0
Mysida indet.	0.0	44.0 ± 19.4	1.4 ± 0.8	0.3 ± 0.2	13.1 ± 11.1	1.9 ± 1.2	0.0	1.6 ± 0.8	0.0	0.0	0.0	0.0

5.3.2.2 Total CPUE, species richness and diversity

There was a significant interaction effect for total CPUE between habitats, regions and seasons (PERMANOVA $p<0.05$, Table 5.3, Figure 5.3). The variation in total CPUE between all factors was mostly due to the habitat and season, but not region (Table 5.3). In the ME, the total CPUE was similar between reef and non-reef habitats across most surveys, apart from spring and summer 2022 (Figure 5.3). In spring 2022, the total CPUE of demersal macroinvertebrates was significantly higher in the reef (median= 23 individuals net^{-1} night^{-1}) than the non-reef habitat (median= 9 individuals^{-1} net^{-1} night^{-1}) (Figure 5.3A, Table 5.3). The opposite pattern was recorded in summer 2022, when the total CPUE was significantly greater in the non-reef (median= 49 individuals net^{-1} night^{-1}) than the reef habitat (median= 19 individuals net^{-1} night^{-1}) (Figure 5.3A, Table 5.3). In the NL, total CPUE was significantly higher in the reef than non-reef habitat during summer and autumn 2023 surveys. For all other surveys, total CPUE was similar between habitats (Figure 5.3B).

The species richness, H' diversity and J' evenness were similar between reef and non-reef habitats (Table 5.3B–D, Appendix D Table S4). For the regions and seasons surveyed, the species richness, and diversity indices H' and J' were significantly different (PERMANOVA $p<0.05$, Table 5.3B–D). In the ME, across seasonal surveys, species richness varied (2–5 species), and the range in diversity indices were 0.36–1.28 for H' and 0.25–0.91 for J' (Appendix D Table S4). In the NL there were between 2–4 species across seasonal surveys, and diversity ranges were 0.14–0.66 for H' and 0.11–0.60 for J' (Appendix D Table S4).

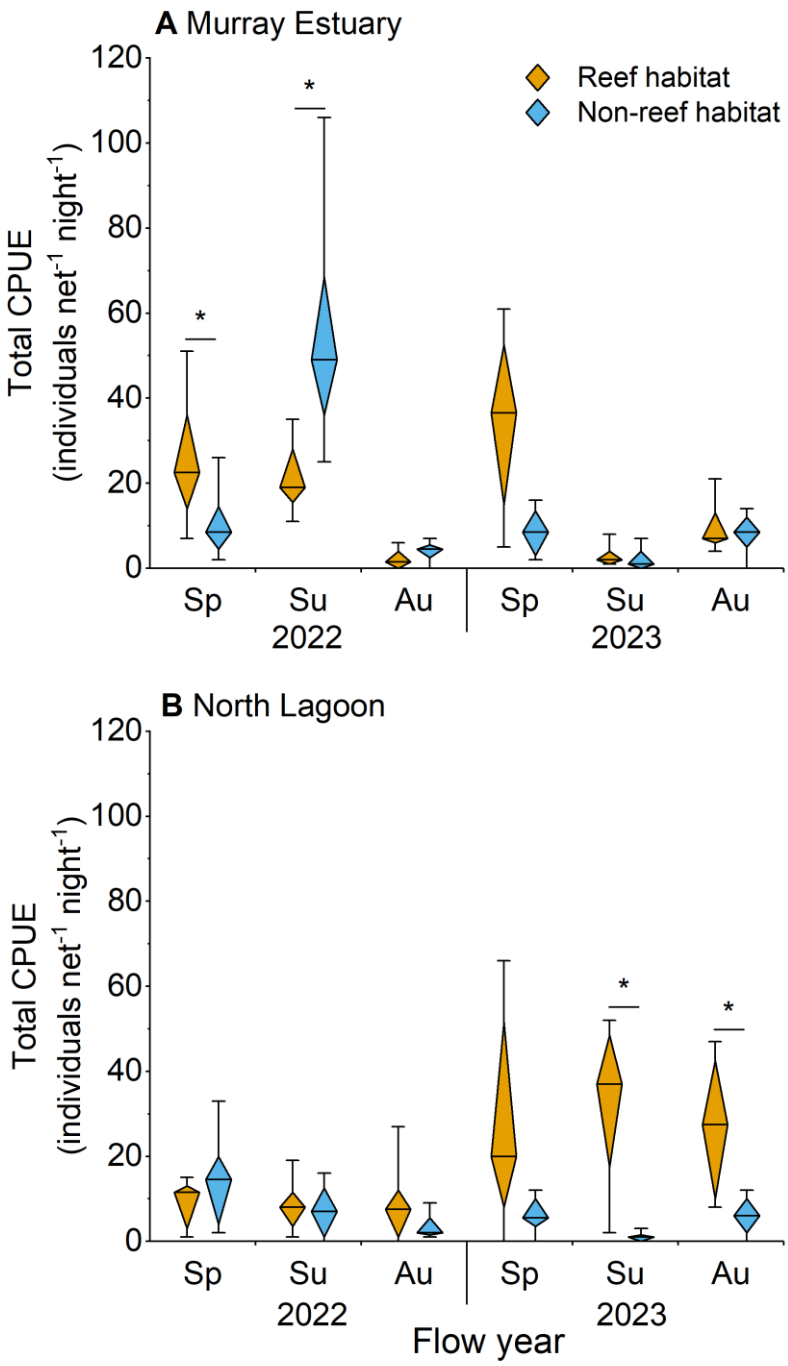

Figure 5.3. Box and whisker plots of the median total demersal macroinvertebrate catch per unit effort (CPUE) (individuals net^{-1} night^{-1}) between reef and non-reef habitats in the **A)** Murray Estuary and **B)** North Lagoon during spring (Sp), summer (Su) and autumn (Au) surveys in flow years 2022 and 2023. Significant pairwise tests are indicated by *.

Table 5.3. Univariate PERMutational ANalysis Of VAriance (PERMANOVA) on **A)** CPUE (individuals net^{-1} night^{-1}), **B)** species richness (S) **C)** Shannon Diversity (H') and **D)** Pielou's Evenness (J') of demersal macroinvertebrates to test for differences between Habitats (Ha) (reef and non-reef), Regions (Re) (Murray Estuary and North Lagoon) and Seasons (Se) (spring, summer and autumn in flow years 2022 and 2023). Significant values ($p<0.05$) are indicated in bold.

Source	df	MS	Pseudo-F	*P*	df	MS	Pseudo-F	*p*
	A) Total CPUE (individuals net^{-1} night^{-1})				**B) Species Richness (S net^{-1} night^{-1})**			
Habitat (Ha)	1	51.47	17.59	**<0.001**	1	0.26	0.37	0.559
Region (Re)	1	5.86	2.00	0.161	1	10.55	15.39	**<0.001**
Season (Se)	5	30.45	10.40	**<0.001**	5	4.94	7.21	**<0.001**
Ha × Re	1	27.59	9.43	**0.002**	1	5.67	8.28	**0.005**
Ha × Se	5	18.37	6.28	**<0.001**	5	3.62	5.28	**<0.001**
Re × Se	5	29.74	10.16	**<0.001**	5	1.48	2.17	**0.062**
Ha × Re × Se	5	12.97	4.43	**<0.001**	5	0.43	0.63	0.666
Residual	168	2.93			168	0.69		
Total	191				191			
	C) Shannon Diversity (H')				**D) Pielou's Evenness (J')**			
Habitat (Ha)	1	0.06	0.67	0.416	1	0.00	0.01	0.902
Region (Re)	1	2.71	29.98	**<0.001**	1	2.58	24.63	**<0.001**
Season (Se)	5	0.45	5.00	**<0.001**	5	0.60	5.76	**<0.001**
Ha × Re	1	0.36	3.93	0.047	1	0.07	0.66	0.421
Ha × Se	5	0.32	3.56	**0.005**	5	0.38	3.58	**0.004**
Re × Se	5	0.10	1.15	0.340	5	0.22	2.11	**0.066**
Ha × Re × Se	5	0.28	3.11	**0.010**	5	0.24	2.24	**0.052**
Residual	168	0.09			168	0.11		
Total	191				191			

5.3.2.3 Community structure

The community structure of demersal macroinvertebrates was significantly different between reef and non-reef habitats across the regions and seasons (PERMANOVA p<0.05, Table 5.4, Appendix D Figure S1). A CAP analysis characterised the differences in the community between habitats which were significant (trace p=0.023, Figure 5.4A). The ME and NL communities varied significantly (PERMANOVA p<0.05, Table 5.4A), and spatial separation by region was pronounced in a CAP analysis (trace p=0.0001) (Figure 5.4B). There was significant temporal variation in the community across the seasons sampled (PERMANOVA p<0.05, Table 5.3A, trace p=0.001 Figure 5.4C).

The demersal macroinvertebrate community in the ME differed between reef and non-reef habitats for four out of six seasonal surveys (spring, summer and autumn in 2022, and spring in 2023) (Table 5.4B). The dissimilarity between habitats in the ME was greatest in autumn 2022 (~72%), due to a higher abundance of *A. laevis* in the reef habitat, and higher abundances of *P. serenus* and *P. gaimardii* in the non-reef habitat (Figure 5.5, Table 5.5A). In the ME during spring 2023, ~68% dissimilarity was observed between habitats, which was due to a higher abundance of mysids in the reef habitat and higher abundances of *P. serenus* and *P. gaimardii* in the non-reef habitat (Figure 5.5, Table 5.5A). Figure 5.5, Table 5.5A

In the North Lagoon, the demersal macroinvertebrate community significantly differed between reef and non-reef habitats for the seasons summer and autumn 2023 (PERMANOVA p<0.05, Table 5.4 B). *Palaemon serenus* was more abundant in the reef habitat on both occasions and contributed to most of the dissimilarity in community structure between habitats (Figure 5.5, Table 5.5B).

Table 5.4. Multivariate PERMmutational ANalysis Of VAriance (PERMANOVA) **A)** main test results and **B)** pairwise test results on differences in the demersal macroinvertebrate community structure between Habitats (Ha) (reef and non-reef) and Regions (Re) (Murray Estuary and North Lagoon). Significant values (p<0.05) are indicated in bold.

A) Demersal macroinvertebrate community				
	df	MS	Pseudo-F	*P*
Habitat (Ha)	1	4526.30	6.11	**<0.001**
Region (Re)	1	38981.00	52.59	**<0.001**
Season (Se)	5	9844.10	13.28	**<0.001**
Ha × Re	1	5328.00	7.19	**<0.001**
Ha × Se	5	3348.20	4.52	**<0.001**
Re × Se	5	9865.60	13.31	**<0.001**
Ha × Re × Se	5	1570.70	2.12	**0.005**
Residual	168	741.23		
Total	191			

B) Pairwise test				
	Murray Estuary (Reef vs non-reef)		North Lagoon (Reef vs non-reef)	
Season	t	*P*	T	*p*
Spring 2022	1.96	**0.029**	1.10	0.299
Summer 2022	3.22	**0.001**	0.57	0.752
Autumn 2022	2.16	**0.029**	1.15	0.276
Spring 2023	2.16	**0.013**	1.39	0.153
Summer 2023	0.82	0.537	4.52	**<0.001**
Autumn 2023	1.37	0.138	2.11	**0.010**

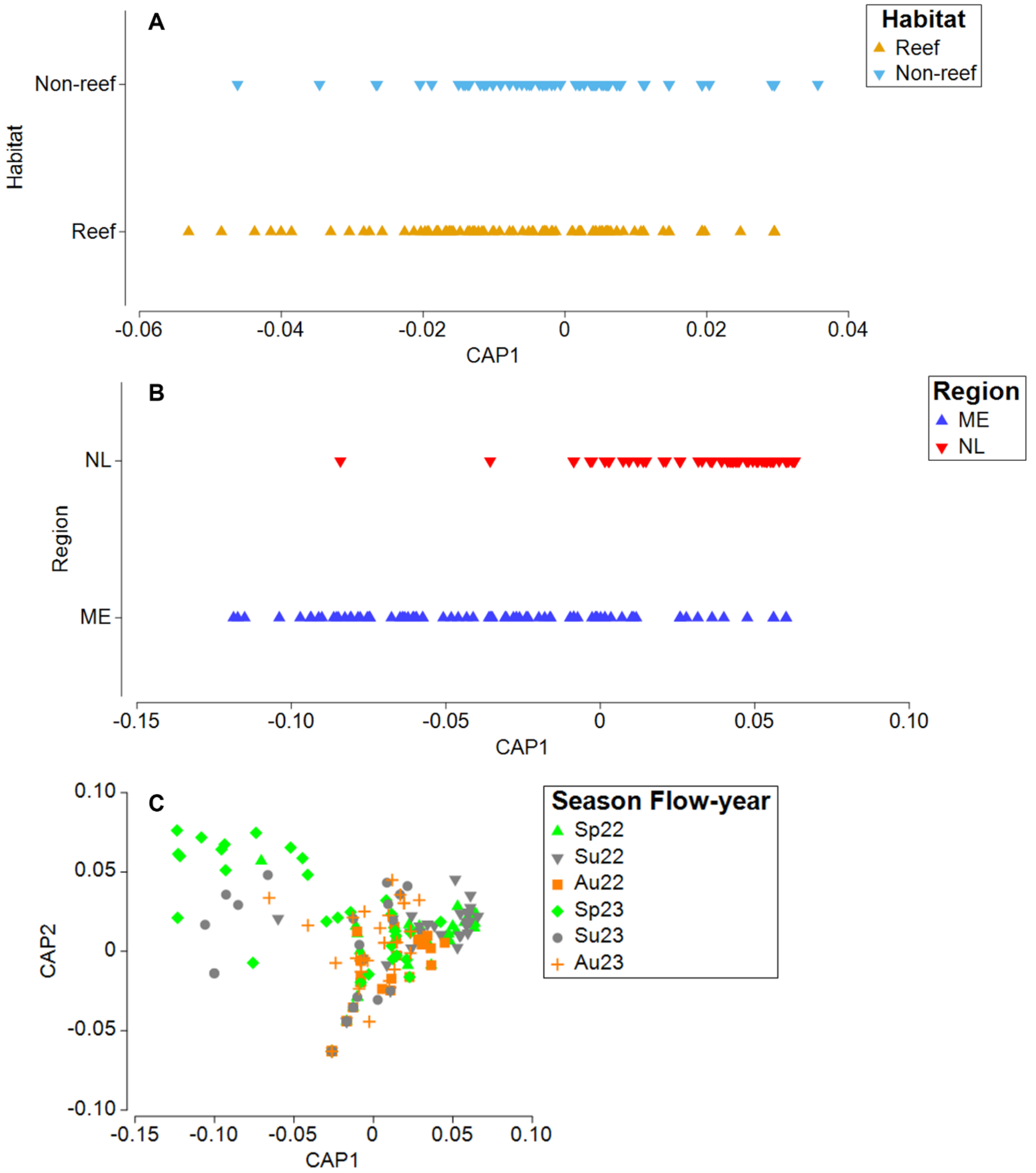

Figure 5.4. CAP (Canonical analysis of principal coordinates) constrained ordination plot of the demersal macroinvertebrate community showing the separation of groups by **A)** habitat (reef and non-reef) (m= 4 axes, 57.29% allocation success rate) **B)** region (Murray Estuary (ME) and North Lagoon (NL)) (m=4 axes, 79.69% allocation success rate) and **C)** season (spring (sp), summer (su), autumn (au) in flow years 2022 and 2023 (m=4, 40.10% allocation success rate).

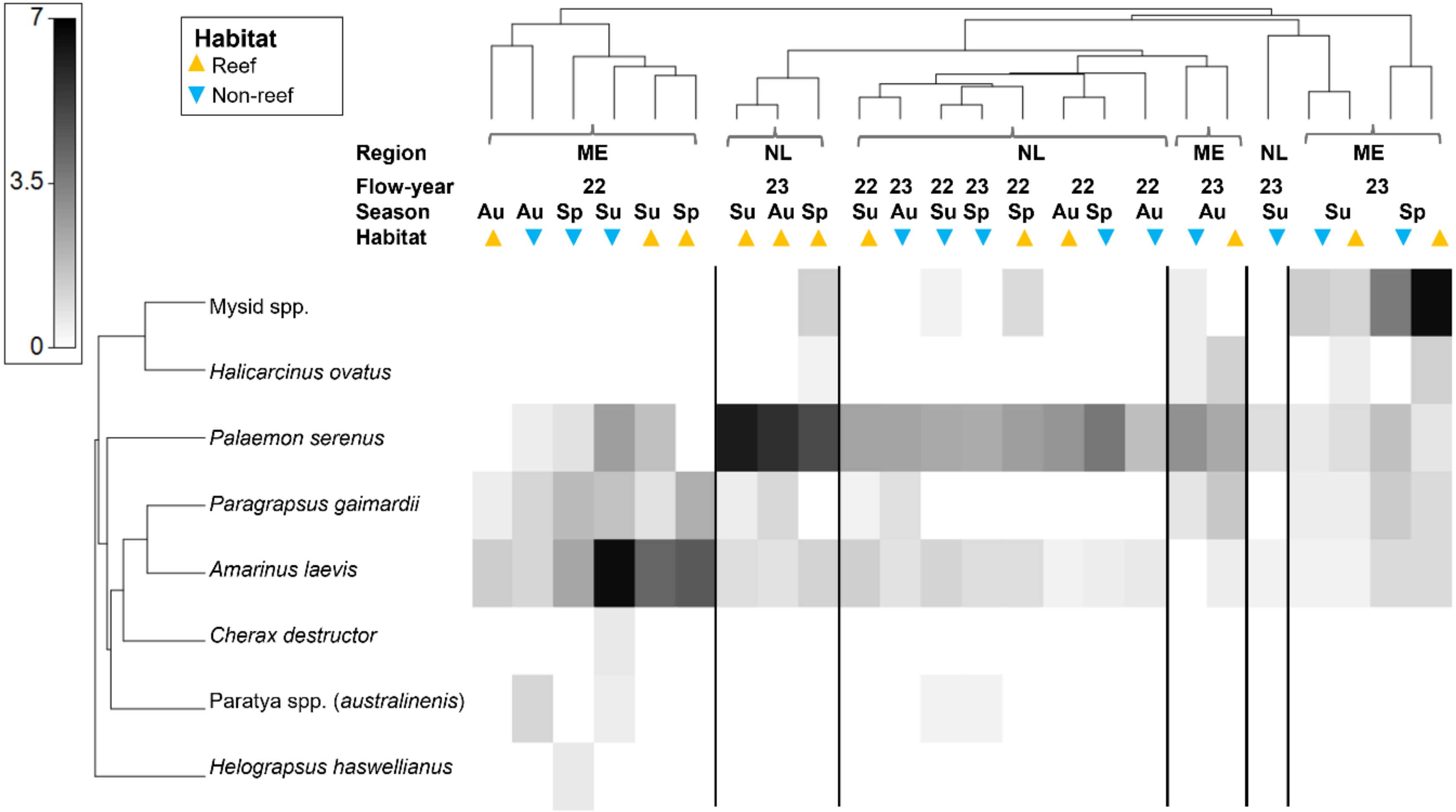

Figure 5.5. Shade plot showing the average CPUE (individuals net^{-1} night^{-1}, square root transformed), in reef and non-reef habitats in each the Murray Estuary (ME) and North Lagoon (NL) during spring, summer and autumn surveys in 2022 and 2023. White squares indicate absence, and black squares indicate high abundance. Sample dendrogram shows clustering of samples by habitat, region and season by CLUSTER analysis. Variable dendrogram shows groupings of species by the index of association.

Table 5.5. SIMPER results showing the demersal macroinvertebrate species contributing to significant differences in the community between reef and non-reef habitats sampled in **A)** the Murray Estuary during spring 2022, summer 2022, autumn 2022 and spring 2023 and **B)** the North Lagoon during summer 2023 and autumn 2023. Values shown are the relative abundances of the species and their cumulative contributions. Highest abundances of taxa in the comparison are underlined.

Species	Reef	Non-reef	Diss/SD	Cum. Contrib. %
A) Murray Estuary				
Spring 2022	**Average dissimilarity= 34.15%**			
Amarinus laevis	4.31	2.3	1.57	59.36
Paragrapsus gaimardii	2.02	1.64	1.24	88.21
Summer 2022	**Average dissimilarity= 32.47%**			
Amarinus laevis	4.1	6.53	1.73	45.82
Paragrapsus gaimardii	0.39	1.56	1.55	70.1
Autumn 2022	**Average dissimilarity= 71.75%**			
Amarinus laevis	1.05	0.96	0.95	38.1
Paratya cf *australiensis*	0	0.95	1.49	66.36
Paragrapsus gaimardii	0.25	0.95	1.32	93.32
Spring 2023	**Average dissimilarity= 67.78%**			
Mysida indet.	5.58	1.78	1.84	54.83
Palaemon serenus	0.43	1.51	1.28	69.95
Paragrapsus gaimardii	0.71	1.15	1.15	80.73
B) North Lagoon				
Summer 2023	**Average dissimilarity= 78.84%**			
Palaemon serenus	5.72	0.64	2.97	85.7
Autumn 2023	**Average dissimilarity= 48.80%**			
Palaemon serenus	5.16	1.95	1.43	74.44

5.3.2.4 The effect of environmental conditions on the community

The five water quality variables included in the DISTLM analysis (salinity, water temperature, water transparency and total monthly flow) accounted for 21.3% of the total variation in the demersal macroinvertebrate community and 85.2% of the fitted variation in the dbRDA axes 1 and 2 (Figure 5.6). Salinity, dissolved oxygen, temperature, and total monthly flow were identified in the best solution as variables that could most strongly predict variation in the demersal macroinvertebrate community, but the strength of these correlations was low (AIC=1364.6, R^2=0.249, Table 5.6). Salinity could best explain variation in the communities along the first dbRDA axis which split the communities by region (Figure 5.6A, Table 5.6). Spring, summer, and autumn surveys in the Murray Estuary during 2022 were characterised by low salinities and high total monthly flow, which corresponded to abundances of freshwater and estuarine crustaceans (*P. australiensis*, *A. laevis* and *P. gaimardii*) (Figure 5.6A and B). Dissolved oxygen was a secondary key environmental driver explaining seasonal variation in both the Murray Estuary and North Lagoon communities (Table 5.6, Figure 5.6A).

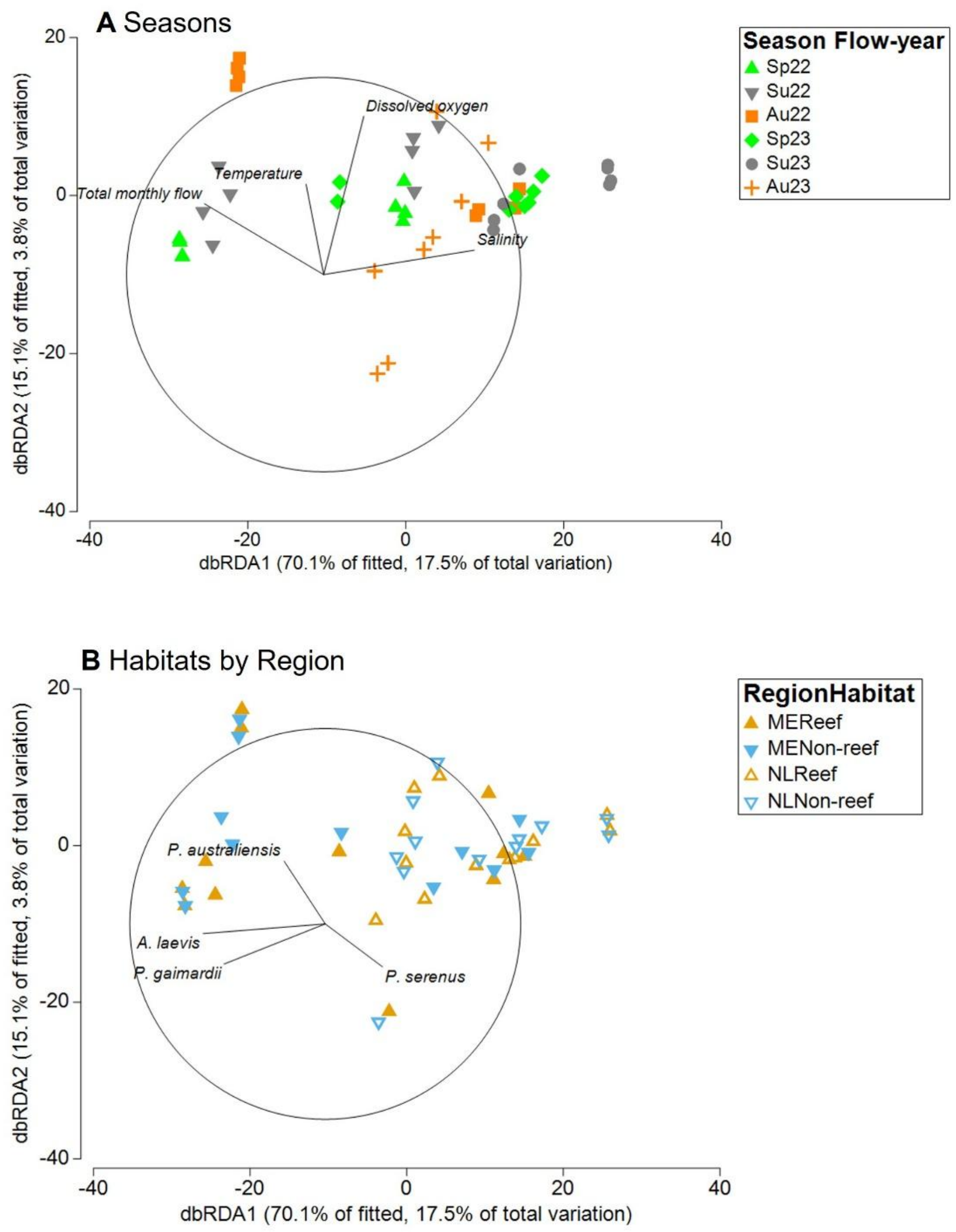

Figure 5.6. Distance based redundancy analysis (dbRDA) ordination of the fitted model of the demersal macroinvertebrate community with the environmental conditions across **A)** Seasons and **B)** Habitats by Region. The vector overlay in A) indicated multiple correlations between the environmental conditions with dbRDA1 and dbRDA2 axes. The vector overlay in B) shows Pearson correlations ≥0.5 for taxa and the community.

Table 5.6. DistLM analysis sequential test results for the best solution of environmental conditions which explained spatial and temporal variation in the demersal macroinvertebrate community, and their Pearson correlation values with the first two dbRDA axes. Significant values ($p<0.05$) are indicated in bold, and the variable with the strongest correlation with each axis shown in bold.

Variable	Pseudo-F	p	Cumulative R^2	Residual df	dbRDA1	dbRDA2
Salinity	38.25	**<0.001**	0.17	190	**0.764**	0.124
Dissolved oxygen	8.29	**<0.001**	0.20	189	0.204	**0.803**
Temperature	6.55	**<0.001**	0.23	188	-0.089	0.458
Total monthly flow	4.98	**0.002**	0.25	187	-0.605	0.359

5.3.3 Benthic macroinvertebrates

5.3.3.1 Catch summary

A total of 22 benthic macroinvertebrate taxa were found across the three substrate types (reef matrix, reef sediment and non-reef sediment) (Table 5.7). In 2023, amphipods and chironomid larvae were the two most abundant benthic taxa in the ME, whereas amphipods and polychaete *Simplisetia aequisetis,* were the two most abundant benthic taxa in the NL (Table 5.7). The average density of amphipods was highest in the reef matrix, intermediate in the reef sediment and lowest in the non-reef sediment, in both the ME and NL during 2023 (Table 5.7). The decapod species *A. laevis* and juvenile Hymenosomatidae indet. were only recorded in the ME reef matrix substrate (Table 5.7). The average carapace width of *A. laevis* and juvenile Hymenosomatidae indet. were 4.3 ± 1.1 mm and 1.0 ± 0.1 mm respectively (Appendix D Table S5). In the NL (2023), the average densities of *S. aequisetis* occurred in the reef matrix compared to the reef sediment and non-reef sediment (Table 5.7). Bivalves were absent from the ME, but present in the NL, with the highest average abundance of *Hiatula alba* (<5mm) occurring in the reef sediment during spring and summer (2023) (Table 5.7).

Table 5.7. Average densities (individuals 88.32 cm^2) (± s.e.) of benthic macroinvertebrates in reef and non-reef habitats, in the Murray Estuary (ME) and North Lagoon (NL) of the Coorong sampled in 2023.

	ME						**NL**					
	ME Reef matrix		**ME Reef sediment**		**ME Non-reef sediment**		**NL Reef matrix**		**NL Reef sediment**		**NL Non-reef sediment**	
Benthic taxa	**Sp**	**Su**	**Sp**	**Su**	**Sp**	**Su**	**Sp**	**Su**	**Sp**	**Su**	**Sp**	**Su**
Amphipoda indet.	4733.7 ± 683.2	8361.2 ± 1687.5	705.8 ± 97.1	1022.5 ± 124.2	431.6 ± 74.1	493.4 ± 86.0	1097.7 ± 140.7	962.4 ± 48.8	614.8 ± 48.9	591.0 ± 45.3	349.8 ± 79.7	404.9 ± 68
Mysida indet.	0.0	0.0	0.6 ± 0.3	0.1 ± 0.1	0.0	0.6 ± 0.3	0.0	0.0	0.0	0.1 ± 0.1	0.9 ± 0.3	0.0
Janiridae indet.	0.0	0.0	0.0	0.0	0.0	0.0	17.5 ± 5.5	4.2 ± 1.4	0.0	0.0	0.0	0.0
Ostracoda indet.	0.5 ± 0.5	0.5 ± 0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amarinus laevis	4.2 ± 1.4	5.3 ± 2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Halicarcinus ovatus	0.5 ± 0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hymenosomatidae indet.	0.0	9 ± 5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paragrapsus gaimardii	0.5 ± 0.5	6.4 ± 3.2	0.0	0.0	0.0	0.0	0.0	0.5 ± 0.5	0.0	0.0	0.0	0.0
Helograpsus haswellianus	0.5 ± 0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae indet. larvae	147.0 ± 30.1	534.3 ± 78.6	276.1 ± 33.2	287.5 ± 35.0	392.6 ± 93.5	292.9 ± 45.5	1.1 ± 0.7	1.6 ± 1.1	0.9 ± 0.4	0.3 ± 0.2	1.9 ± 0.6	3.8 ± 1.1
Dolichopodidae indet.larvae	0.0	1.1 ± 1.1	0.1 ± 0.1	0.0	0.1 ± 0.1	0.1 ± 0.1	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae indet. larvae	1.1 ± 1.1	0.5 ± 0.5	0.0	0.0	2.6 ± 2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae indet. larvae	0.0	0.0	0.0	0.0	0.0	0.1 ± 0.1	0.0	0.0	0.0	0.0	0.0	0.0
Stratiomyidae indet. larvae	0.0	0.0	0.0	0.0	0.0	0.1 ± 0.1	0.0	0.0	0.0	0.0	0.0	0.0

Table 5.7. cont.

	ME						NL					
	ME Reef matrix		ME Reef sediment		ME Non-reef sediment		NL Reef matrix		NL Reef sediment		NL Non-reef sediment	
Benthic taxa	**Sp**	**Su**	**Sp**	**Su**	**Sp**	**Su**	**Sp**	**Su**	**Sp**	**Su**	**Sp**	**Su**
Simplisetia aequisetis	5.3 ± 1.3	6.9 ± 2.4	1.4 ± 0.4	1.6 ± 0.8	0.3 ± 0.2	0.4 ± 0.3	131.6 ± 18.4	179.3 ± 27.8	48.6 ± 8.1	50.3 ± 5.8	71.1 ± 9	50.8 ± 5.2
Aglaophamus australiensis	0.0	0.0	0.0	0.0	0.1 ± 0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Australonereis ehlersi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3 ± 0.3	0.1 ± 0.1	0.0	0.0
Boccardiella limnicola	110.4 ± 33.2	36.1 ± 7.4	18.1 ± 8.9	17.6 ± 5.4	20.0 ± 5.8	10.3 ± 3.1	2.1 ± 2.1	0.0	0.0	0.1 ± 0.1	0.0	0.0
Capitellidae indet.	1.6 ± 1.1	2.1 ± 1.4	0.0	0.0	0.3 ± 0.2	0.3 ± 0.3	2.7 ± 1.1	0.0	0.0	4.3 ± 1.8	1.8 ± 0.7	0.1 ± 0.1
Oligochaeta indet.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8 ± 0.8	0.0
Arthritica semen	0.0	0.0	0.0	0.0	0.0	0.0	15.4 ± 5.7	11.1 ± 4.2	13.6 ± 8.8	10.6 ± 2.3	0.9 ± 0.6	1.6 ± 0.5
Hiatula alba (>5mm)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1 ± 1.1	2.4 ± 1.1	6.0 ± 1.6	3.3 ± 0.7	6.0 ± 1.0
Hiatula alba (<5mm)	0.0	0.0	0.0	0.0	0.0	0.0	30.8 ± 6.7	10.1 ± 5.4	63.8 ± 9.3	104.9 ± 12.3	2.5 ± 0.8	5.6 ± 1.4
Spisula trigonella (>5mm)	0.0	0.0	0.0	0.0	0.0	0.0	0.5 ± 0.5	0.5 ± 0.5	2.6 ± 0.8	1.6 ± 0.6	0.1 ± 0.1	0.8 ± 0.4
Spisula trigonella (<5mm)	0.0	0.0	0.0	0.0	0.0	0.0	0.5 ± 0.5	0.0	0.1 ± 0.1	0.0	0.0	0.0
Truncatelloidea indet.	2.1 ± 2.1	13.8 ± 6.3	0.1 ± 0.1	0.5 ± 0.2	29.6 ± 27.4	2.8 ± 1.2	8.0 ± 3.4	1.6 ± 0.8	3.0 ± 1.7	4.0 ± 1.8	1.1 ± 0.9	0.4 ± 0.3
Salinator fragilis	0.0	0.0	0.0	0.0	0.0	0.0	0.5 ± 0.5	0.0	0.0	0.0	0.1 ± 0.1	0.0

5.3.3.2 Total abundance, species richness and diversity

Total abundance of benthic macroinvertebrates differed significantly between substrates, regions and seasons sampled (PERMANOVA $p<0.05$, Figure 5.7, Table 5.8A). The total abundance of benthic macroinvertebrates was highest in the reef matrix, intermediate in the reef sediment and lowest in the non-reef sediment (Figure 5.7). This pattern between substrates of the reef matrix, reef sediment and non-reef sediment was independent of time, as indicated by a non-significant interaction effect between substrates and seasons (Table 5.8A). Pairwise tests were only non-significant in the ME during spring (2023) when the total abundance between the reef and non-reef sediments was not significantly different (Figure 5.7A). In the NL, pairwise tests between each habitat were all significantly different in both spring and summer (2023) (Figure 5.7B).

For both regions combined, the species richness was highest in the reef matrix (19 taxa), intermediate in the non-reef sediments (17 taxa) and lowest in the reef sediments (12 taxa). Species richness and diversity indices H’ and J’ were different between substrates in the ME versus NL, as indicated by an interaction effect between substrates and regions, but there were no seasonal differences between spring and summer surveys (Table 5.8B–D, Table 5.9). In the ME, species richness was significantly greater in the reef matrix (14 taxa) versus reef sediment (7 taxa) and non-reef sediment (12 taxa) (PERMANOVA $p<0.05$, Table 5.8B, Table 5.9A Appendix D Figure S2A). In contrast, the indices of diversity H’ and evenness J’ were significantly lower in the reef matrix, intermediate in the reef sediment and highest in the non-reef sediment (Table 5.8B–C, Table 5.9A, Appendix D Figure S2B and C). In the NL, all three substrate types had a similar species richness and evenness J’ (Table 5.8B, Table 5.9B). H’ diversity was similar between substrate comparisons except for the reef matrix and reef sediment due to a significantly greater H’ in the reef sediment (Table 5.8B, Table 5.9B, Appendix D Figure S2B).

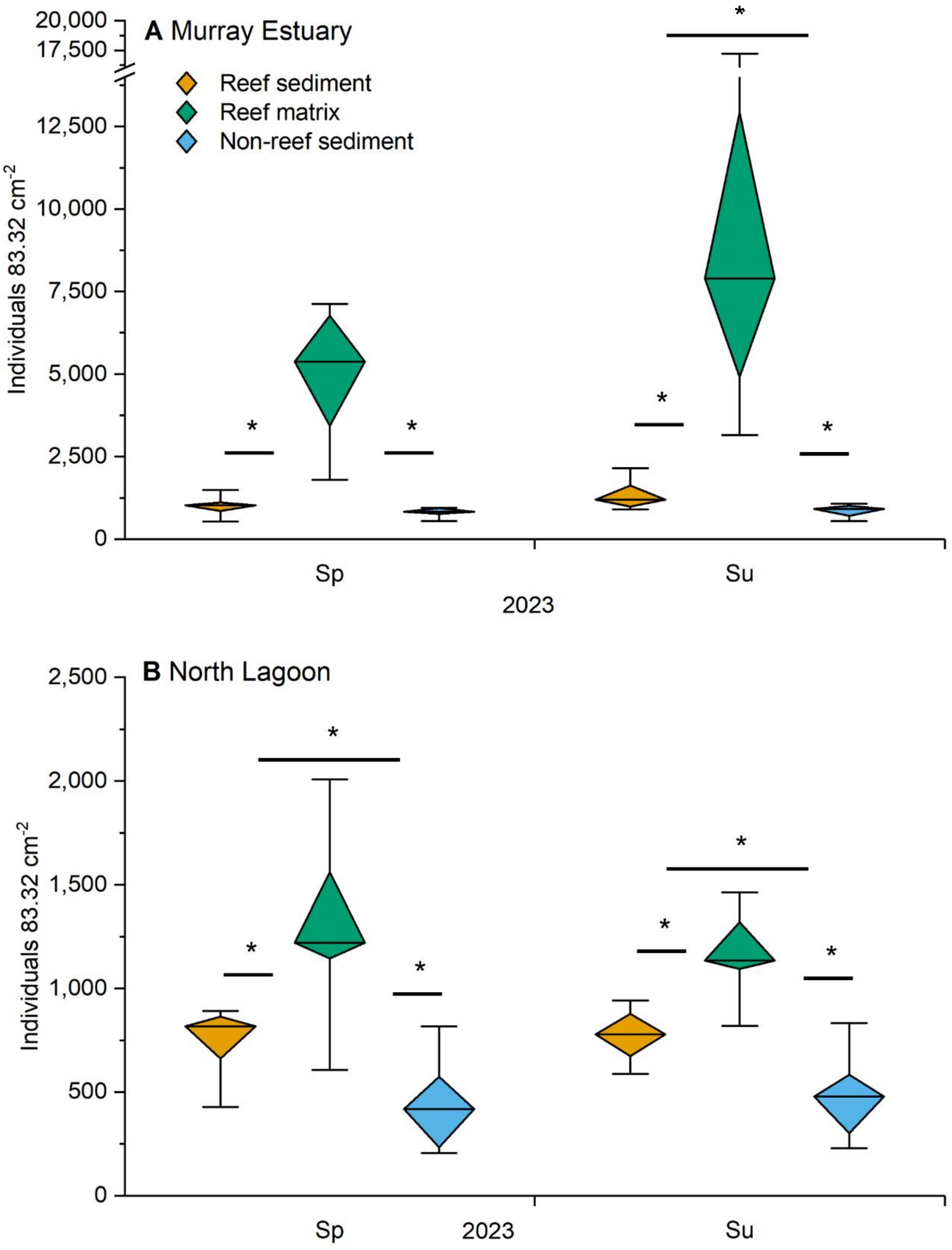

Figure 5.7. Box and whisker plots of total benthic macroinvertebrates (individuals 83.32 cm^{-2}) between substrates of reef sediment, reef matrix and non-reef sediment in the **A)** Murray Estuary and **B)** North Lagoon during spring (Sp) and summer (Su) in flow year 2023. Significant pairwise tests are indicated by *.

Table 5.8. Univariate PERMutational ANalysis Of VAriance (PERMANOVA) on **A)** total abundance (individuals 83.32 cm^{-2}) **B)** species richness (S) **C)** Shannon Diversity (H') and **D)** Pielou's Evenness (J') of benthic macroinvertebrates to test for differences between Substrates (reef matrix, reef sediment and non-reef sediment), Regions (Re) (Murray Estuary and North Lagoon) and Seasons (Se) (spring and summer in flow-year 2023). Significant values ($p<0.05$) are indicated in bold.

Source	df	MS	Pseudo-F	*P*	Df	MS	Pseudo-F	*p*
	A) Total abundance				**B) Species Richness (S)**			
Substrate (Su)	2	9947.40	103.27	**<0.001**	2	5.38	3.06	0.051
Region (Re)	1	9378.60	97.36	**<0.001**	1	28.17	16.01	**<0.001**
Season (Se)	1	408.18	4.24	**0.040**	1	0.042	0.02	0.852
Su × Re	2	3974.90	41.27	**<0.001**	2	16.17	9.19	**<0.001**
Su × Se	2	246.38	2.56	0.070	2	0.67	0.38	0.692
Re × Se	1	411.32	4.27	**0.040**	1	5.04	2.87	0.097
Su × Re × Se	2	386.57	4.01	**0.020**	2	4.54	2.58	0.081
Residual	84	96.33			84	1.76		
Total	95				95			
	C) Shannon Diversity (H')				**D) Pielou's Evenness (J')**			
Substrate (Su)	2	0.60	33.32	**<0.001**	2	0.32	42.79	**<0.001**
Region (Re)	1	0.13	7.45	**0.008**	1	0.02	2.29	0.129
Season (Se)	1	0.01	0.33	0.572	1	0.00	0.41	0.516
Su × Re	2	0.38	21.35	**<0.001**	2	0.27	36.27	**<0.001**
Su × Se	2	0.01	0.72	0.483	2	0.00	0.32	0.732
Re × Se	1	0.00	0.00	0.999	1	0.01	1.49	0.225
Su × Re × Se	2	0.06	3.15	0.052	2	0.01	0.79	0.456
Residual	84	0.02			84	0.01		
Total	95				95			

Table 5.9. Benthic macroinvertebrate species richness (S), Shannon Diversity (H’), and Pielou’s Evenness (J’) in **A)** the Murray Estuary and **B)** North Lagoon across Substrates (reef matrix, reef sediment and non-reef sediment) for combined spring and summer surveys in flow-year 2023.

Substrate by Region	**S**	**H’**	**J’**
A) Murray Estuary			
Reef matrix	14	0.29	0.11
Reef sediment	7	0.64	0.33
Non-reef sediment	12	0.86	0.35
B) North Lagoon			
Reef matrix	12	0.62	0.25
Reef sediment	11	0.75	0.31
Non-reef sediment	11	0.59	0.25

5.3.3.3 Abundance of major taxa groups

Overall, crustaceans had the highest total abundance of the major taxa groups (Figure 5.8). The average abundance of crustaceans differed significantly in abundance between the three substrate types (PERMANOVA $p<0.05$, Figure 5.8A, Appendix D Table S6A and Figure S3A). Insects were the second most dominant taxon but showed inconsistent patterns between substrate types in each season and region (Figure 5.8B, Appendix D Table S6B and Figure S3B). The abundances of annelids (Figure 5.8C) were significantly greater in the reef matrix in comparison to the reef and non-reef sediments (PERMANOVA $p<0.05$, Appendix D Table S6C and Figure S3C), but similar between the reef and non-reef sediment on all occasions (Figure 5.8C and Appendix D Figure S3C). Gastropods occurred in low abundance (Figure 5.8). Pairwise tests indicated gastropod abundances were highest in the reef matrix (ME summer and NL spring 2023) (Figure 5.8D, Appendix D Table S6D and Figure S3D). Bivalves were recorded only from the North Lagoon (Figure 5.8E), where their abundances were significantly higher in the reef sediment, intermediate in the reef matrix and lowest in the non-reef sediment during spring (PEMRANOVA $p<0.05$, Appendix D Table S6E and Figure S3E). During summer, bivalve abundances were again significantly higher in the reef sediment (PERMANOVA $p<0.05$) but similar between the reef matrix and non-reef sediment (Figure 5.8E and Appendix D Figure S3E).

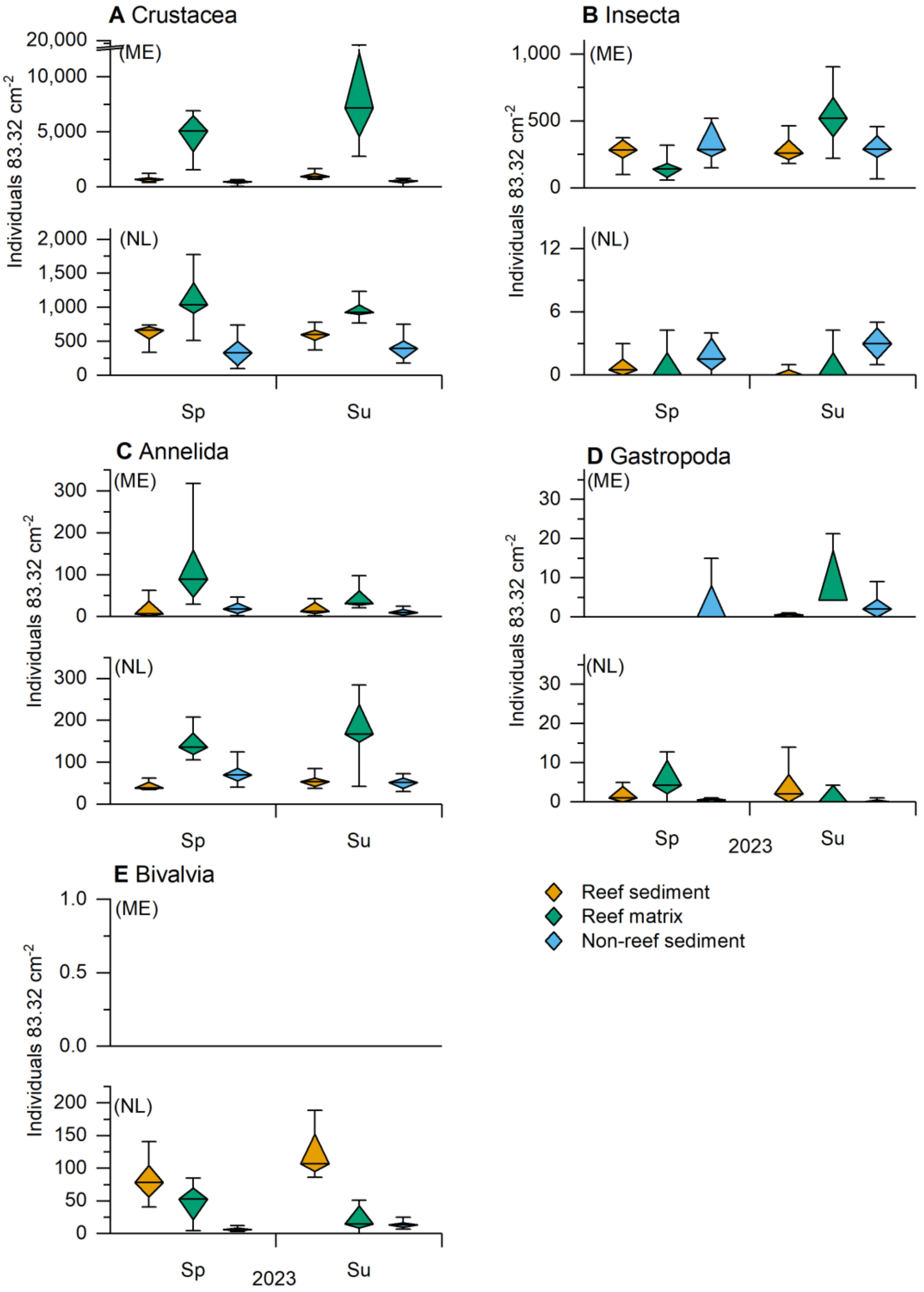

Figure 5.8. Box and whisker plots of benthic macroinvertebrates (individuals 83.32cm^{-2}) by taxonomy group between substrates of reef sediment, reef matrix and non-reef sediment in the Murray Estuary and North Lagoon during spring (Sp) and summer (Su) in flow year 2023. Groups include **A)** Crustacea, **B)** Insecta, **C)** Annelida, **D)** Gastropoda and **E)** Bivalvia.

5.3.3.4 Total biomass

Total biomass of benthic macroinvertebrates did not differ across seasons (PERMANOVA $p>0.05$), but there was a significant interaction effect between substrates and regions (PERMANOVA $p<0.05$, Table 5.10, Figure 5.9A). The total biomass in the ME was significantly greater in the reef matrix compared to the reef sediment and non-reef sediment, with no difference between the reef and non-reef sediments (Table 5.10B, Figure 5.9A). In the NL, total biomass was significantly different between all three substrates, and highest in the reef matrix followed by the reef sediment and non-reef sediment (Table 5.10B, Figure 5.7A).

In the reef matrix from the ME, Amphipoda indet. and *A. laevis* were the two main taxa that contributed the greatest proportion to the total biomass (Figure 5.9B). In the reef and non-reef sediments of the ME, Amphipoda indet. also contributed to the greatest proportion of the biomass followed by Chironomidae (Figure 5.9B). In the reef matrix from the NL, Amphipoda indet. and the polychaete, *S. aequisetis* contributed the greatest proportion to the total biomass, whereas the polychaete *Australonereis ehlersi* and the bivalve species *S. trigonella* and *H. alba* contributed mostly to the total biomass in the reef and non-reef sediments of the NL (Figure 5.9B).

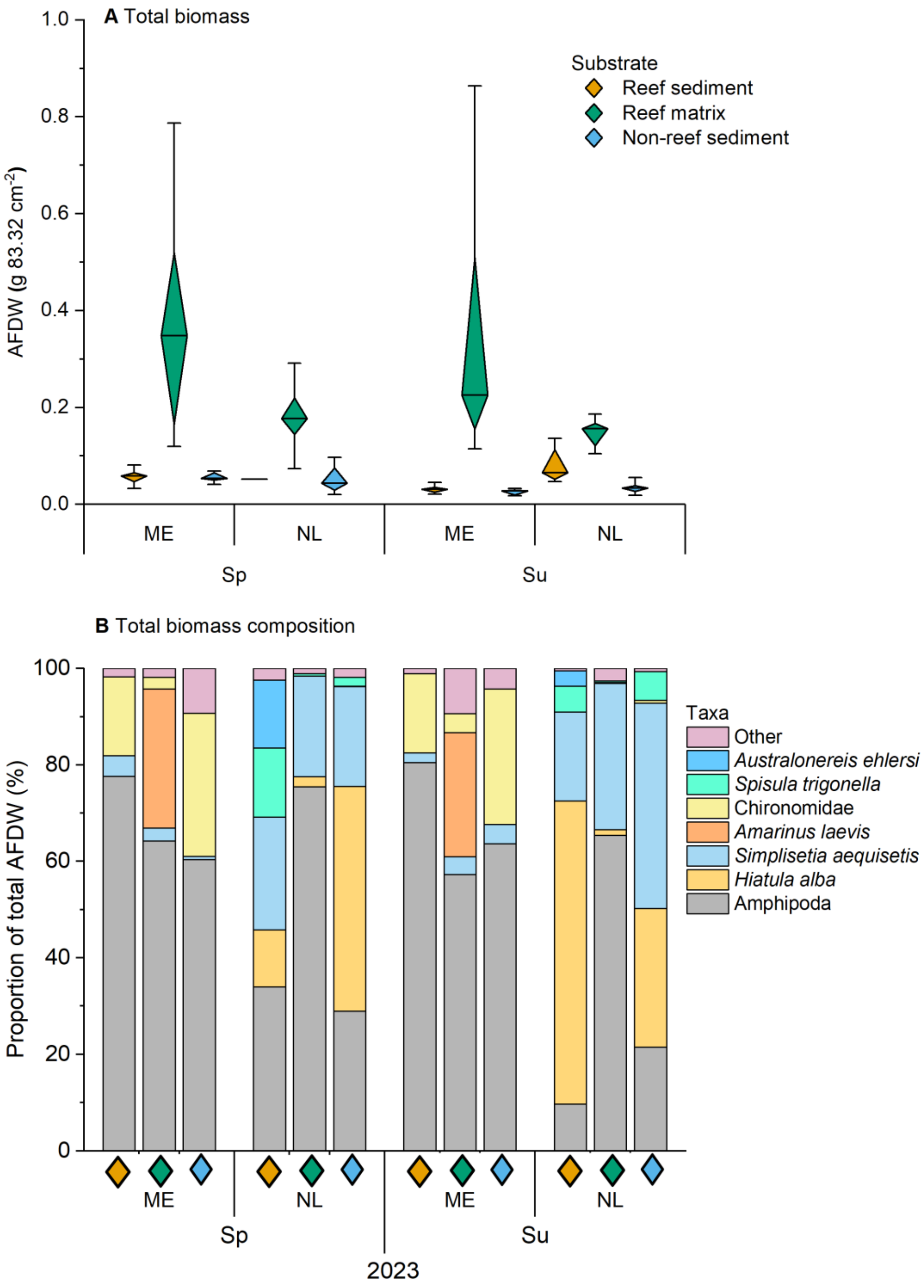

Figure 5.9. A) Box and whisker plots of the median total biomass of benthic macroinvertebrates in ash-free dry weight (AFDW g 83.32 cm^{-2}) between substrates of reef sediment, reef matrix and non-reef sediment in the Murray Estuary (ME) and North Lagoon (NL) during spring (Sp) and summer (Su) surveys in flow year 2023. **B)** Contribution of the main taxa to total biomass (proportion in % of total AFDW).

Table 5.10. Univariate PERMmutational ANalysis Of VAriance (PERMANOVA) **A)** main test results and **B)** pairwise test results on differences in the total biomass of benthic macroinvertebrates between Substrates (Su) (reef sediment, reef matrix and non-reef sediment), Regions (Re) (Murray Estuary and North Lagoon) and Seasons (Se) (spring and summer in flow year 2023). Significant values ($p<0.05$) are indicated in bold.

A) Total biomass (AFDW g 83.32 cm^{-2})				
	df	MS	Pseudo-F	*p*
Substrate (Su)	2	0.47	37.19	**<0.001**
Region (Re)	1	0.06	4.76	**0.029**
Season (Se)	1	<0.01	0.25	0.631
Su × Re	2	0.13	10.18	**<0.001**
Su × Se	2	<0.01	0.50	0.631
Re × Se	1	<0.01	0.54	0.482
Su × Re × Se	2	<0.01	0.44	0.654
Res	84	0.01		
Total	95			

B) Pairwise test		
Region (Substrate)	t	*p*
Murray Estuary		
Reef matrix vs reef sediment	5.01	**<0.001**
Reef matrix vs non-reef sediment	5.08	**<0.001**
Reef sediment vs non-reef sediment	1.08	0.293
North Lagoon		
Reef matrix vs reef sediment	2.90	**0.004**
Reef matrix vs non-reef sediment	8.69	**<0.001**
Reef sediment vs non-reef sediment	1.75	**<0.001**

5.3.3.5 Community structure

There was significant variation in the benthic macroinvertebrate community between substrates, regions, and seasons (PERMANOVA $p<0.05$, Figure 5.10, Table 5.11). The communities varied by region between the Murray Estuary and the North Lagoon (PERMANOVA $p<0.05$, Table 5.11A, Figure 5.10A). There was a greater distinction between the communities of the reef matrix compared with the reef sediment and non-reef sediment in the Murray Estuary compared to the North Lagoon (Figure 5.10B). There was no seasonal difference between the spring and summer communities in each of the regions (PERMANOVA $p>0.05$, Table 5.11A, Figure 5.10C).

In the Murray Estuary, the community structure in the reef matrix differed significantly to both the reef sediment and non-reef sediment (Table 5.11B). The community structure of the reef matrix was characterised by higher abundances of amphipods, *Boccardiella limnicola*, Truncatelloidea spp., *S. aequisetis* and *A. laevis* (Table 5.12A, Figure 5.11). In the reef sediment, amphipod, *B. limnicola*, and *S. aequisetis* were more abundant compared to the non-reef sediment (Table 5.12A, Figure 5.11). Pairwise tests showed that the reef sediment and non-reef sediment communities were significantly different in spring but not in summer (Table 5.11B).

In the North Lagoon, the community structure varied between the three substrate types, regardless of season sampled (Table 5.11B, Figure 5.10). The reef matrix had lower abundances of the bivalve species *H. alba* and *S. trigonella* but higher abundances of Janiridae spp. and *S. aequisetis* compared to the reef sediment (Table 5.12B, Figure 5.11). The dissimilarity between the reef matrix and non-reef sediment community reflected higher abundances of Amphipoda, *Arthritica semen*, Janiridae spp. and Truncatelloidea spp. (Table 5.12B). The communities of the reef and non-reef sediments were also different (Table 5.11B) with higher abundances of all three bivalve species (*H. alba, A. semen, S. trigonella*) in the reef sediments and higher abundances of *Chironomidae* in the non-reef sediments (Table 5.12B).

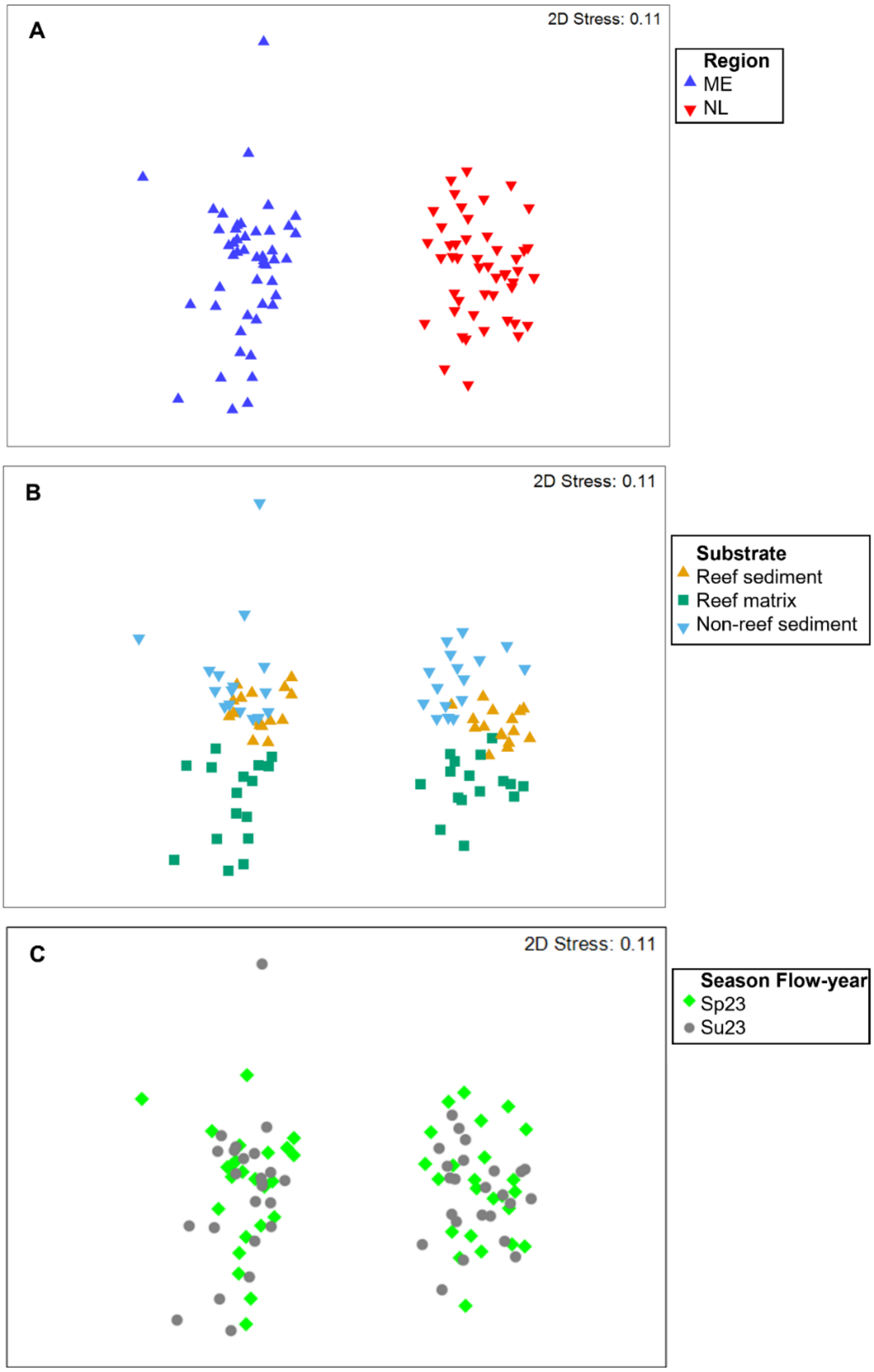

Figure 5.10. Non-metric multidimensional scaling (MDS) plots comparing the benthic macroinvertebrate communities between **A)** region (Murray Estuary (ME) and North Lagoon (NL)) **B)** substrates (reef sediment, reef matrix and non-reef sediment), and **C)** season flow-year (spring (sp) and summer (su) in 2023).

Table 5.11. Multivariate PERMmutational ANalysis Of VAriance (PERMANOVA) **A)** main test results and **B)** pairwise test results on differences in the benthic macroinvertebrate community structure between Substrates (Su) (reef sediment, reef matrix and non-reef sediment), Regions (Re) (Murray Estuary and North Lagoon) and Seasons (Se) (spring and summer in flow year 2023). Significant values (p<0.05) are indicated in bold.

A) Benthic macroinvertebrate community				
	Df	MS	Pseudo-F	*p*
Substrate (Su)	2	4919.10	25.77	**<0.001**
Region (Re)	1	49993.00	261.86	**<0.001**
Season (Se)	1	67.44	0.35	0.797
Su × Re	2	2254.40	11.81	**<0.001**
Su × Se	2	241.90	1.27	0.258
Re × Se	1	781.51	4.09	**0.017**
Su × Re × Se	2	850.12	4.45	**0.003**
Residual	84	190.91		
Total	95			

B) Pairwise test	Spring 2023		Summer 2023	
Region (Substrate)	T	*p*	T	*p*
Murray Estuary				
Reef matrix vs reef sediment	3.94	**<0.001**	4.15	**<0.001**
Reef matrix vs non-reef sediment	3.68	**<0.001**	3.42	**<0.001**
Reef sediment vs non-reef sediment	1.73	**0.013**	1.47	0.072
North Lagoon				
Reef matrix vs reef sediment	2.73	**<0.001**	3.92	**<0.001**
Reef matrix vs non-reef sediment	2.99	**<0.001**	3.82	**<0.001**
Reef sediment vs non-reef sediment	3.45	**<0.001**	4.08	**<0.001**

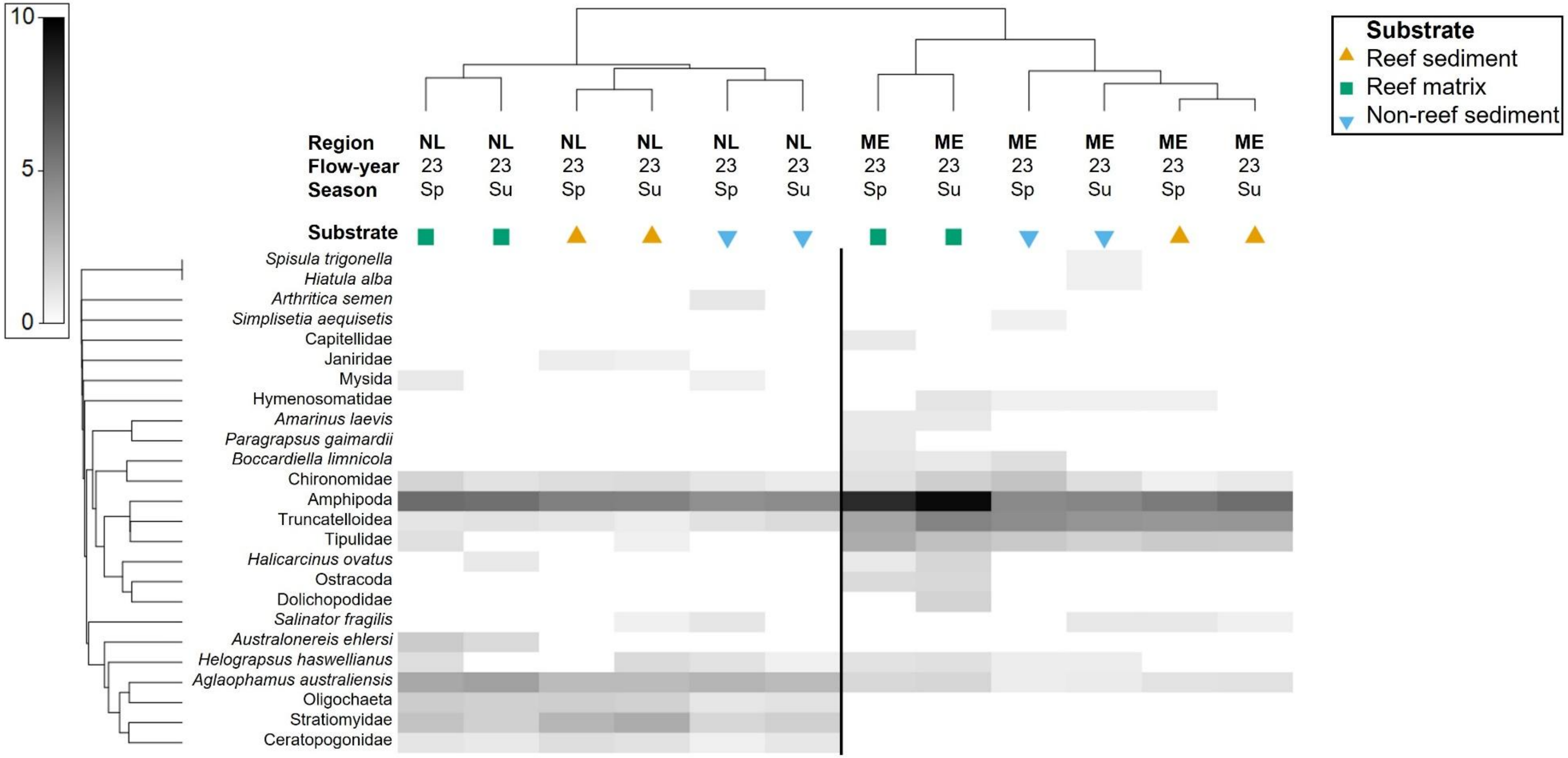

Figure 5.11. Shade plot showing the average density of benthic macroinvertebrates (individuals 83.32 cm^{-2}, fourth root transformed) per substrate type (reef matrix or reef sediment or non-reef sediment) in spring (sp) and summer (su) surveys in the Murray Estuary (ME) and North Lagoon (NL) for flow year 2023. White squares indicate absence, and black indicates high abundance. Sample dendrogram shows clustering of samples by substrate, region and season based on CLUSTER analysis. Variable dendrogram shows groupings of species by the index of association.

Table 5.12. SIMPER results showing the benthic macroinvertebrate taxa contributing to differences in the community between Substrates (reef matrix, reef sediment and non-reef sediment) in **A)** the Murray Estuary and **B)** North Lagoon during combined surveys in spring and summer in flow-year 2023. Values shown are the relative abundances of the species and their cumulative contributions. Highest abundances of taxa in the comparison are underlined.

Species	Pairwise comparison		Diss/SD	Cum. Contrib. %
A) Murray Estuary				
	Reef matrix	**Reef sediment**		
	Average dissimilarity= 30.28%			
Amphipoda indet.	8.72	5.35	3.03	32.89
Boccardiella limnicola	2.73	1.68	1.2	44.9
Truncatelloidea	1	0.31	1.24	53.92
Amarinus laevis	0.94	0	1.11	62.59
Simplisetia aequisetis	1.23	0.8	1.36	71.11
	Reef matrix	**Non-reef sediment**		
	Average dissimilarity=36.21%			
Amphipoda indet.	8.72	4.43	3.25	35.65
Boccardiella limnicola	2.73	1.62	1.11	45.79
Simplisetia aequisetis	1.23	0.26	1.55	55.16
Truncatelloidea indet.	1	0.8	1.12	64.01
Amarinus laevis	0.94	0	1.11	71.33
	Reef sediment	**Non-reef sediment**		
	Average dissimilarity=20.56%			
Amphipoda indet.	5.35	4.43	1.02	19.78
Boccardiella limnicola	1.68	1.62	1.18	37.86
Truncatelloidea indet.	0.31	0.8	0.91	54.13
Simplisetia aequisetis	0.8	0.26	1.28	68.07
Chironomidae indet. larvae	4.05	4.18	1.15	78.69
B) North Lagoon				
	Reef matrix	**Reef sediment**		
	Average dissimilarity= 28.08%			
Hiatula alba	1.55	3.02	1.21	18.32
Janiridae indet.	1.21	0	1.24	31.51
Spisula Trigonella	0.27	1.05	1.76	42.57
Simplisetia aequisetis	3.45	2.62	2.03	52.64
Truncatelloidea indet.	0.91	0.89	1.24	62.67
	Reef matrix	**Non-reef sediment**		
	Average dissimilarity=32.86%			
Amphipoda indet.	5.63	4.28	1.83	15.27
Arthritica semen	1.54	0.61	1.46	28.22
Janiridae indet.	1.21	0	1.24	40.77
Hiatula alba	1.55	1.67	1.48	51.95
Chironomidae indet. larvae	0.38	1.12	1.64	62.65
	Reef sediment	**Non-reef sediment**		
	Average dissimilarity=26.86%			
Hiatula alba	3.02	1.67	3.46	18.34
Arthritica semen	1.62	0.61	1.45	33.38
Chironomidae indet. larvae	0.41	1.12	1.46	44.65
Spisula trigonella	1.05	0.33	1.5	55.88
Truncatelloidea indet.	0.89	0.36	1.22	66.94

5.3.3.6 The effect of macrophytes, feeding mode and environmental conditions on the community

Macrophytes were only present in the reef matrix substrate, and not in the reef sediment and non-reef sediment. In the Murray Estuary, filamentous green algae (Enteromorpha) were dominant, and the density of amphipods increased with macroalgal biomass (Figure 5.12A). In the North Lagoon, the red macroalgae Hypnea sp., was common in the reef matrix and in one sample, the seagrass *Ruppia tuberosa*. In the NL reef matrix, there was no relationship between the density of amphipods and macroalgal biomass (Figure 5.12B).

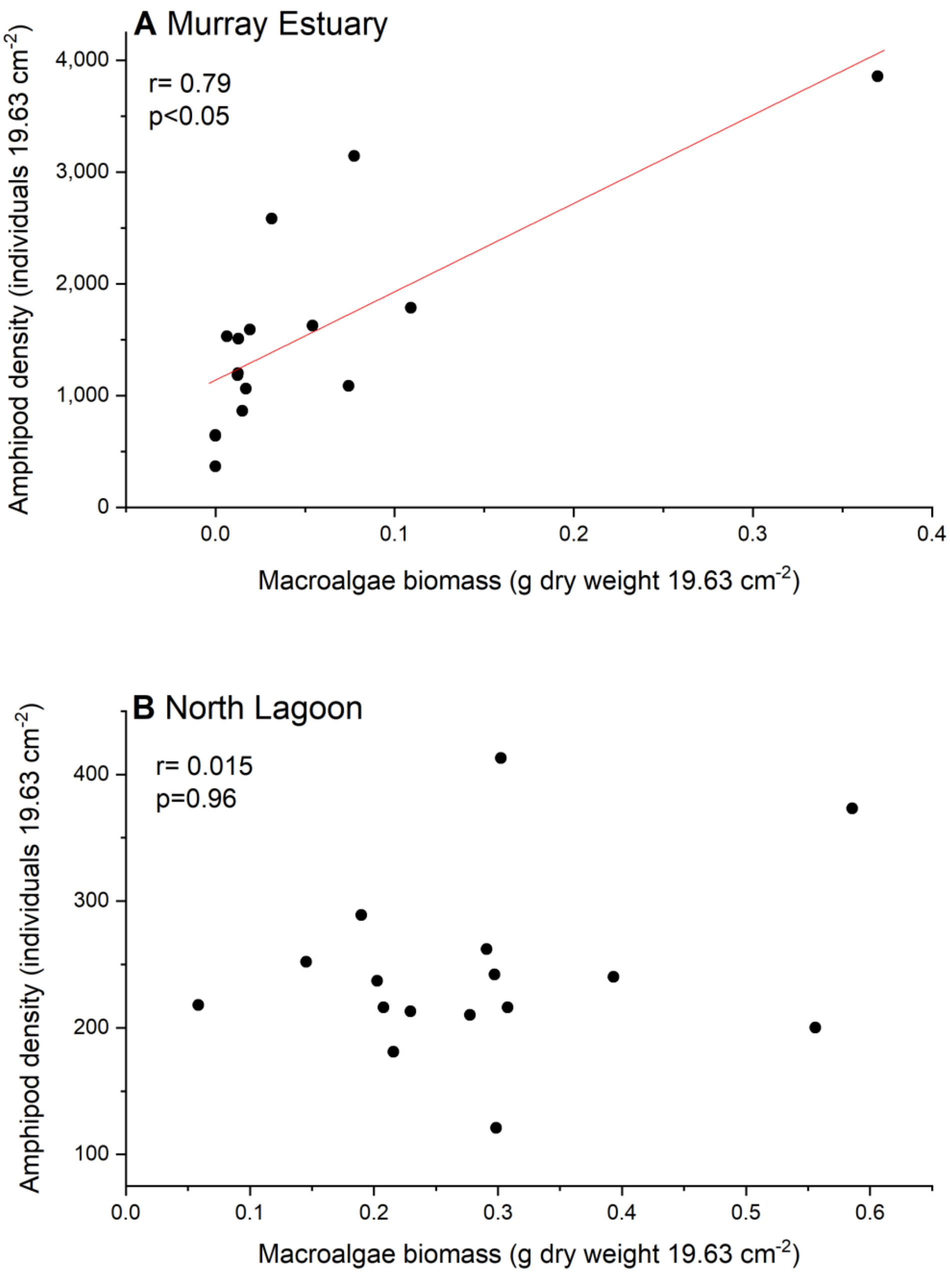

Figure 5.12. Scatter plot between macroalgae biomass and density of amphipods in the reef matrix from **A)** the Murray Estuary and **B)** North Lagoon. The Spearman correlation coefficient (r) and p value are shown.

In the reef matrix, the feeding modes most expressed based on community weighted means (CWM) were scavenger/opportunist, sub-surface deposit feeder and filter/suspension feeder (Figure 5.13). There were small and significant variations in CWM between the reef matrix compared to the reef and non-reef sediments for the feeding modes of filter feeder, predator, scavenger/opportunist and sub-surface filter feeder, which often varied with region and or season (Appendix D Table S7). The CWM of deposit feeder and predator were significantly greater in the NL compared to the ME (Figure 5.13, Appendix D Table S7).

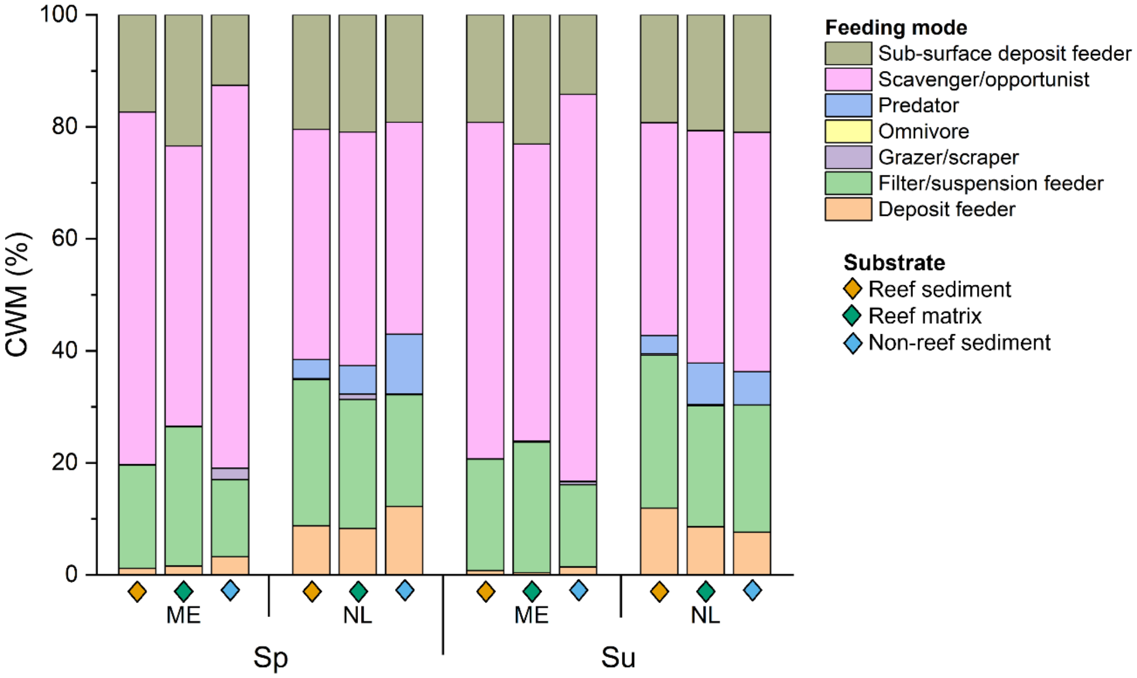

Figure 5.13. Community weighted mean (CWM) (%) of feeding mode expression. The percentage contribution of CWM is averaged by sampling regions, seasons and substrates. Seasons include spring (sp) and summer (su), and regions include the Murray Estuary (ME) and North Lagoon (NL).

The DISTLM analysis of four water quality variables (DO, water temperature, salinity, water transparency) and three sediment variables (AFDW %, median grain size, sorting coefficient) accounted for 73.2% of the total variation in the benthic macroinvertebrate community of the reef and non-reef sediments across regions (Figure 5.14A). In the first two dbRDA axes, 95.1% of the community variation was fitted, and there was strong separation between the two regions of the Murray Mouth and North Lagoon along dbRDA axis 1 (Figure 5.14A). Salinity, dissolved oxygen and sorting coefficient (σG) best explained variation in the community, and the strength of these correlations was high (AIC=137.4, R^2=0.77, Table 5.13).

In the Murray Estuary, the sorting coefficient (σG) significantly explained variation in the benthic macroinvertebrate community and positively correlated with variation in the non-reef sediments in contrast to reef sediments (Figure 5.14B, Table 5.13). The median grain size D50 (μm) weakly correlated with the non-reef sediment community (Figure 5.14B).

In the North Lagoon, the sorting coefficient (σG) and median grain size D50 (μm) significantly explained variation in the benthic macroinvertebrate community (Figure 5.14C, Table 5.13). The community variation in non-reef sediments was mainly explained by the sorting coefficient (σG) and median grain size D50 (μm). Organic matter partially explained the community variation in the reef sediments (Figure 5.14C).

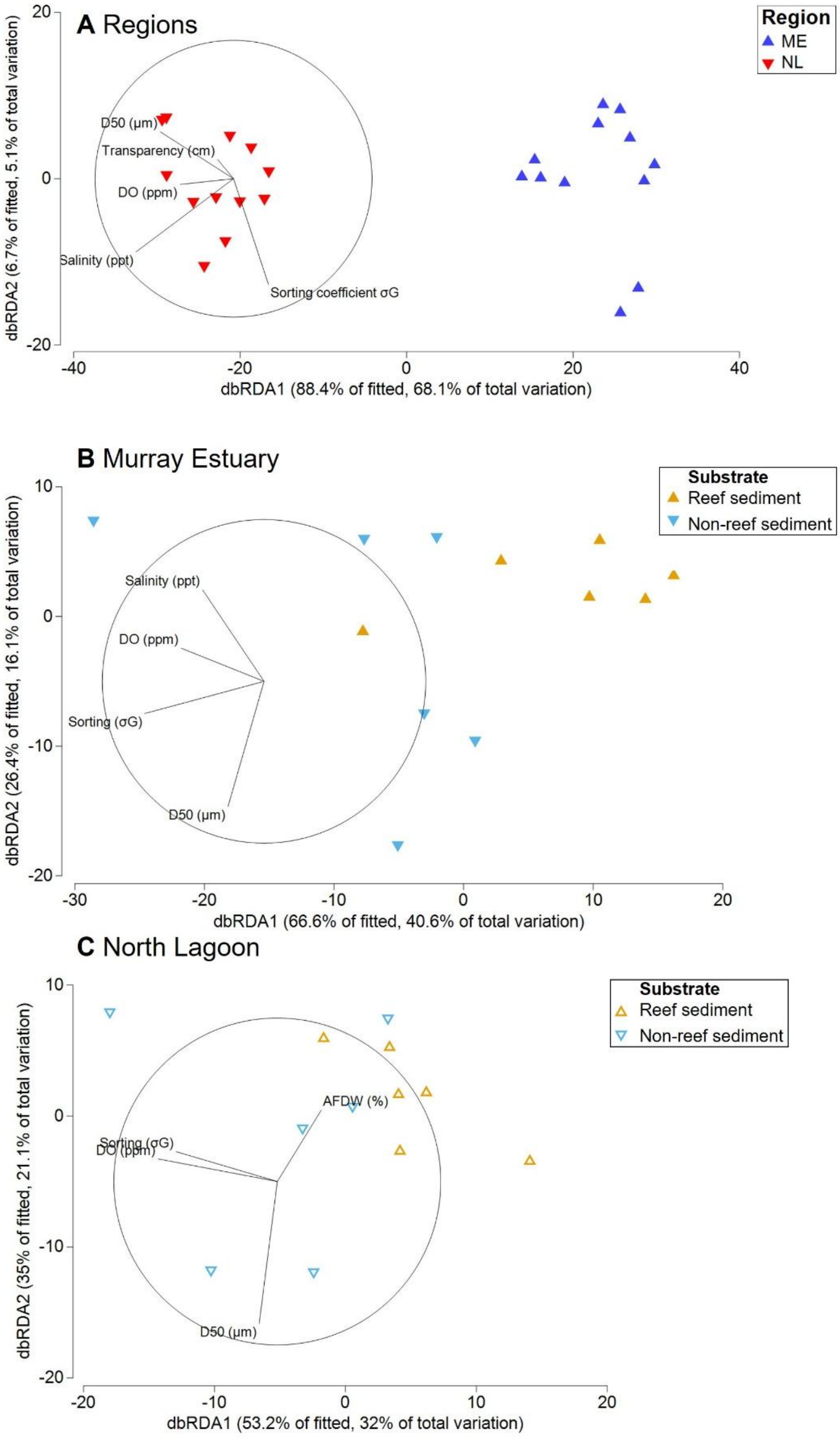

Figure 5.14. Distance based redundancy analysis (dbRDA) ordination of the fitted model of the benthic macroinvertebrate community with the environmental conditions across **A)** Regions **B)** Murray Estuary reef and non-reef substrates and **C)** North Lagoon reef and non-reef substrates. The vector overlays indicate multiple correlations between the environmental conditions (water quality and sediment conditions) with dbRDA1 and dbRDA2 axes.

Table 5.13. DistLM analysis sequential test results for the best solution of environmental conditions which explained spatial and temporal variation in the benthic macroinvertebrate community for **A)** both the Murray Estuary (ME) and North Lagoon (NL), **B)** the ME and **C)** the NL. Significant values ($p<0.05$) are indicated in bold, and the variable with the strongest correlation with each axis shown in bold.

Variable	Pseudo-F	p	Cumulative R^2	Residual df	dbRDA1	dbRDA2
A) ME and NL						
Salinity (ppt)	2.99	**0.037**	0.48	21	**-0.704**	-0.529
DO (ppm)	13.88	**<0.001**	0.69	20	-0.385	-0.041
Sorting coefficient (σG)	3.01	**0.026**	0.72	20	0.253	**-0.765**
D50 (µm)	2.09	0.108	0.75	19	-0.529	0.339
Transparency (cm)	1.63	0.192	0.77	18	-0.114	0.138
B) Murray Estuary						
Sorting coefficient (σG)	3.73	**0.016**	0.27	10	**-0.738**	-0.199
Salinity (ppt)	1.90	0.135	0.40	9	-0.38	0.565
DO (ppm)	1.98	0.148	0.52	8	-0.512	0.205
D50 (µm)	1.65	0.208	0.61	7	-0.223	**-0.774**
C) North Lagoon						
D50 (µm)	2.09	**0.095**	0.17	10	-0.111	**0.87**
DO (ppm)	1.84	0.128	0.31	9	**-0.729**	-0.138
Sorting coefficient (σG)	3.26	**0.018**	0.51	8	-0.62	-0.183
AFDW (%)	1.56	0.218	0.60	7	0.268	-0.436

5.3.4 Demersal versus benthic macroinvertebrate community

The global R values from a 3-way ANOSIM test on the demersal macroinvertebrate community show that communities are identical and similar across the three factors of habitat (0.13), region (0.48), and season (0.32). In comparison, a 3-way ANOSIM test on the benthic macroinvertebrate communities indicated that region (0.97) had the largest effect, whereas habitat (0.435) and season (0.14) had little effect. Thus, habitat had a low effect on communities, but a slightly higher difference was observed in the benthic versus demersal communities between reef and non-reef habitats.

5.4 Discussion

As ecosystem engineers, polychaete reefs can modulate resources for other biota, and this study showed that *F. enigmaticus* reef habitats influence both the associated demersal and benthic macroinvertebrate communities. In this study within the Coorong estuary in southern Australia, the macroinvertebrate community was not only influenced by reef habitat, but also the region (estuary or lagoon). The results supported hypothesis (1) a higher abundance and diversity of demersal and benthic macroinvertebrates in reef versus non-reef habitat and substrate. Hypothesis (2) was supported by the results where community composition differed between reef versus non-reef habitat and substrates. Hypothesis (3) was not supported and for both demersal and benthic macroinvertebrates, the community composition varied across regions within the estuary. Hypothesis (4) was supported only by the results of seasonal variation in the demersal macroinvertebrate community. However, a seasonal effect on benthic macroinvertebrate communities was not detected. Lastly, hypothesis (5) was not supported by the ANOSIM results, which indicated only slightly higher habitat differences for benthic versus demersal macroinvertebrate communities.

5.4.1 Higher macroinvertebrate abundances associated with reefs

A higher abundance of macroinvertebrates in association with reefs was more pronounced in benthic compared to demersal macroinvertebrates. For the substrates sampled, the benthic macroinvertebrate abundance were highest in the reef matrix, intermediate in the reef sediment and lowest in the non-reef sediment. Amphipods were driving the pattern in total abundance. In the ME, average amphipod densities were up to 8-fold greater in the reef matrix compared to reef sediment. Also, in the ME, amphipods were up to 2-fold greater in the reef sediment compared to non-reef sediment. In the NL, average amphipod densities were around 2-fold greater in the reef matrix compared to reef sediment and 2-fold greater in the reef sediment versus non-reef sediment. The results correspond with previous studies that have found high individual densities of amphipods in *F. enigmaticus* reefs (Bruschetti et al., 2009; Heiman & Micheli, 2010; Thomas & Thorp, 1994) and other serpulid reefs (Palmer et al., 2021). In the Mar Chiquita lagoon (Argentina), *F. enigmaticus* reefs increased the abundance of the amphipod *Melita palmata*, by 600-fold in the upper reef matrix in comparison to the surrounding mudflat sediments (Bruschetti et al., 2009). Similarly, *F. enigmaticus* reefs in the Elkhorn Slough (California) supported high densities of amphipods compared to mudflat sediments, and amphipods from similar families (Corophiidae, Melitidae) (Heiman & Micheli, 2010). Heiman & Micheli (2010) and Martinez et al. (2020) explain the association of amphipods with reefs from a provision of shelter for recruitment and juvenile survival. Amphipods can also benefit from macrophytes attached to reefs, which provide an additional refuge and can trap detritus or food (Vázquez-Luis et al., 2012; Ferreira et al., 2025). The high abundances of amphipodsin the reef matrix found in this study were partially explained by macrophyte cover on reefs, corresponding with findings by Bazterrica et al. (2021) and Martinez et al. (2020).

The polychaetes *Simplisetia aequisetis* and *Boccardiella limnicola* also contributed to the overall pattern of higher macroinvertebrate abundance in the reef matrix. Polychaetes inhabited the empty tubes and spaces in the reef matrix and were more abundant there. The polychaete *S. aequisetis* brood their young (De Roach, 2007), thus the reef matrix may provide enhanced protection compared to soft sediments (e.g., Bruschetti et al., 2009; Heiman et al., 2008; Schwindt & Iribarne, 1998). The habitat offered by reefs may also explain the association with other polychaetes, such as *B. limnicola.* Spionid polychaetes were exclusively found in *F. enigmaticus* reefs in the Mar Chiquita lagoon (Martinez et al., 2020). The feeding modes of both *S. aequisetis* and *B. limnicola* include deposit feeding (De Roach, 2007; Lam-Gordillo et al., 2020; Lautenschlager et al., 2014), which could reflect higher organic matter from bio-deposits of *F. enigmaticus* reefs (Bruschetti et al., 2011). Associations between deposit feeders and biogenic reefs were also recorded in mussel beds (Dittmann, 1990) and other serpulid reefs (Palmer et al., 2021). While species with a capacity to deposit feed were present in higher abundances in the reef matrix, the trait analysis (CWMs) did not reflect a greater expression of the deposit feeding mode in the reef matrix.

In soft sediments, benthic macroinvertebrates were higher in abundance in the reef compared to non-reef sediments. In this study, annelids, amphipods and bivalves contributed to the higher abundances in the reef sediment. This pattern must be interpreted with reference to the distance from the reef (i.e., one metre), as previous studies found decreased abundances in reef sediments directly around reef edges of *F. enigmaticus* due to crab foraging (Heiman and Michelli, 2010; Schwindt et al., 2001).

The physical structure of *F. enigmaticus* reefs can reduce flow speeds and affect the bedload sediment transport by facilitating the deposition of fine sediments on the top of the reef and leeward sides (Schwindt et al., 2004a). In the Coorong, currents are primarily wind driven in shallow water (Chilton, 2024), and reefs may impede wind-induced sediment resuspension (e.g., Schwindt et al., 2004a). Thus, the changed hydrodynamics from reefs may be reflected in the fine and well sorted reef sediments compared to poorly sorted, and in some cases greater median grain size in the non-reef sediments. The grain sizes in this study showed mostly fine and well sorted sediments in the reef habitat. Further sampling involving increased replication across each habitat is needed to ascertain this trend in grain size in the reef habitat. The higher abundance of annelids in the reef sediments, as found in this study, could partially be due to their preference for fine sediments. Grain size and sorting strongly influence benthic fauna, for example free-living organisms (e.g., polychaetes) benefit from increases in fine and well sorted sediments for burrowing (Lam-Gordillo et al., 2021) or acquiring food resources (Semeniuk & Wurm, 2000). The hydrodynamic effect of reefs can also cause larvae to settle in the vicinity of reefs (Breitburg et al., 1989). The bivalves *S. trigonella* and *H. alba* have planktonic larvae (Semeniuk & Wurm, 2000; Matthews & Fairweather, 2006) and were more abundant in the sediments in the vicinity of reefs.

The higher abundances of annelids, amphipods and bivalves in reef sediments compared to non-reef sediments, may also reflect a higher availability of resources (e.g., detritus, micro-phytobenthos, organic matter, nutrients) in the reef sediment. In this study there was a greater organic matter content in reef versus non-reef sediments, but mainly in the North Lagoon. Living *F. enigmaticus* produce bio-deposits that are enriched in nutrients and can be delivered as a source of organic matter to surrounding soft sediments (Bruschetti et al., 2011). Other sources of organic matter in the vicinity of reef sediments could be derived from macrophytes which commonly attach to reefs and largely contribute to organic matter in sediments in the Coorong (Priestley et al., 2022). Organic matter provides an important trophic link for benthic macroinvertebrates as seen in other biogenic reefs (McLeod et al., 2020; Zhou et al., 2006). Annelids, amphipods and bivalves deposit feed in some capacity, or switch between feeding modes (Riisgård & Schotge, 2007; Evan Ward & Shumway, 2004). Stable isotope analysis from another estuary in Southern Australia indicated organic matter for macroinvertebrates, including key species in this study (e.g., *H. alba*, *A. helmsi*, *S. aequisetis*), is derived from autochthonous sources, and included marine seaweed in the estuary versus freshwater and estuarine macrophytes upstream (Lautenschlager et al., 2014).

The outcomes of the trait analysis in this study showed similar feeding modes of benthic macroinvertebrates between reef and non-reef sediments. As a filter feeder, *F. enigmaticus* did not have a negative effect on the presence of filter feeding bivalves in the sediments in the vicinity of reefs. This finding contrasts an amensalistic relationship between the filter feeding reef species and other filter feeding macroinvertebrates in the sediments described for other biogenic reefs such as mussel beds (Dittmann, 1990). The co-existence of both living reefs and filter feeding bivalves could reflect niche for particle sizes selected by *F. enigmaticus* from the water column (Davies et al., 1989). Bivalves could also be switching from filter feeding to deposit feeding (Evan Ward & Shumway, 2004) to take advantage of increased organic matter in the reef sediments (Bruschetti et al., 2011) or increased benthic primary productivity from the reefs (Bruschetti et al., 2008).

In contrast to benthic communities, a higher abundance of demersal macroinvertebrates in reef versus non-reef habitats only occurred in the North Lagoon, and only during spring and summer of 2023. Mysids and the red-handed shrimp (*Palaemon serenus*) were more abundant in reef habitats. High abundances of hyperbenthic fauna in the vicinity of reefs constructed by the sand-mason (*Lanice conchilega*) included mostly Mysids and brown shrimps *Crangon crangon* (De Smet et al., 2015). The reefs changed the hydrodynamics and concentrated total organic carbon which explained the close association between mysids and shrimps with polychaete reefs (i.e., feeding preference for detritus, algae and zooplankton) (De Smet et al., 2015). The results from this study aligned with De Smet et al. (2015), showing that reefs structure not only the benthic community, but also the epibenthos and hyperbenthos communities.

5.4.2 Higher macroinvertebrate diversity associated with reefs

The species richness of demersal macroinvertebrates was similar between the reef and non-reef habitats. In contrast, a higher species richness of benthic macroinvertebrates occurred in the reef matrix compared to soft sediments. This finding corroborates previous studies on *F. enigmaticus* reefs which showed positive effects on the diversity of benthic macroinvertebrates in the reef matrix (Heiman & Micheli, 2010; Martinez et al., 2020; McQuaid & Griffiths, 2014). This pattern can reflect the recruitment of species, where juveniles shelter amongst the reef matrix (Bruschetti et al., 2009; Heiman & Micheli, 2010; Schwindt & Iribarne, 1998). In this study, several benthic macroinvertebrate taxa were only recorded in the reef matrix (e.g., Janiridae) as were juveniles of crabs (*Halicarcinus ovatus, Helograpsus haswellianus, Amarinus laevis* and *Paragrapsus gaimardii*). Juvenile *A. laevis* and *P. gaimardii* were dominant in the reef matrix, while larger individuals of juveniles were recorded from the demersal community in the vicinity of reefs. This pattern was similar to studies showing ontogenic changes in crab associations with *F. enigmaticus* reefs (Spivak et al., 1994). The Mar Chiquita coastal lagoon serves as a key example of the ecosystem engineering effect of reefs on the increased density and survival of the native crab, *Cyrtograpsus angulatus* (Spivak et al., 1994; Schwindt et al., 2001). Juveniles of *C. angulatus* recruited to the crevices within *F. enigmaticus* reefs (Spivak et al., 1994), whereas adults occur outside the reef (Schwindt et al., 2001). In the reef matrix, species richness may have been underestimated in this study. The taxonomic resolution presented here was affected by the preservation method of freezing samples. Amphipods were the dominant taxa group in the reef matrix, and likely represented a complex of different species, therefore diversity may have been higher and community relationships more complex beyond what was observed.

5.4.3 Differences in macroinvertebrate communities between reef and non-reef habitats

The provision of reef habitat influenced both the demersal and benthic macroinvertebrate communities. The dissimilarity in demersal macroinvertebrate community between the reef and non-reef habitat varied across regions and seasons. In the ME during spring 2023, mysids were more abundant in the reef habitat, leading to ~70% habitat dissimilarity. In the NL, the abundance of shrimps was ~9-fold and ~3-fold greater in reef compared to non-reef habitats respectively during summer and autumn of 2023. For sand-mason reefs, higher abundances of mysids and shrimps in the reefs have been recorded by De Smet et al. (2015). In this study, crab abundances were variable and driving differences in the demersal community in reef versus non-reef habitats. In the estuary, tidal cycles may influence crab movements between deeper channel sections and the intertidal shallow sections, or greater migrations between freshwater, estuarine or sea environments (Carr et al., 2004; Morgan et al., 2006; Zarrella-Smith et al., 2022). High mobility in crabs may reflect behaviours such as spawning aggregations, selecting habitats for feeding, or to avoid predation by larger fish or birds (Carr et al., 2004; Hewitt et al., 2023).

The comparison between three substrates showed a similar trend of benthic macroinvertebrate community in the reef matrix compared to reef and non-reef sediments. This finding corresponds with Martinez et al. (2020) for *F. enigmaticus* reefs in the Mar Chiquita, where community structure was different in the reef matrix compared to soft sediments, due to an overall greater diversity and abundance of benthic macroinvertebrates. In the present study, the results from the North Lagoon where reef and non-reef soft sediments also differed in community structure, corresponds with previous studies showing that reefs increase environmental heterogeneity (Martinez et al., 2020; De Smet et al., 2015). The similarity between reef and non-reef sediment communities in the Murray Estuary in this study may indicate that the effect of reefs is confounded by stronger abiotic or biotic variables, which could have impacted both types of sediment (e.g., flood related sediment deposition) (Reddering & Esterhuysen, 1987; Dyer, 1995).

5.4.4 Regional differences in macroinvertebrate communities

The estuarine or lagoon region sampled had an influence on the macroinvertebrate communities in reef and non-reef habitats. The background environmental setting has been investigated once before for mixed reefs of *Hydroides dianthus* and *F. enigmaticus* across different lagoons (Brundu & Magni, 2021). Brundu and Magni (2021) showed that the macroinvertebrate community of reefs was dependent on reef size, density, and the lagoon (location, confinement and marine connectivity). The present study showed benthic communities vary between substrates of *F. enigmaticus* reef matrix and sediment, and non-reef sediments, and are subject to the environmental setting (i.e., the estuarine or lagoon region). The reef matrix enhances benthic macroinvertebrate communities (diversity and abundance), in comparison to soft sediments. In future studies, the effect of reef type could be investigated by comparing similar reef types (e.g., morphology size) found in different environmental settings (estuary versus lagoon). Other features of reefs could be measured on an individual reef scale (e.g., edge perimeter, rugosity, vertical relief, reef condition, distance to reef) to explore the generality of the pattern in relation to other components of reef structural complexity. Furthermore, identification of frozen specimens could have been affected by this preservation method (Nitschke et al., 2024). Taxonomic resolution was thus kept at a higher level and more complex relationships between macroinvertebrates and reefs could have been missed.

5.4.5 The effect of the environment on the macroinvertebrate community

The association between macroinvertebrates and reefs were found to vary for the demersal catch, subject to the environmental conditions, which included a flood event. The major flood which occurred in summer of flow year 2022, had a freshening effect in the Coorong. The fresh to brackish conditions in reef habitats likely explained the greater demersal catches of estuarine crabs *A. laevis* and *P. gaimardii*, and freshwater shrimp *P. australiensis* in flow year 2022 versus 2023. A combination of abiotic conditions from the flood or trophic linkages (i.e., increased plankton or detritus) may explain the response of these demersal species to freshwater flow (Kimmerer, 2002). In addition to temporal change, there were spatial changes in the demersal catches. Reef habitats in the North Lagoon experienced some freshening but were mostly characterised by higher salinities than in the Murray Estuary. Estuarine and freshwater species were more common in the ME reef habitats (*A. laevis*, *P. gaimardii, P. australiensis*) while the marine shrimp *P. serenus* was more common in the North Lagoon reef habitats. Marine opportunistic species, such as *P. serenus* may have moved into the North Lagoon, as part of a seasonal movement to find a suitable nursery habitat (Henderson & Bird, 2010).

While no temporal changes were detected between spring and summer in the benthic macroinvertebrate community, there were some spatial changes due to the varying environmental conditions. The association between benthic macroinvertebrates and reef differed in biomass, between the Murray Estuary and North Lagoon. The higher biomass in the reef matrix of the Murray Estuary than the reef matrix of the North Lagoon could have been explained by the prevailing lower salinities in the Murray Estuary. Amphipods, which made up most of the biomass, are often recorded in high abundances after flood events (Dittmann et al., 2015; Mosley et al., 2024).

5.4.6 The effect of habitat on the demersal versus benthic macroinvertebrate community

Habitat had a low effect on communities from the ANOSIM test results, but a slightly higher difference was observed between habitats for the benthic versus demersal communities. Instead, region was identified as the main factor which had the largest effect on the benthic community. This finding suggests that when interpreting patterns in relation to reef habitat, it is important to consider the environmental setting. While the findings did not suggest a clear difference in the immediate provision of reef habitat to demersal versus benthic macroinvertebrates, it builds on previous studies comparing multiple faunal components (i.e., sediment versus water column). Demersal macroinvertebrates in the water column are likely to undertake greater migrations or disperse with water currents (e.g., Morgan et al., 2006; Zarrella-Smith et al., 2022). Future investigations comparing the associations of macroinvertebrates from multiple components (e.g., sediment vs. water column) should consider replication from the individual reef perspective, and measure additional reef parameters (e.g., size, diameter, height, porosity).

5.5 Conclusion

The ecosystem engineer, *F. enigmaticus*, enhanced benthic macroinvertebrate fauna and had a positive effect on some demersal macroinvertebrate species in a large temperate estuary in southern Australia. There was significant variation in the macroinvertebrate community between substrate types (reef matrix, reef sediment or non-reef sediment) and between regions (estuary and lagoon) where the environmental setting differed. The abundances of benthic macroinvertebrates were often highest in the reef matrix, intermediate in the reef sediments and lowest in the non-reef sediments. The findings demonstrate associations of benthic macroinvertebrates with *F. enigmaticus* reefs but also showed that the patterns are not universal as they varied between the estuary or lagoon, and seasons. Investigation of multiple components of the ecology of reefs, including larger demersal macroinvertebrates, showed that reefs structure the benthic community more than the demersal community. Environmental conditions including changes from a large flood event explained variation in the demersal communities, whereas sediment conditions primarily explained variation in the benthic communities. Estuarine macroinvertebrates benefit from the habitat heterogeneity provided by *F. enigmaticus* reefs, whereby reef associated demersal and benthic macroinvertebrate communities varied with the environmental setting.

Chapter 6. General Discussion

Biogenic reefs are complex, three-dimensional structures which are essential habitats for the functioning of marine and estuarine ecosystems (Sheehan et al., 2015; Stewart-Sinclair et al., 2020). Typical biogenic reefs like coral and shellfish are known to provide nursery habitat, contribute to productivity and species diversity, sediment stability, nutrient cycling and benthic-pelagic coupling (Boström et al., 2011; zu Ermgassen et al., 2020; Lefcheck et al., 2019). Globally, polychaete reefs are increasingly recognised as ecosystem engineers, yet aspects of their ecological functions are not well known in comparison to typical biogenic reefs (Montefalcone et al., 2022; Lefcheck et al., 2019). There has been limited understanding of how large calcareous reefs constructed by serpulid polychaetes influence components of the biotic community, including macroinvertebrate and fish fauna, and their value as nursery habitat (Montefalcone et al., 2022). This thesis advanced the understanding of the ecology of polychaete reefs, and generated new knowledge highlighting that polychaete reefs provide ecosystem functions that are similar to other typical biogenic reefs in marine and estuarine ecosystems.

To address knowledge gaps on the ecosystem functions of polychaete reefs, investigations were carried out in the Coorong, a large temperate estuary in southern Australia, where no other type of biogenic reefs occurs. The polychaete reefs studied were of *Ficopomatus enigmaticus* (Serpulidae), a cosmopolitan species which is also a marine alien species in some parts of the world (Alvarez-Aguilar et al., 2022). The true origin of *F. enigmaticus* remains unclear, but the putative native range includes Australia, where little is known about its ecology (Styan et al., 2017).

To understand the ecosystem processes and functions of data-limited biogenic reefs, it is first important to investigate the scale of structural complexity offered by the habitat (Loh et al., 2018; Bateman and Bishop, 2017). Chapter 2 fulfilled a knowledge gap on the characteristics and spatial distribution of polychaete reefs within the Coorong in southern Australia, and how their sizes and density related to environmental conditions. Changes which occurred in the Coorong over the past decades include reduced flushing following upstream water extraction, and increased eutrophication, that raised the question whether the growth of large and expansive reefs identified from Chapter 2 coincided with anthropogenic impacts on the environment. Chapter 3 used radiocarbon dating to investigate polychaete reef ages and identified links between the environmental history and the naturalisation of polychaete reefs in the Coorong. The reef classification and maps developed in Chapter 2 guided subsequent field investigations on the ecosystem functioning of reefs (Chapter 4 and Chapter 5).

Chapters 4 and 5 together advanced the known ecosystem functions from polychaete reefs, and particularly serpulid reefs, for faunal communities in estuaries. Chapter 4 investigated fish communities associated with the large calcareous reefs constructed by serpulid polychaetes. In chapter 5, the associations of demersal and benthic macroinvertebrates with serpulid reefs were investigated. A stronger association with reef habitat was found for benthic than demersal macroinvertebrates. Benthic macroinvertebrate abundances were higher in soft sediments in reef versus non-reef habitats in all surveys. The differences in the community of macroinvertebrates, in substrates found in both reef and non-reef habitats, often varied in the estuary compared to the lagoon. Below, I summarise the main findings of each data chapter (Figure 6.1) and review how these new findings on the ecology of polychaete reefs compare to the ecosystem functions provided by other biogenic reefs. Lastly, I discuss the implications of my research outcomes for the conservation and management of polychaete reefs and future directions for research.

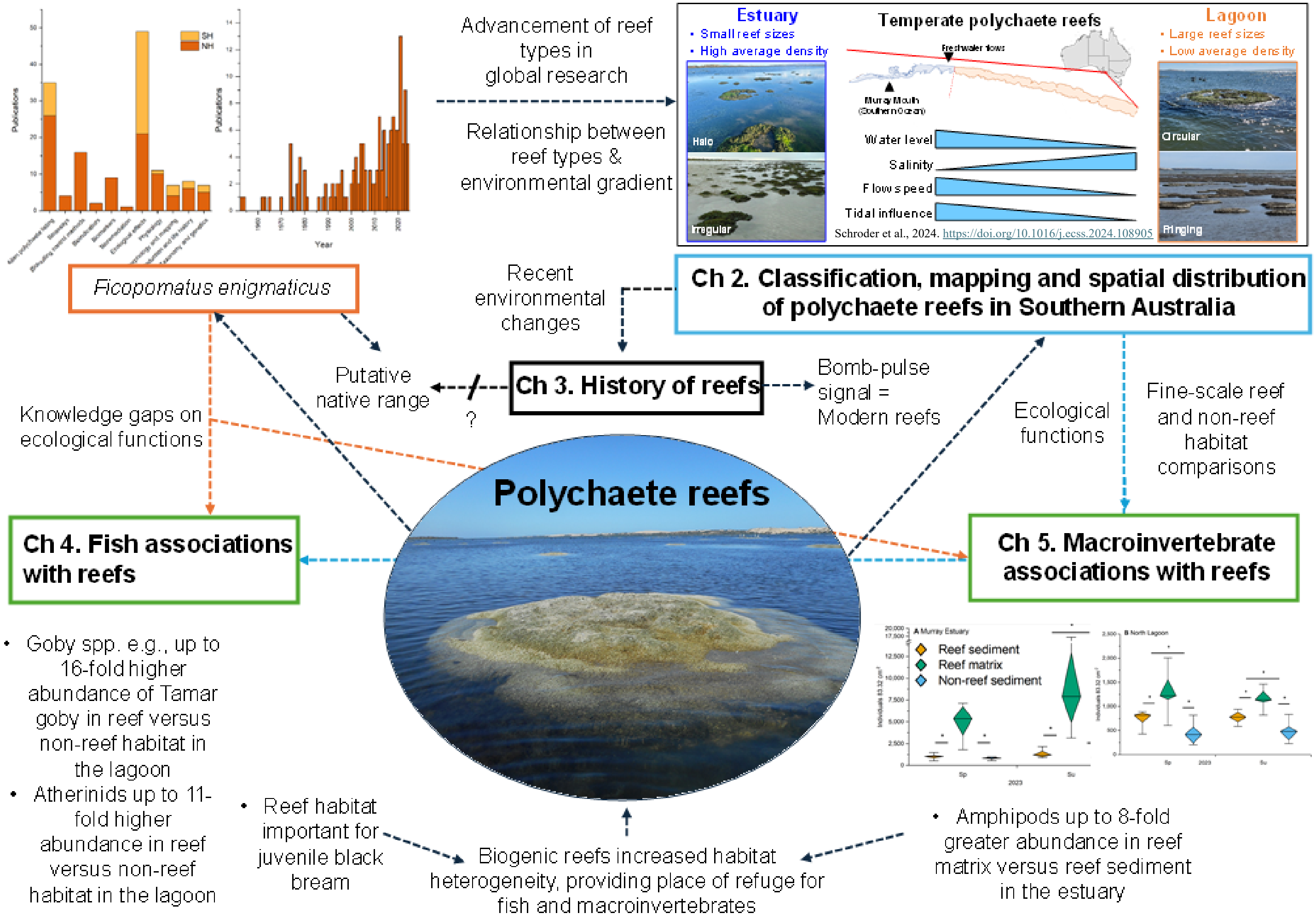

Figure 6.1. Literature review on global distribution of *Ficopomatus enigmaticus* (Chapter 1, Fig 1.1), and overview of the main results from each of the four data chapters in this thesis. The data chapters presented are inter-linked, as the results on the polychaete reef classification and mapping (Chapter 2) raised questions on the history of reefs (Chapter 3) and guided the survey design for subsequent field investigations to fill knowledge gaps on the ecosystem functioning of polychaete reefs (Chapter 4 and 5).

6.1 Overview of main results

6.1.1 Chapter 2- Classification and mapping of polychaete reefs

My findings revealed extensive polychaete reefs of *F. enigmaticus* in a large temperate estuary in southern Australia, which included some of the largest circular reefs recorded globally (Schroder et al., 2024). A new classification was described for polychaete reef types according to their morphology and size, from 200 reefs analysed from digital aerial imagery, which was checked with an accuracy assessment. Five reef classes were described, which provided coherent terminology for polychaete reefs of *F. enigmaticus* found globally: halo, irregular, circular, platform or fringing reefs.

My spatial analysis of 2,376 ha showed an expansive range of *F. enigmaticus* reefs and striking differences in reef classes and density across the environmental gradient in the Coorong. The estuary was characterised by smaller sized reefs of halo, irregular, circular and small platform classes, whereas reefs in the lagoon were larger sized reefs and mostly circular, platforms or fringing classes. Reef density reached up to 525 reef ha^{-1} in the estuary compared to 191 reefs ha^{-1} in the lagoon. Reef density was patch dependent, however, the median reef density found in the estuary (224 reefs ha^{-1}) was lower than in the Mar Chiquita (Schwindt et al., 2004b). Previous mapping of *F. enigmaticus* showed individual density to vary with substrate availability (Bezuidenhout and Robinson, 2020; Bianchi and Morri, 1996), benthic assemblages (Brundu and Magni, 2021) and growth rates over time (Schwindt et al., 2004b).

Reef sizes and density were analysed with mean environmental conditions in the Coorong, which positively correlated larger circular reefs in low densities with salinity, bicarbonate, chlorophyll a, and Trophic Index (TRIX). My findings highlighted that reef sizes (i.e., growth) benefited from the higher salinities (lower freshwater flows) and eutrophic conditions which have prevailed in the lagoon over several decades (Mosley et al., 2023). The findings from this chapter raised curiosity about their history within the Coorong estuary and lagoon (Chapter 3) and ecological functions (Chapter 4 and Chapter 5).

6.1.2 Chapter 3- History of polychaete reefs in southern Australia

The history of polychaete reefs, built by *F. enigmaticus*, was examined in the Coorong, southern Australia. This chapter presented an original approach by taking cores directly from reefs, and radiocarbon dating polychaete tubes along intervals from the surface to the deepest part of the core. A snapshot of the history along a core was indicated by changes in the percent of modern radiocarbon ($F^{14}C$), given that a living sample reflected the approximate atmospheric conditions.

My findings provide new evidence that reefs are modern (i.e., younger than the 1950s), when $F^{14}C$ peaked during global nuclear bomb testings. This was an unexpected result given the presence of fossil serpulids from the same region (Bone and Wass, 1990). However, new evidence from Chapter 3 compliments the interpretation of the finding from Chapter 2, where the timing of major environmental change (e.g., eutrophication) in the modern Coorong (Mosley et al., 2023) must have coincided with the establishment of large and expansive polychaete reefs present today (Schroder et al., 2024). This finding corresponds to other estuaries where *F. enigmaticus* reefs proliferate under eutrophic conditions (Keene, 1980; Zaouali and Baeten, 1983). The putative native range of *F. enigmaticus* includes Australia (Dew, 1959) and given the presence of fossil serpulids dated to 700 BP in the Coorong (Bone and Wass, 1990) my findings alone cannot disprove the native status of *F. enigmaticus.* It remains unknown whether *F. enigmaticus* replaced a native serpulid known from the fossils, as occurred in Argentinean estuaries (Ferrero et al., 2005). However, the expansion of modern reefs in the Coorong estuary and lagoon reflects the environmental changes this ecosystem experienced in recent decades.

6.1.3 Chapter 4- Estuarine fish associated with polychaete reefs

Fish surveys from a total of 192 overnight fyke net deployments across polychaete reef and non-reef habitats in each the estuary and lagoon found a total of 22 native species and distinct native fish communities in reefs. Fish community composition significantly varied between habitats, regions and seasons surveyed. The *F. enigmaticus* reefs serve as shelter for estuarine fish especially during the juvenile life stage. These findings provide a first insight into the functional roles of *F. enigmaticus* for fish communities and are later discussed when considering the nursery function of polychaete reefs for fishes (Rabaut et al., 2010; Rabaut et al., 2013; De Smet et al., 2015). In addition, fish communities were highly dynamic due to confounding variation from environmental stressors (e.g., flood event). A large flood event coincided with the start of fish surveys and caused fresh salinities (0 ppt) in the estuary. Total monthly flow (total freshwater flow across all barrages into the Coorong, GL $month^{-1}$) was the strongest environmental variable explaining fish dynamics.

6.1.4 Chapter 5- Estuarine macroinvertebrates associated with polychaete reefs

Demersal catch of macroinvertebrates from 192 overnight fyke net deployments (Chapter 4) combined with benthic macroinvertebrate surveys of 60 replicate cores, found a total of 23 species associated with polychaete reefs or soft-sediments in the vicinity of reefs. Demersal macroinvertebrate community composition significantly varied between reef and non-reef habitats, between regions and between seasons. The benthic macroinvertebrate community composition significantly varied between substrates (reef matrix, reef sediment and non-reef sediment) and between regions. The mean abundance of the total benthic macroinvertebrates was highest in the reef matrix, intermediate in the reef sediment and lowest in the non-reef sediment. A comparison between the reef and non-reef sediments showed that the abundances of crustaceans, annelids and bivalves were higher in abundance in soft sediments located 1 m away from reefs. Demersal macroinvertebrate communities were dynamic and varied seasonally. Environmental conditions (e.g., salinity and freshwater flow) influenced demersal fauna which corresponded with the increased mobility and dispersion of demersal fauna (i.e., epi-benthos and hyper-benthos) in relation to polychaete reefs (De Smet et al., 2015).

6.2 Comparison of ecosystem functions of polychaete reefs and other biogenic reefs

Recently, there has been topical discussions on polychaete reefs, and in particular serpulid reefs and their role in providing ecosystem functions and services to aquatic ecosystem services worldwide (Bruschetti, 2019; Montefalcone et al., 2022). Emerging ecosystem functions of polychaete reefs are analogous to other biogenic reefs, such as shelter, nursery sites for juveniles, sediment accumulation and benthic-pelagic coupling (Bruschetti, 2019; Montefalcone et al., 2022). While the refuge of biogenic reefs for fish fauna is well known (Brandl et al., 2019; Gilby et al., 2018; Pratchett et al., 2008; Pratchett et al., 2011; Reeves et al., 2020; Stella et al., 2011), there were few examples investigating the relevance of polychaete reefs for fish communities (e.g., Chong et al., 2021).

Previous investigations on fish associations with polychaete reefs have focused on Sabellariidae (sandmasons) (Chong et al., 2021; De Smet et al., 2015; Rabuat et al., 2010; Rabuat et al., 2013) compared to Serpulidae reefs (Poloczanska et al., 2004; Palmer et al., 2021). My findings (Chapter 4) added to the understanding of the ecosystem functioning of polychaete reefs by filling a knowledge gap on the association between fish and polychaete reefs and was the first investigation on fish associated with serpulid reefs built by *F. enigmaticus*.

The discussion below compares the ecosystem functions of serpulid reefs with other biogenic reefs occurring in similar biogeographic locations. The comparison thus focused on shellfish reefs due to their overlapping occurrence in temperate and mediterranean climates, coastal habitats (i.e., estuaries) and environmental conditions (i.e., brackish salinities) (Reeves et al., 2020). The comparison thus excludes coral reefs which are mostly tropical (Hughes et al., 2002).

6.2.1 Shelter for fish

My findings of distinct fish communities in serpulid, polychaete reef compared to non-reef habitats, provided evidence of the shelter provision of polychaete reefs for fish (Chapter 4). All biogenic reefs offer a form of three-dimensional structure providing crevices, edges, and patches where fish can seek refuge or hide to escape predation (Lefcheck et al., 2019). For temperate and estuarine fish communities, polychaete reefs can offer a similar shelter function as oyster reefs, where species-specific patterns have been found (e.g., Grabowski et al., 2022;

Martínez-Baena et al., 2022). From Chapter 4, demersal gobies that were estuarine residents were strongly associated (i.e., found in higher abundances) with reef compared to non-reef habitats, and were found to shelter or hide amongst the reefs or under edges in *F. enigmaticus* reefs. Similarly, cryptic species such as blennies and gobies were more common in oyster reefs than adjacent soft sediments, using finer scale complexity for shelter (e.g., dead shells, crevices) (Martínez-Baena et al., 2022; Lewis et al., 2021).

Some species of blenny and goby also show high site fidelity to oyster reefs and occupy the habitat as nesting sites in estuarine ecosystems (Harding et al., 2020; Lewis et al., 2021). Gobies often use nests, either burrows or other structure and in some species, females lay demersal and adhesive eggs on physical structures (e.g., vegetation, rock) which the male guards (Houde et al., 2022; Lintermans, 2007). Polychaete reefs could provide a similar nesting place or laying substrate for gobies, and this study provided indirect evidence as there was a high association between reefs and goby species during spring and summer (Chapter 4) which coincides with their breeding season (Bice, 2010; Cheshire et al., 2013).

The shelter offered to gobies may be unique in polychaete reefs compared to oyster reefs, such that sediment scouring below the base of polychaete reefs (e.g., Bruschetti et al., 2011) creates unique overhang ledges which are used by individuals to hide under (Chapter 4). A similarity of the biogenic reefs created by polychaetes and shellfish is that they alter flow speeds, creating sheltered conditions on the leeward sides of reefs (Schwindt et al., 2004b; Kitsikoudis et al., 2020), which could be beneficial for resident and demersal fishes for sheltering (e.g., Martínez-Baena et al., 2022).

6.2.2 Foraging opportunities for fish

The foraging activity of some fishes with polychaete reef habitats (Chapter 4) may reflect a greater availability of macroinvertebrate prey resources as part of the reef infauna and reef associated sediments (Chapter 5). Although gobies mostly used reefs for shelter, they undertook foraging bouts and made lunges toward reef infauna (Chapter 4), likely feeding upon amphipods which were abundant in the reef matrix (Chapter 5) and are a key dietary item for gobies (Hossain et al., 2017; Giatas et al., 2022). These findings are similar to patterns found on temperate oyster reefs which host higher abundances of invertebrate prey which explains their interactions with fish fauna (Grabowski et al., 2021). Other trophic interactions between fish and oyster reefs, have been found for reef-residents which consume not only infauna but also detritus on the reefs (Abeels et al., 2012).

Oyster reefs do not completely exclude soft-bottom feeders, for example, flounders forage on sediments in the vicinity of reefs (Grabowski et al., 2021). In the soft sediments near polychaete reefs, higher abundances of crustaceans, annelids and bivalves were present than in sediments in non-reef areas (Chapter 5). The apparent effect is that polychaete reefs are enhancing the productivity of macroinvertebrate prey in nearby soft sediments (Chapter 5), which could have important trophic links. For example, goby, congolli and yellow-eye mullet were common in the fish community from polychaete reef habitats (Chapter 4) and could have benefited from highly available macroinvertebrate prey items in nearby reef sediments, which are known in their diets (Ye et al., 2020). For both polychaete reef and oyster reefs, there are similar indirect effects of reefs on the ecosystem, for example, increasing macroinvertebrate prey (i.e., food) resources available to fish fauna (Palmer et al., 2021; Grabowski et al., 2021).

6.2.3 Nursery sites for fish and macroinvertebrates

While the nursery function of shellfish reefs is well known (Lefcheck et al., 2019), there are few examples of polychaete reefs as nursery habitat for fish (Bruschetti et al., 2019). Previous evidence for polychaete reefs as nurseries comes from juvenile flatfish and seabream associations with sabellid reefs (Ventura et al., 2024; Rabuat et al., 2013; Rabuat et al., 2010) and little is known about serpulid reefs which are more permanent and stable structures in the environment (Montefalcone et al., 2022). New findings from Chapter 4 show that serpulid reef habitats support the recruitment and greater abundances of juveniles of estuarine species (e.g., small mouth hardyhead and black bream) than in non-reef habitats. On some occasions, juvenile greenback flounder were also more abundant in reef compared to non-reef habitats (Chapter 4), which corroborates with the findings from Rabuat et al. (2010; 2013) where nursery sites for flatfish occurred in the vicinity of reefs of *Lanice conchilega* (Sabellidae).

The co-existence of polychaete reefs with macrophytes further highlights their importance as nursery sites. Submerged aquatic vegetation provides a key nursery role for both fish and invertebrates, which can help to exclude predators, and enhance juvenile density, growth and survival (Lefcheck et al., 2019). The polychaete reefs (*F. enigmaticus*) investigated in this study were the only substrate for attachment by the red macroalage *Hypnea* spp. in the North Lagoon. This is similar to the red macroalga, *Polysiphonia* sp. which only grows on *F.*

enigmaticus in the Mar Chiquita coastal lagoon, Argentina, and provides positive effects for associated invertebrates (Bazterrica et al., 2013). The findings of a positive association between crustaceans (i.e., amphipods) with macroalgae (Chapter 5), and association of juvenile fish of estuarine species that rely upon macrophytes (e.g., black bream) (Woodland et al., 2019), suggest that reefs and macrophytes work in conjunction to create important nursery sites.

The reef matrix of polychaete reefs is unique compared to other biogenic reefs like oyster and mussels and may explain different patterns in associated epibenthos. In polychaete reefs, the reef matrix is porous, with spaces between tubes that can act as a sediment trap, and many smaller holes and crevices are common the reef surface (Ventura et al., 2020; Gravina et al., 2018; Schwindt et al., 2001). The high abundance of benthic macroinvertebrates in the reef matrix was a pattern found regardless of the reef type (e.g., size, density of reefs) (Chapter 5) which could reflect that shelter is important only at micro-habitat level, which consists of empty tubes, spaces in-between tubes or smaller holes and crevices amongst the tubes. The nursery role of polychaetes was also evident at the micro-habitat level, where juvenile crabs were only found sheltering in the reef crevices (Chapter 5). This finding coincided with previous studies on juvenile crab associations with polychaete reefs (Luppi and Bas, 2002; Aviz et al., 2021)

In comparison to polychaete reefs, the micro-habitat of shellfish reefs differs such that the surface area of the substrate (i.e., shells) is greater for epibiota (Bateman and Bishop, 2017). This may explain why shellfish reefs (e.g., oyster, mussel, razorfish) host more diverse and abundant epibiota (e.g., sponges, cnidarians, ascidians, echinoderms, algae) (Buschbaum et al., 2009; Rabaoui et al., 2015) than polychaete reefs (typically bryozoans) (Chapter 5). In addition, the empty or dead shells from shellfish reefs can provide a nursery site for juvenile crabs and can increase their survival rates (Longmire et al., 2021; Tiller et al., 2024). Thus, the type of micro-habitat offered to juvenile crabs by shellfish reefs may differ to that by polychaete reefs, but they are providing the same ecological function as a nursery site.

6.3 Conservation and management of polychaete reefs in southern Australia

Polychaete reefs of *F. enigmaticus* are found globally in estuaries, marinas and coastal lagoons (Bruschetti, 2019). Across many regions in the world, *F. enigmaticus* can be highly invasive, fouling on infrastructure or other animals (e.g., turtles), causing irreversible abiotic and biotic changes in the environment, facilitating the establishment of other non-native species, and outcompeting native species (Alvarez-Aguilar et al., 2022). While the true origin of the species remains unknown, the putative native range includes Australia (Dew, 1959). Recent molecular evidence identified three cryptic species of *F. enigmaticus* across southern Australia, but phylogenetic patterns in distribution were not reflective of a marine native species (Styan et al., 2017). In the Coorong, radiocarbon dating of bryozoan and serpulid build-ups was 700 BP (Bone and Wass, 1990). Fossil serpulid tubes preserve well through time and morphological analysis can shed light on their taxonomy (Ippolitov et al., 2014), yet no attempt was made by Bone and Wass (1990) to identify nor preserve reference samples of the fossils. My findings (Chapter 3) of the radiocarbon dating from large platform *F. enigmaticus* reefs from the Coorong estuary raised further uncertainty of the naturalisation of *F. enigmaticus* reefs given they were relatively recent formations.

The new knowledge on the distribution and ecology of polychaete reefs in the Murray Estuary and North Lagoon of the Coorong (Chapters 2–5), a Ramsar listed wetland of international importance, motivates the need for management actions to balance the positive and negative implications of reefs on the natural environment. My findings in Chapter 4 and 5 demonstrate the positive effects for native biota such as fish and macroinvertebrates which were associated with reefs for nursery habitat or shelter. On a broad scale, estuarine habitats are already important nursery grounds for fish (Lefcheck et al., 2018), but finer scale habitats such as polychaete reefs could offer enhanced protection for juveniles from larger predatory fish (Bruschetti et al., 2019). Reefs also enhance macroinvertebrate abundances within the reef matrix (Chapter 5), suggesting reefs provide shelter or buffer harsh conditions (e.g., water movement) (Giangrande et al., 2020). Resilience in macroinvertebrate populations in the estuary during times of disturbance (e.g., flood event) or recovery, may be facilitated by polychaete reefs as refuge, as demonstrated in oyster reefs (Searles et al., 2022). The patterns in benthic macroinvertebrate abundances in relation to reefs were universal and irrespective of the type of reef (e.g., size, density) (Chapter 5), demonstrating the ecosystem engineering role of *F. enigmaticus* reefs in the environment (Bruschetti et al., 2019).

Reefs are a vital hard substrate for macrophytes to attach, which contributes to a more complex nursery habitat, and for instance directly benefits crustaceans like amphipods (Chapter 5), but may also benefit juvenile estuarine fish such as black bream (Chapter 4). The positive associations from my findings (Chapter 4 and Chapter 5) already demonstrate a conservation value of reefs given their ecosystem functions and services in the Coorong Murray Estuary and

North Lagoon. Further functions, which were not investigated as part of this study, could arise for birds and water quality. Birds can use reefs as resting sites (pers. observations), and migratory shorebird species can forage upon epifaunal and infaunal prey in the reefs (e.g., Bruschetti et al., 2009). Another benefit of the ecosystem functioning role of *F. enigmaticus* reefs in the Coorong is that the tubeworms are efficient filter feeder, which could help to clear the water column and improve transparency (Davies et al., 1989), thus benefiting other macrophyte communities or benthic-pelagic coupling (Bruschetti et al., 2008).

Freshwater flow is critical for the future management of *F. enigmaticus* reefs, to balance their potential negative impacts on the environment. For instance, during the height of the Millenium Drought, freshwater flows into the Coorong completely ceased, which caused estuarine water to seep into the Lower Lakes, spreading *F. enigmaticus* larvae (Kingsford et al., 2011). During this time, *F. enigmaticus* was a nuisance species fouling on infrastructure, jetties, boats and other native animals (e.g., mussels, turtles), and caused large mortalities of freshwater native turtles from overgrowth on their shells (Kingsford et al., 2011; Benger, 2010). Since the end of the Millennium Drought, freshwater flows have resumed and *F. enigmaticus* was no longer problematic in the Lower Lakes (Dittmann et al., 2011).

Environmental water has assisted in the recovery and maintained estuarine habitats in the Coorong in-between natural flood events (Lester et al., 2013; Dittmann et al., 2015; Ye et al., 2013). However, southern sections of the North Lagoon, and the South Lagoon of the Coorong, have been affected by reduced flushing which has led to salinisation and eutrophication over the last two decades (2000 to 2022) (Mosley et al., 2023). Reefs are now absent in the South Lagoon due to extreme salinisation, and these conditions could potentially come into the North Lagoon and cause reef mortality. The eutrophic conditions can already explain recent changes of *F. enigmaticus* reef distributions in the Coorong. For example, larger reefs are now characteristic to the southern sections of the North Lagoon (Chapter 2), which is a confined section of the lagoon and subject to eutrophic waters (Mosley et al., 2023). This highlights the need for consistent freshwater flow deliveries (volume and frequency) for flushing the southern sections of the North Lagoon, to decrease eutrophication.

Improving flushing would reduce eutrophic conditions that otherwise facilitate rapid growth of reefs (e.g., Diawara et al., 2008). This would have reciprocating benefits reducing the risk that large circular reefs choke up the narrow sections of the North Lagoon in the Coorong. Thus, if higher rates of flushing are maintained, it can be expected that reefs would not cause issues for the restriction of water flow and vital connectivity between the North and South Lagoons. The removal of any reefs of *F. enigmaticus* would not be an option, given they are already established throughout the estuary and lagoon (Chapter 2) making them impossible to eradicate. Also, any removal method could trigger mass spawning events which would lead to further spread (Kupriyanova et al., 2001). A key management action that should be taken to ensure reefs do not proliferate further would be maintaining freshwater flows into the Coorong lagoons, and improving water quality (i.e., less eutrophic conditions). Secondly, the new reef distribution maps (Chapter 2) can be used to increase the awareness of reefs by boat users and avoid disturbance and further spread by boating activities or propellor strikes (e.g., Ferrario et al., 2024).

6.4 Outlook and final concluding remarks

While effects of coral and shellfish reefs are well studied, scientific attention has only recently turned to polychaete reefs as ecosystem engineers in coastal environments (Bruschetti, 2019). The aim of this PhD thesis was to investigate the ecosystem functioning of polychaete reefs, particularly serpulid reefs.

The findings showed new evidence that polychaete reefs constructed by *Ficopomatus enigmaticus* are expansive throughout the Coorong, a large temperate estuary in southern Australia, and vary in their morphology, size and density. A classification of different reef types provided evidence that the structural complexity of *F. enigmaticus* reefs varies across a broad spatial scale in the Coorong. At a smaller spatial scale, the reef matrix was more important than reef type (e.g., reef size and density) for macroinvertebrates and explained their universal associations with reefs. The structural complexity (e.g, size, density) was, however, important for fish communities, but as confounding environmental stressors occurred over the study period, future research should investigate the associations further.

The history of *F. enigmaticus* reefs from its putative native range in southern Australia revealed that the expansion of reefs coincided with eutrophication over the past few decades. Further research can build upon the methodology of using radiocarbon dating to reconstruct the age of polychaete reefs, such as modelling a bomb-curve to match calendar year to depth in the core and combining it with other isotope signatures to reconstruct an environmental history over recent decades. Findings modern reefs of *F. enigmaticus* in the Coorong invites future studies on their origin. Multiple cryptic species of the *F. enigmaticus* senso lato group have been previously identified across southern Australia (Styan et al., 2017), but no material from the Coorong was used in that study. Future molecular studies could investigate whether populations in the Coorong are related to populations in other estuaries of southern Australia.

Positive ecological associations were found between native macroinvertebrate and fish communities with *F. enigmaticus* reefs in the Coorong, due to the provision of shelter. The new findings from this thesis demonstrated that polychaete reefs can offer similar ecological functions (e.g., habitat provisioning) as shellfish reefs in estuarine and marine environments. Future work can expand on the trophic ecology and investigate differences in foraging behaviour and diet of fish in relation to the vicinity and type of polychaete reefs.

This study advanced the knowledge of the nursery role of polychaete reefs, and particularly serpulid reefs, for both macroinvertebrates and fish. The patterns found in this thesis revealed that the fine-scale of reef complexity (i.e., reef matrix) was important for juvenile macroinvertebrates. This pattern could be explored further with technological advances in three-dimensional scanning to obtain fine-scale structural complexity measures (e.g., porosity, crevices, spaces in the reef matrix) (e.g., Ventura et al., 2024) that could be correlated fish densities of juvenile macroinvertebrates and fish. On a fine spatial scale, polychaete reefs have a greater porosity with many small interstitial spaces within their matrix, which differs to other biogenic reefs (e.g., shellfish) built from larger shells with a greater surface area. Further work could investigate how this could relate to differences for epi-and infaunal macroinvertebrate associations.

The recognition of the multiple ecological functions, such as shelter provision, and nursery habitat for native species of macroinvertebrates and fish, implies that reefs have conservation value in the Coorong estuary and lagoons. Investigations found significant variation in the fish communities between habitats, regions and seasons. Also, the macroinvertebrate communities differed by substrate type and region. The complex patterns identified in this work provide an avenue for future research; to explore the effects of environmental settings on the ecosystem functions of reefs.

Invasive freshwater fish species were also recorded in the reef habitat, but their presence in the estuary was flood related. Although reefs have conservation values, it is still important to monitor their occurrence in the environment by assessing changes in their spatial distributions and reef sizes. Anthropogenic impacts need to be reduced (e.g., eutrophication) to minimise the risk of reef proliferation as this could potentially restrict water movements and connectivity between the North and South Lagoon in the Coorong. The ubiquity of relationships found between *F. enigmaticus* reefs and the environmental conditions (e.g, salinity, chlorophyll a, water level, Trophic Index) can be tested across ecosystems elsewhere in the world.

The outcomes of this PhD thesis demonstrated that ecosystem functions provided by polychaete reefs are similar to other biogenic reefs (e.g., shellfish). The increased knowledge on the ecosystem functions of biogenic reefs is essential for the conservation and management of these ecosystems and their provisioning services.

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Appendices

Appendix A. Supplementary material for Chapter 2

Table S1. Summary of previous morphological classifications of *Ficopomatus enigmaticus* reefs from estuaries and coastal lagoons.

Reef classification	Description of reef morphology	Reef size (diameter, height)	Substrate	Spatial distribution	Coastal lagoon	Reference
Hemispherical	A patch reef that has collapsed to be hemispherical in shape	0.6 m height, 1.6 m diameter	Shell (e.g. bivalve), broken fragment of old reef (i.e. worm tubes), rocks/ boulders from cliff faces.	Shallow lagoon areas 0.5-1.5 m	Albufera of Menorca in the Balearic Islands (Western Mediterranean)	Fornós et al. 1997
Micro-atoll	A patch reef that has collapsed at the centre					
Cauliflower-like	A patch reef that has a reduced development or erosion at their base.	1.2-2.4 m height, 2.5-4.5 m diameter		Central and deep parts of lagoon (i.e. narrow channel parts where deeper)		
Fringing reef	Horizontally protruding platforms, growing from the rocky shoreline	Several to many m^2 (up to 20 m in diameter, and vertical walls more than 1 m in height (up to 3m thick)	Rocky	Littoral zone		
Circular reef	Circular in shape	Up to 4 m in diameter, and 0. 5 m in height. Maximum height dependent on water level.	Shells, bottles, rocks, pillars and bones	Reef abundance decreases towards mouth of lagoon at higher salinities	Mar Chiquita coastal lagoon, Argentina	Schwindt and Iribarne, 1998

Table S1. cont.

Reef classification	Description of reef morphology	Reef size (diameter, height)	Substrate	Spatial distribution	Coastal lagoon	Reference
Fused reef	Pairs of reefs that fuse together	Not described	Shells, bottles, rocks, pillars and bones	Not described	Mar Chiquita coastal lagoon, Argentina	Schwindt and Iribarne, 1998
Elongated reef	Elongate shape, parallel to current direction (uni-directional flow)	Not described	Shells, bottles, rocks, pillars and bones	Common reef shape observed in channels and creeks		
Circular reef	Circular in shape	Up to 7 m in diameter and 0.5 m in height. (Average diameter of 2.5 m)	Not described	Shallow and brackish lagoon areas, 0.1-0.5 m water level	Mar Chiquita coastal lagoon, Argentina	Schwindt et al. 2004a
Platform/ terrace reefs	Aggregates that coalsesce	Not described	Hard substrate	Not described	Mar Chiquita coastal lagoon, Argentina	Obenat and Pezzani 1994
Halo reef	Accumulation of sediments inside the reef causes the mortality of the oldest organisms	na	na	na	Mar Chiquita coastal lagoon, Argentina	Schwindt and Iribarne 1998, Keene 1980
Round reef	Rounded structures	Several metre in diameter	na	Northern and southern basin, 0.5-2 m, water level.	Prokops Lagoon, Western Greece	Ntzoumani et al. 2024
Atoll-shaped reef	Collapsed inner part, and only outer ring present					
Irregular reef	Irregular structures					

Table S2. Spectral differentiation between sediment and *F. enigmaticus* reefs by pixels in each band A) green, B) red and C) blue. Assessed with 2-way ANOVA and presented are pairwise Tukey tests for the mean difference in each region and location.

A Green	**Class 1**	**Class 2**	**Mean difference**	**q value**	**Alpha**	**Sig**
Murray Estuary	Reef	Sediment	-64.02	42.11	0.05	1
North Lagoon	Reef	Sediment	-45.51	82.45	0.05	1
B Red	**Class 1**	**Class 2**	**Mean difference**	**q value**	**Alpha**	**Sig**
Murray Estuary	Reef	Sediment	-65.93	43.37	0.05	1
North Lagoon	Reef	Sediment	-49.85	90.30	0.05	1
C Blue	**Class 1**	**Class 2**	**Mean difference**	**q value**	**Alpha**	**Sig**
Murray Estuary	Reef	Sediment	-51.29	33.74	0.05	1
North Lagoon	Reef	Sediment	-19.00	34.41	0.05	1

Table S3. Spectral thresholds and variance of *F. enigmaticus* reefs by pixel value in each region and locality.

		Pixel summary data (Green Band)				**Pixel variance summary data (Min-Max)**		
Region/Location	**Class**	**Minimum**	**Mean**	**Median**	**Threshold**	**Green**	**Red**	**Blue**
Murray Estuary	Reef	22	72.94	75	93	99	121	89
North Lagoon	Reef	27	62.30	56	75	23	134	80

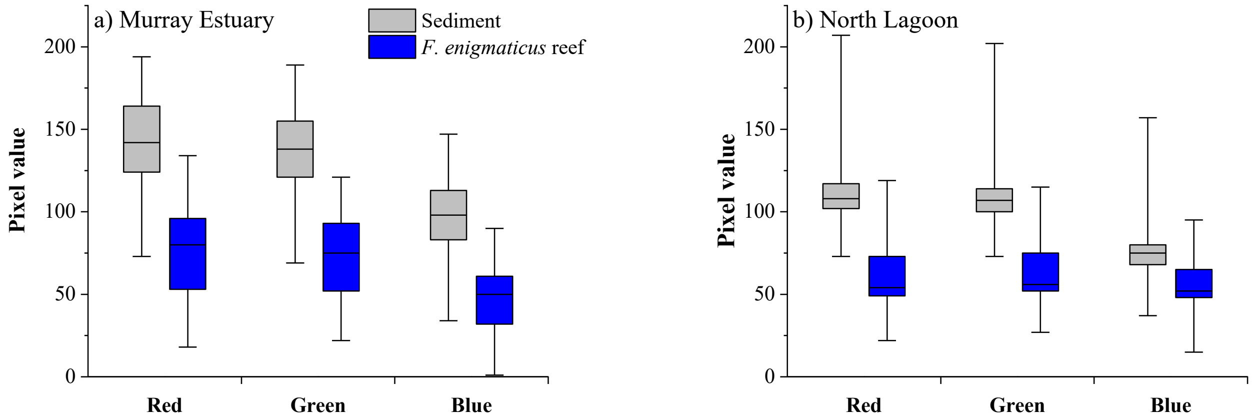


Figure S1. Spectral differentiation of sediment and *F. enigmaticus* reef in each region of the Murray Estuary and North Lagoon, derived from DEW 2018 Coorong digital aerial imagery (n=20 per substrate type in each region).

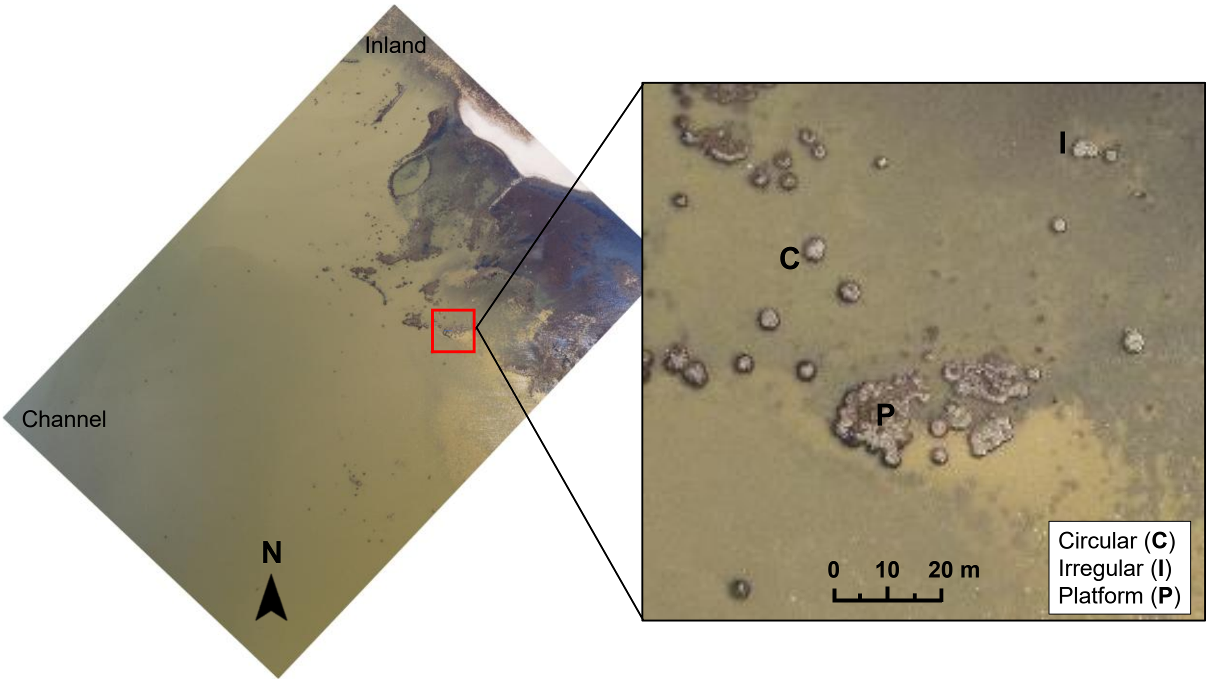


Figure S2. Large circular (C) and irregular (I) reef morphologies of *F. enigmaticus* in the Coorong North Lagoon, with some fused together to form platform (P) structures. Imagery scale of 1:27,308, taken in 2020. Reproduced with permission from Airborne Research Australia.

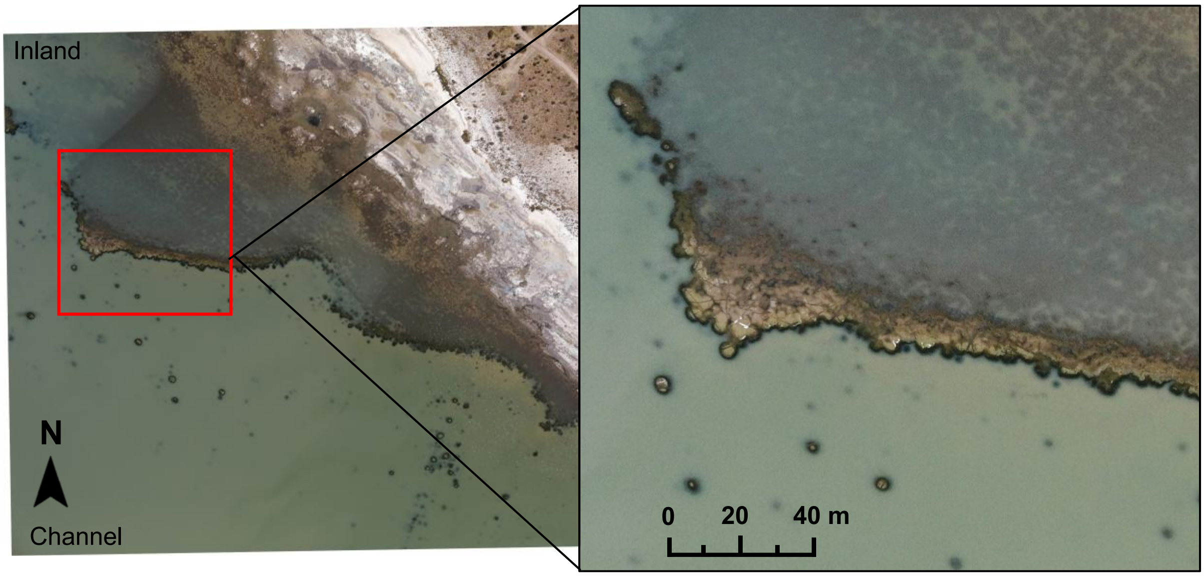


Figure S3. Fringing reef of *F. enigmaticus* growth in the Coorong North Lagoon. Right, shows a close up of the fringing reef and filamentous algal cover. Imagery scale of 1:27,308, taken in 2020. Reproduced with permission from Airborne Research Australia.

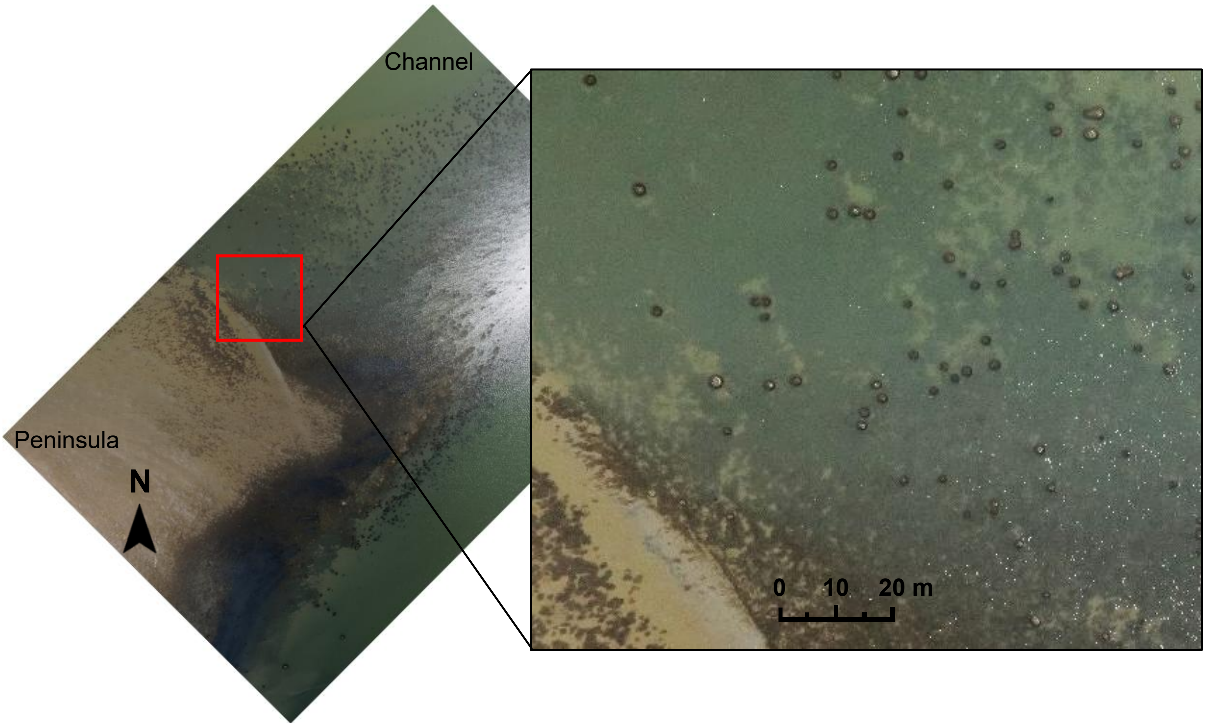


Figure S4. Aerial imagery showing an example of a sand spit on the peninsula side of the Coorong North Lagoon. Right, shows the high densities of small patch reefs of *F. enigmaticus,* including both circular and irregular morphologies. Imagery scale of 1:27,308, taken in 2020. Reproduced with permission from Airborne Research Australia.

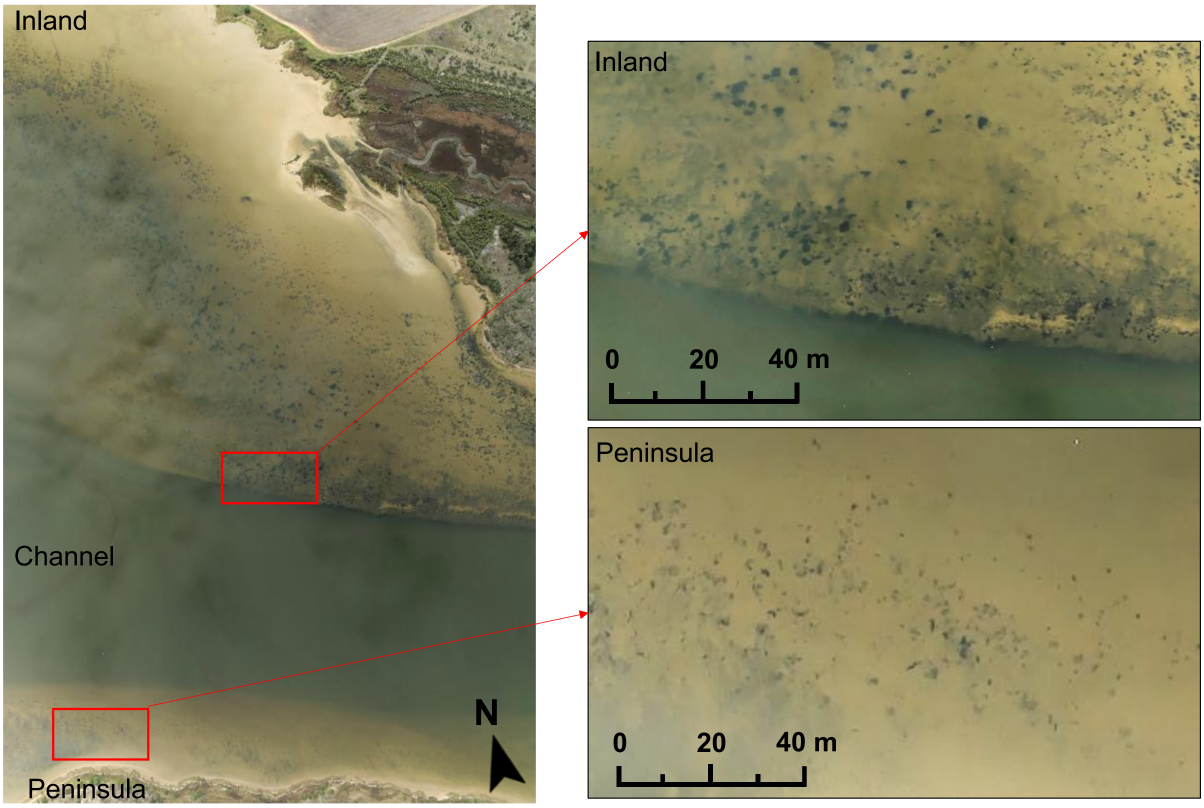


Figure S5. Cross section of the Coorong Murray Estuary (Goolwa Channel), where small patch reefs of *F. enigmaticus* are evident on shallow intertidal areas on either margins of the channel. Imagery scale of 1:27,308, taken in 2017. Reproduced with permission from Airborne Research Australia.

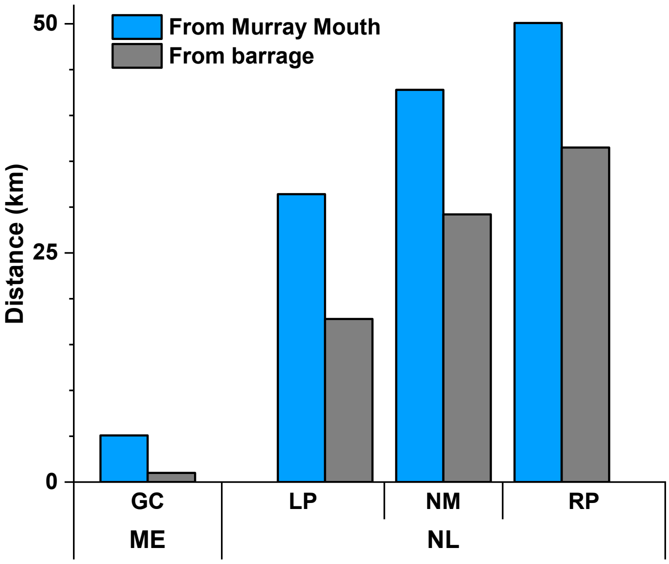


Figure S6. The distance of study sites at Goolwa Channel (GC) in the Murray Estuary (ME) and Long Point (LP), Noonameena (NM), Rob's Point (RP) in the North Lagoon (NL) from the Murray Mouth and nearest barrage (Goolwa barrage for GC and Tauwitchere barrage for LP, NM and RP).

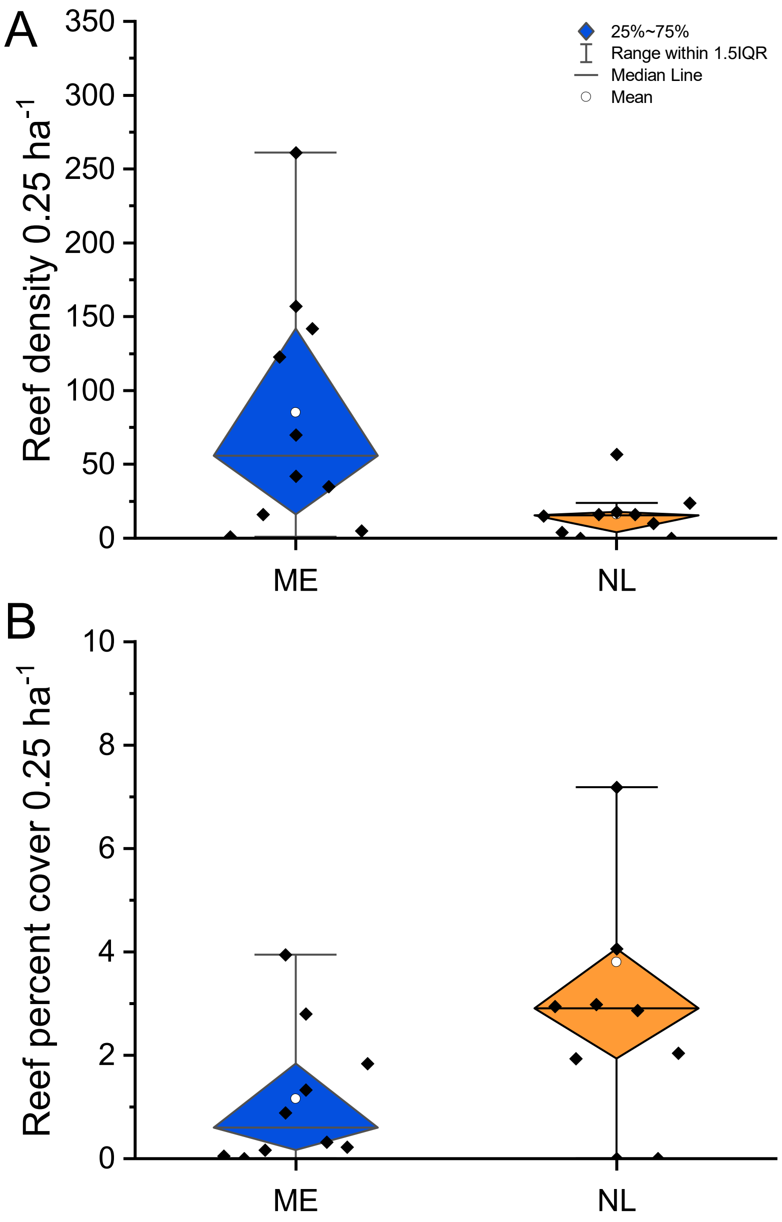


Figure S7. Box plot with data overlay of A) reef density and B) reef percent cover per 0.25 ha plot, for ten randomly surveyed plots in the Murray Estuary (ME, blue box) and North Lagoon (NL, orange box) of the Coorong. The mean is indicated by a white symbol and the median is represented by a horizontal bar with error bars showing 1.5 interquartile range (IQR).

Appendix B. Supplementary material for Chapter 3

Figure S1. Reef core 1 and reef core 2 collected with a stainless steel gauge auger.

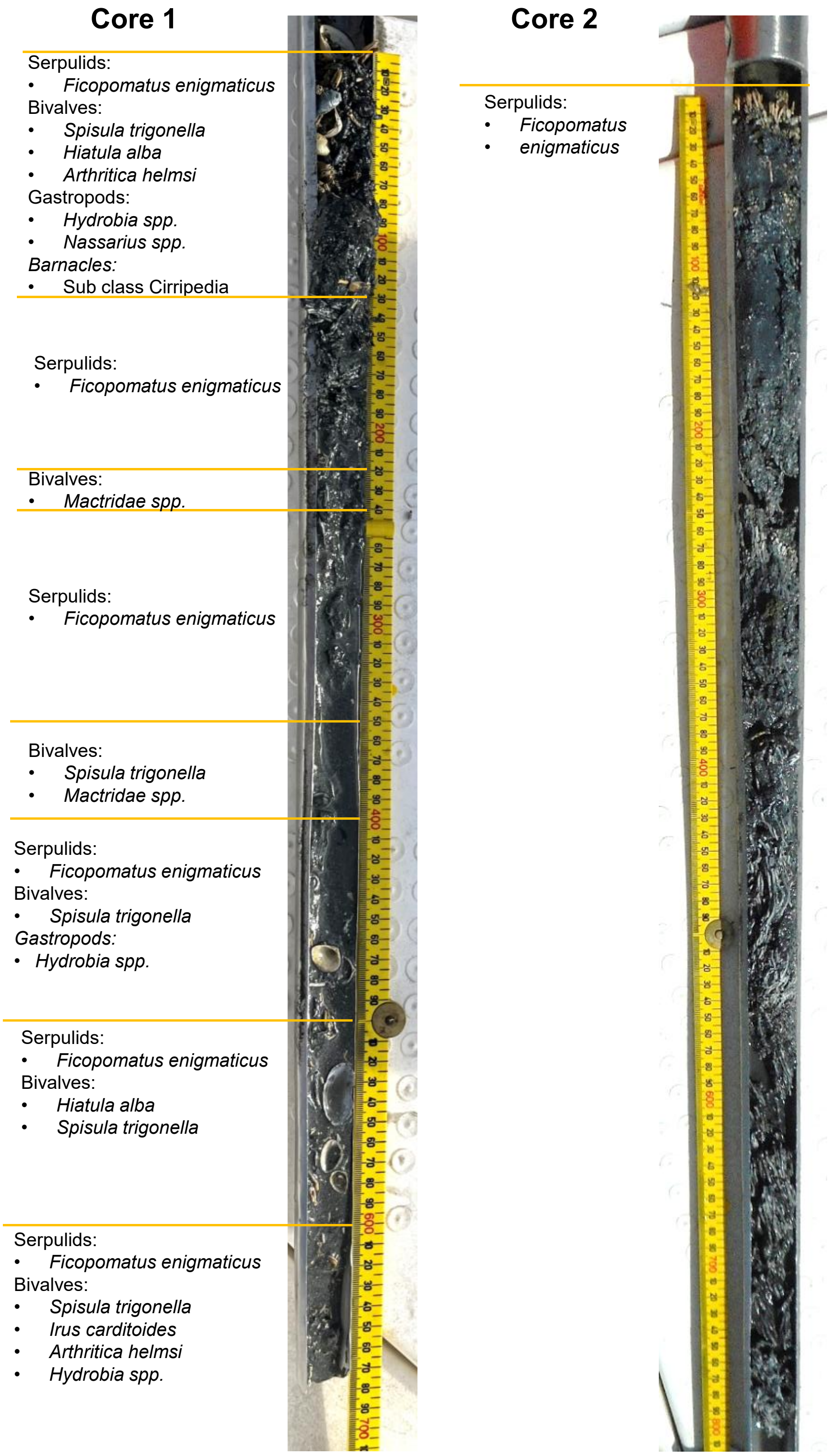


Figure S2. Reef core 4 collected with a stainless steel gauge auger.

Table S1. Published literature on the marine reservoir correction factor used in radiocarbon dating studies in the Coorong estuary, South Australia.

Reference	Correction factor (yrs)	Correction factor details
Lower, C.S., Cann, J.H., Haynes, D., 2013. Microfossil evidence for salinity events in the Holocene Coorong Lagoon, South Australia. Australian journal of earth sciences 60, 573-587.	84 ± 57	Not given
Dick, J., Haynes, D., Tibby, J., Garcia, A., Gell, P., 2011. A history of aquatic plants in the Coorong, a Ramsar-listed coastal wetland, South Australia. Journal of Paleolimnology 46, 623-635.	84 ± 57	Average of available ΔR for the three closest locations to the Coorong (Reimer and Reimer 2001).
Fluin, J., Haynes, D., Tibby, J., 2009. An environmental history of the Lower Lakes and the Coorong, A report for the Department of Environment and Heritage (South Australia). University of Adelaide, Adelaide (2009).	84 ± 57	Average of available ΔR for the three closest locations to the Coorong (Reimer and Reimer 2001).
George, C.S., Wallis, L.A., Keys, B., Wilson, C., Wright, D., Fallon, S., Sumner, M., Hemming, S., Heritage Committee, N., 2013. Radiocarbon dates for coastal midden sites at Long Point in the Coorong, South Australia. Australian Archaeology 77, 141-147.	72 ± 55	Regional average correction for SA (Average of 10 locations) (Ulm 2006)
Disspain, M., Wallis, L., Fallon, S., Sumner, M., St George, C., Wilson, C., Wright, D., Gillanders, B., Ulm, S., 2017. Direct radiocarbon dating of fish otoliths from mulloway (*Argyrosomus japonicus*) and black bream (*Acanthopagrus butcheri*) from Long Point, Coorong, South Australia. Journal of the Anthropological Society of South Australia 41, 3-17.	61 ± 104	Sub-regional average for Gulf St Vincent (Ulm 2006)
Chamberlayne, B., 2015. Paleohydrology from mollusc geochemistry (Dating of *Arthritica* shell from Coorong). University of Adelaide.	62± 61	Average of available ΔR for the seven locations in the region (from Marine Reservoir Correction Database- http://www.calib.qub.ac.uk/marine/)
Chamberlayne, B.K., Tyler, J.J., Haynes, D., Shao, Y., Tibby, J., Gillanders, B.M., 2023. Hydrological change in southern Australia over 1750 years: a bivalve oxygen isotope record from the Coorong Lagoon. Clim. Past 19, 1383-1396.	169±10	Calculated by subtracting the ^{210}Pb-inferred ^{14}C age ($^{14}C_{210Pb}$) from measured ^{14}C for the first occurrence of *Pinus* pollen in the sediments. Note: determined for the Coorong South Lagoon.

Appendix C. Supplementary material for Chapter 4

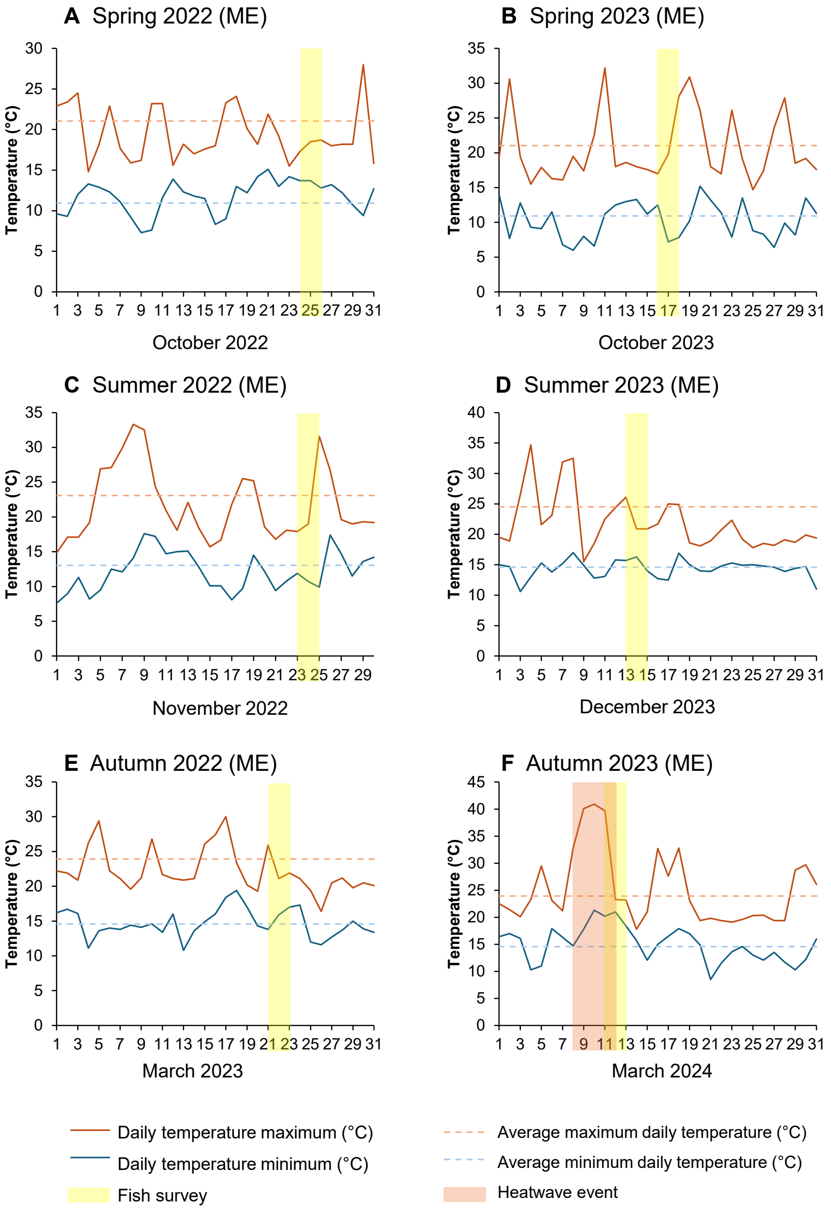


Figure S1. Daily air temperature (°C) during Murray Estuary (ME) fish surveys in seasons **A–B)** spring **C–D)** summer and **E–F)** autumn in flow years 2022 and 2023. Dotted lines indicate the average daily maximum and minimum for the given month. Heatwave events are highlighted in orange when there is abnormally high maximum and minimum temperatures for the given month, for a duration of ≥3 days. Data were obtained from the Bureau of Meteorology (Commonwealth of Australia 2024) to the weather station closest to the ME fish survey location (~5km apart), Hindmarsh Island, SA (Station 023894; 35.52°S, 138.87°E).

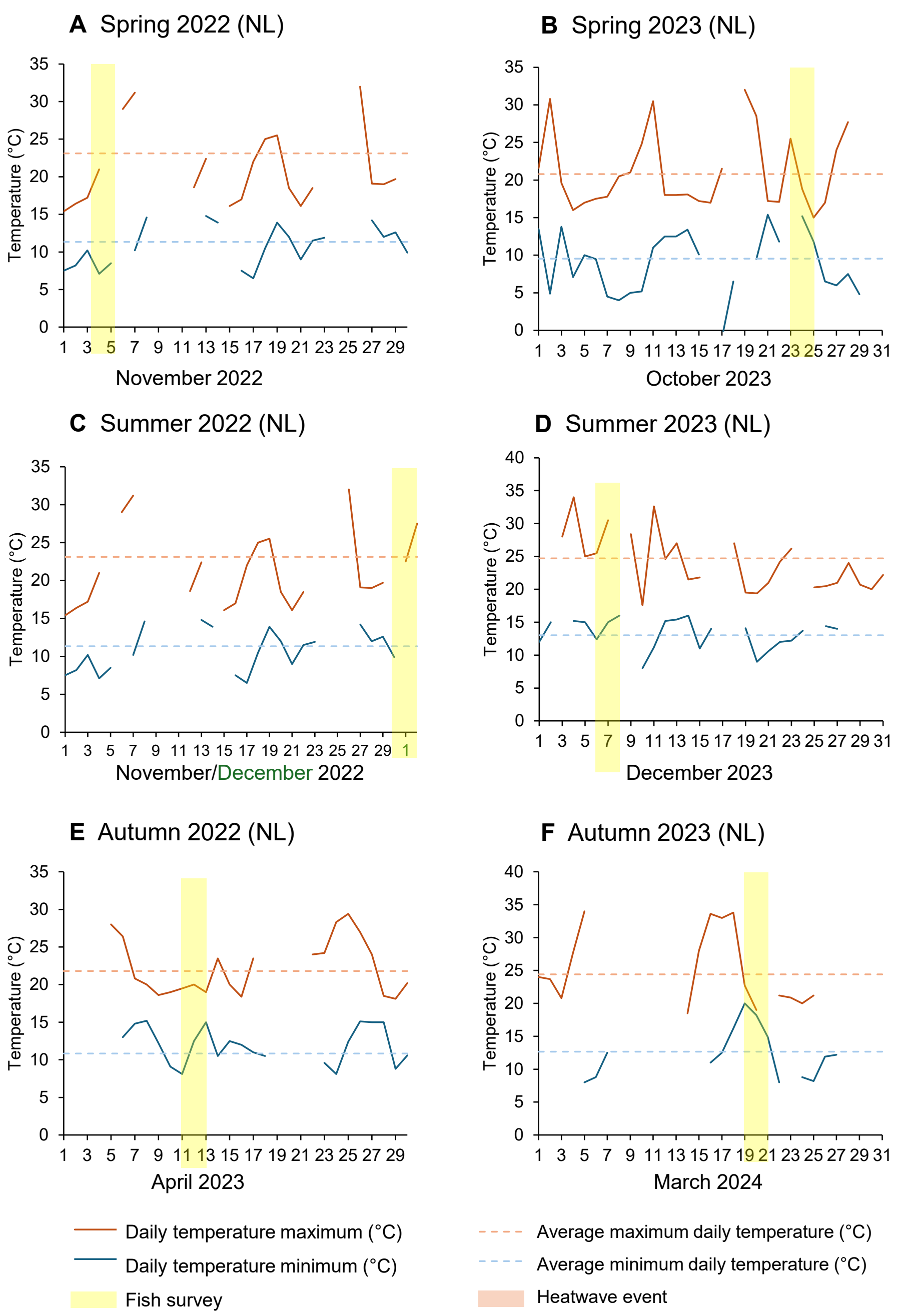


Figure S2. Daily air temperature (°C) during North Lagoon (NL) fish surveys in seasons **A–B)** spring **C–D)** summer and **E–F)** autumn in flow years 2022 and 2023. Dotted lines indicate the average daily maximum and minimum for the given month. Heatwave events are highlighted in orange when there is abnormally high maximum and minimum temperatures for the given month, for a duration of ≥3 days. Data were obtained from the Bureau of Meteorology (Commonwealth of Australia 2024) to the weather station closest to the NL fish survey location (~15 km apart), Meningie, SA (Station 024518; 35.69°S, 139.34°E).

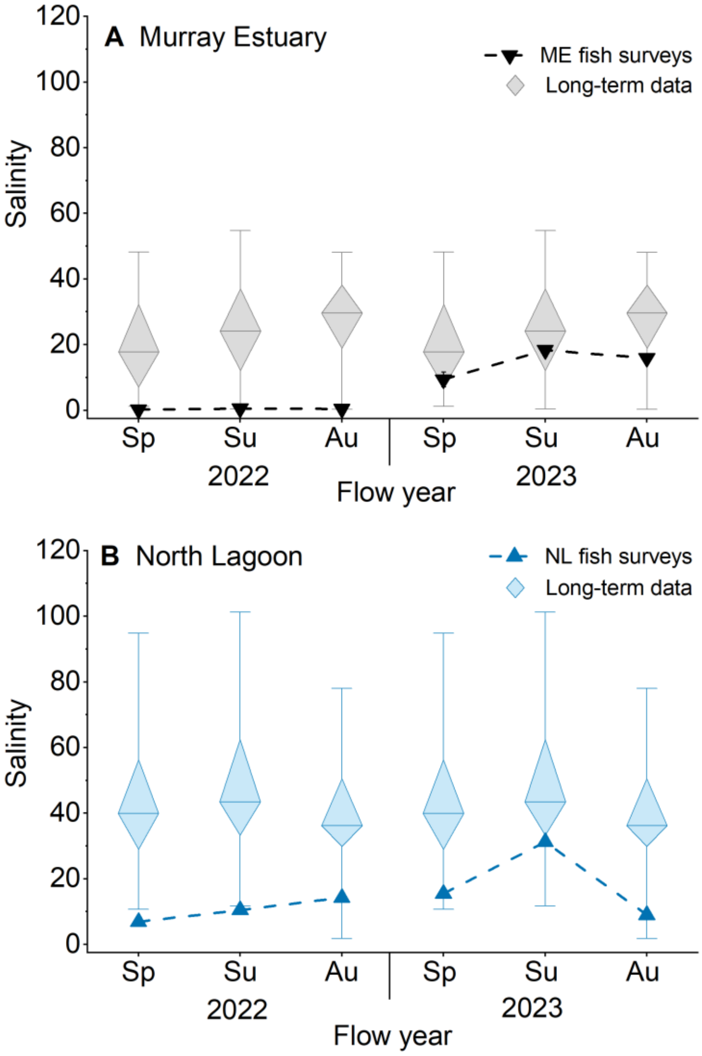
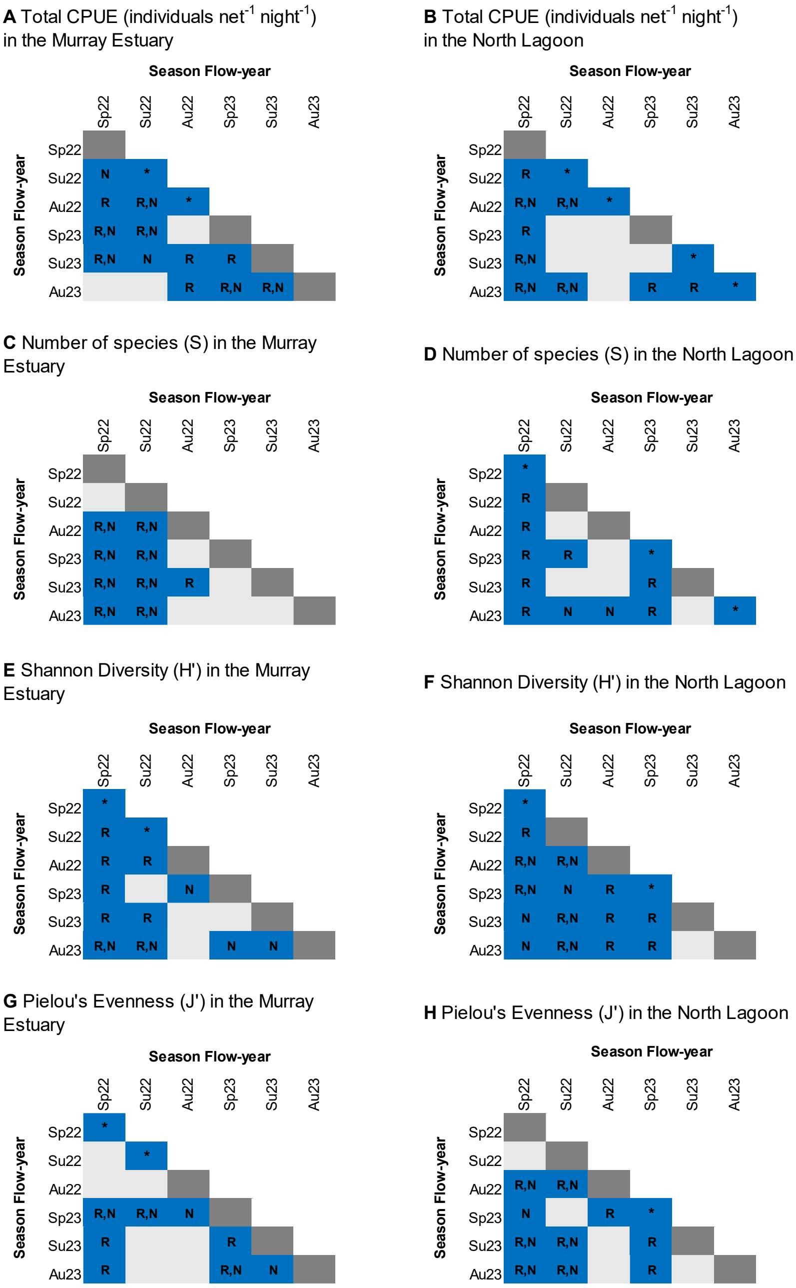


Figure S3. Salinity during fish surveys in this study (Flow year 2022 and 2023) compared to long term data (2000-2022) in **A)** the Murray Estuary and **B)** North Lagoon of the Coorong over spring (Sp), summer (Su) and autumn (Au) seasons. Daily data were averaged across all months within a given season and sourced from Water Data SA (DEW, 2025).



A Total CPUE (individuals net^{-1} night^{-1}) in the Murray Estuary

B Total CPUE (individuals net^{-1} night^{-1}) in the North Lagoon

C Number of species (S) in the Murray Estuary

D Number of species (S) in the North Lagoon

E Shannon Diversity (H') in the Murray Estuary

F Shannon Diversity (H') in the North Lagoon

G Pielou's Evenness (J') in the Murray Estuary

H Pielou's Evenness (J') in the North Lagoon

Figure S4. Visual summary of PERMANOVA pairwise test results of native fish **A–B)** total catch-per-unit effort (CPUE) (individuals net^{-1} night^{-1}) **C–D)** Number of species (S) **E–F)** Shannon Diversity index (H') and **G–H)** Pielou's Evenness (J') in the Murray Estuary and North Lagoon of the Coorong. Habitat x season-year interaction: *= significant difference $p<0.05$ between reef and non-reef habitats within a given season-year, R= significant difference $p<0.05$ in reef habitats between season-year pairwise comparison and N= significant difference $p<0.05$ in non-reef habitats between season-year pairwise comparison. Labels indicate season; Sp: spring; Su: summer; Au: autumn and flow year; 22: 2022; 23: 2023.

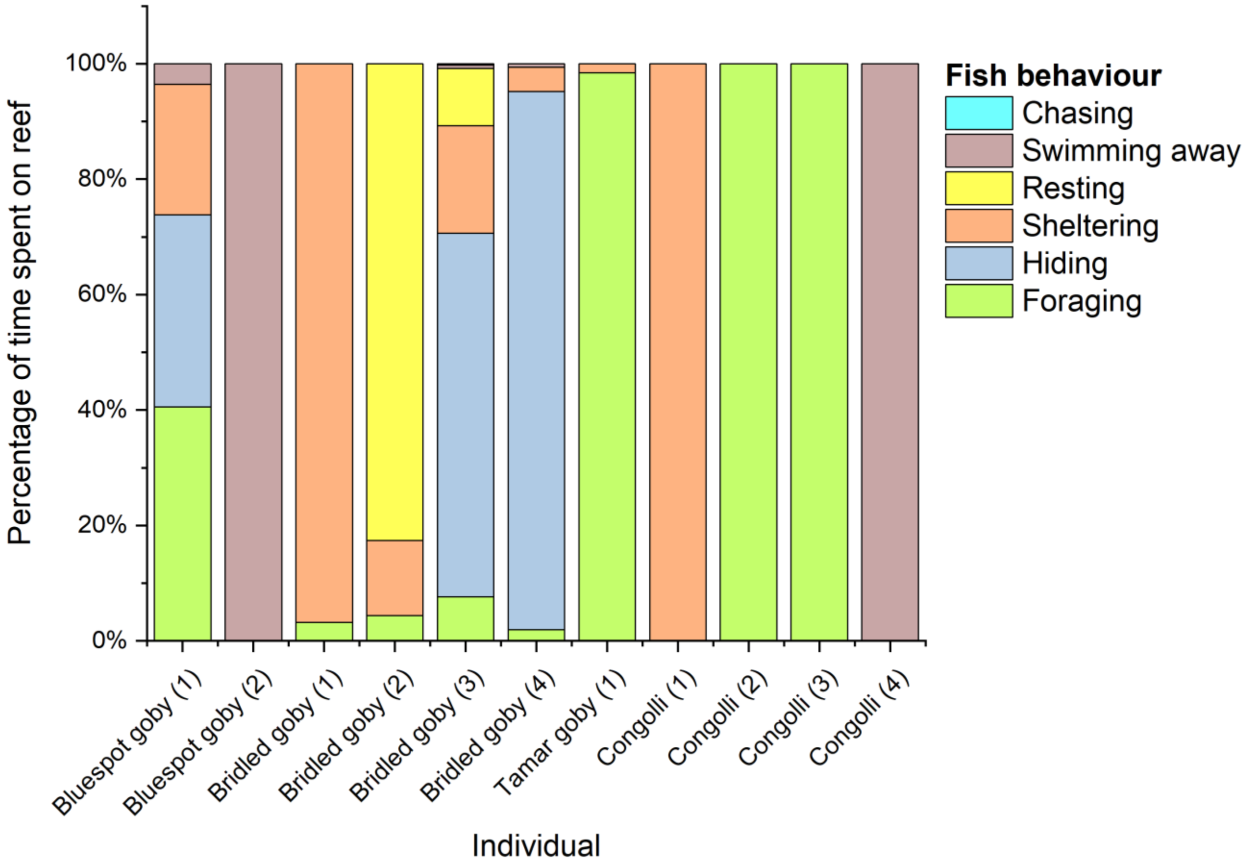


Figure S5. Underwater video observation of fish behaviour's from a 30-minute deployment at a *Ficopomatus enigmaticus* reef in the North Lagoon during summer 2023. Video footage was obtained using an unbaited remote underwater video station (UBRUVS)[7] set at a depth of 1.5 m at Long Point on the 5/12/2023. Individuals were tracked from the time first spotted in the video until swimming out of the field of view. Recorded behavior's were chasing: an individual fish chasing toward another individual fish; swimming away: individual fish swimming past the reef; resting: individual fish is still and visible in the vicinity of the reef; sheltering: individual fish is still and present in a reef crevice or under the reef edge; hiding: individual fish goes into a reef crevice or under a reef edge for some time before reappearing from the same spot in the reef.

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[7] Ebner B.C., Morgan D.L., 2013. Using remote underwater video to estimate freshwater fish species richness. Journal of Fish Biology 82,1592–612. https://doi:10.1111/jfb.12096.

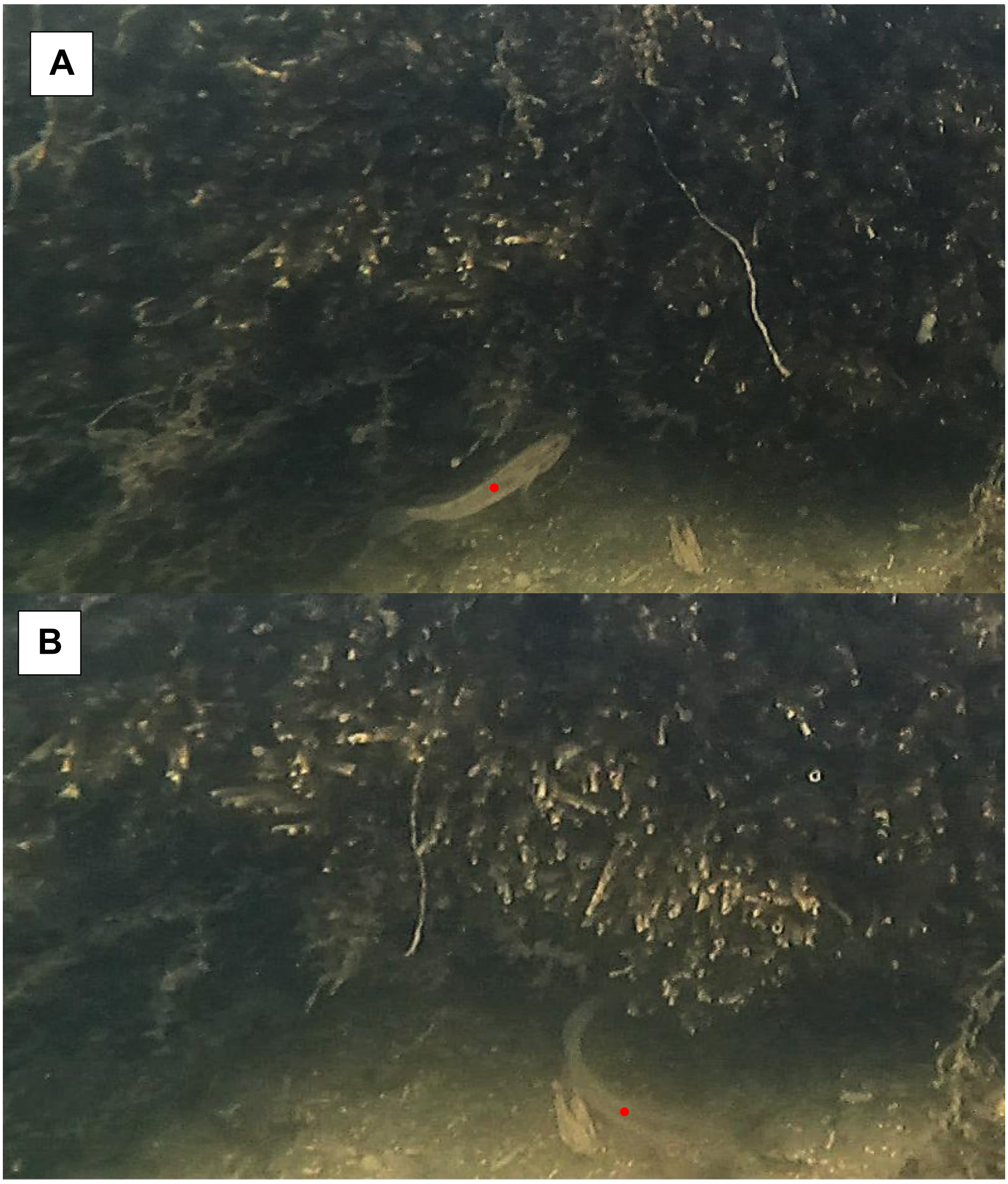

Fig S6. Example of trophic interaction between bridled goby and *Ficopomatus enigmaticus* reef in the North Lagoon of the Coorong where **A)** bridled goby makes a lunge to the reef edge, biting tube edges and **B)** feeding crowns of *F. enigmaticus* retract into tubes, exposing the white tube tips of reef, and same individual of bridled goby departs reef. Video footage was obtained using an unbaited remote underwater video station (UBRUVS)[8] set at a depth of 1.5 m for 30 minutes at Long Point on the 5/12/2023.

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[8] Ebner B.C., Morgan D.L., 2013. Using remote underwater video to estimate freshwater fish species richness. Journal of Fish Biology 82,1592–612. https://doi:10.1111/jfb.12096.

Table S1. Surveys dates in flow years 2022 and 2023, including season, month and dates for fish surveys conducted in the Murray Estuary (ME) and North Lagoon (NL) regions of the Coorong.

Flow Year	Season	ME survey dates	NL survey dates
2022	Spring	24–26/10/22	3–5/11/22
2022	Summer	23–25/11/22	30/11–2/12/22
2022	Autumn	21–23/3/23	11–13/4/23
2023	Spring	16–18/10/23	23–25/10/23
2023	Summer	13–15/12/23	6–8/12/23
2023	Autumn	11–13/3/24	19–21/3/24

Table S2. Criteria thresholds for stressors were categorised as either none, moderate or extreme. Environmental stressors that were present during the surveys included a flood, heatwave and cyanobacteria (blue-green algae, 'BGA' bloom), and their criteria thresholds were based on historical flood data for the Coorong (Ryan, 2018) and Australian guidelines for a heatwave based on atmospheric conditions (BOM, 2024) and cyanobacteria bloom (Australian Government, 2008). The biological stressor of invasives (fish) on native fish during the surveys were scored based on the percentage of invasives contributing to the total catch.

	Stressor score		
Stressor	None	Moderate	Extreme
Flood	Freshwater flows <4,723 GL $year^{-1}$ (less than post-regulation mean discharge)	Freshwater flows >4,723 GL $year^{-1}$ (greater than post-regulation mean discharge)	Freshwater flows >12,233 GL $year^{-1}$ (greater than pre-regulation mean discharge)
Heatwave	None	Days ≥3, abnormally high maximum and minimum temperatures	Days ≥ 4, abnormally high maximum and minimum temperatures
Cyanobacteria bloom	Blue-green algae biovolume <0.4 mm^3 L^{-1}	Blue-green algae biovolume ≥ 0.4 mm^3 L^{-1}	Blue-green algae biovolume > 4 mm^3 L^{-1} (toxic BGA dominant) or >10 mm^3 L^{-1} (toxic BGA non-dominant)
Invasives	Invasive freshwater stragglers (i.e. European carp, redfin perch, goldfish and oriental weatherloach) <10% of total catch	Invasive freshwater stragglers (i.e. European carp, redfin perch, goldfish and oriental weatherloach) <75% of total catch	Invasive freshwater stragglers (i.e. European carp, redfin perch, goldfish and oriental weatherloach) ≥75% of total catch

Table S3. Environmental stressor data for fish surveys in the Murray Estuary (ME) and North Lagoon (NL) during spring (sp), summer (su) and autumn (au) in flow years 2022 and 2023. Highlighted boxes indicate stressor scoring (none, moderate or extreme) for each survey, from thresholds given in Table S2. Barrage flow data was sourced from Water Data SA (2024), heatwave data were sourced from BOM (2024) and presented in Figure S3 and 4), blue-green algae (BGA) data were sourced from Mosley et al. (2023), and invasive catch data were collected in this study.

A ME surveys		**Flood**	**Heatwave**	**Cyanobacteria bloom**			**Invasives**
Season-Flow year	Fish survey date	Barrage flow (GL year^{-1})	Duration (dates)	BGA water sampling date	BGA biovolume (mm^3 L^{-1})	Toxic BGA biovolume (mm^3 L^{-1})	Invasive fish catch (% of total catch)
Sp-22	24–26/10/22	16,597	None	9/11/2022	0.02	0.00	0.6
Su-22	23–25/11/22		None	23/11/2022	0.03	0.00	21.9
Au-22	21–23/3/23		None	14/3/2023	1.66	0.02	86.2
Sp-23	16–18/10/23	5,129	None	27/9/2023	0.27	0.00	15.7
Su-23	13–15/12/23		None	No data	No data	No data	8.9
Au-23	11–13/3/24		8–11/3/24	20/3/2024	0.03	0.00	0.0
Sp-22	3–5/11/22	16,597	None	9/11/2022	0.00	0.00	0.0
Su-22	30/11–2/12/22		None	23/11/2022	0.02	0.00	4.7
Au-22	11–13/4/23		None	12/4/2023	0.04	0.00	0.2
Sp-23	23–25/10/23	5,129	None	27/9/2023	0.00	0.00	0.6
Su-23	6–8/12/23		None	No data	No data	No data	0.0
Au-23	19–21/3/24		None	20/3/2024	0.00	0.00	0.0

Table S4. The density of juvenile fish (CPUE) for each species sampled at the reef and non-reef habitats in each the Murray Estuary (ME) and North Lagoon (NL) across seasons spring (Sp), summer (Su) and autumn (Au) for surveys pooled over two consecutive flow years (2022 and 2023). Fish species are listed by functional guild (Potter et al, 2015) and ticks are given for small bodied species (SB, <15 cm TL at size of maturity). For each species, the range in total length (TL, minimum–maximum) for individuals caught and the TL of size of maturity is included (estimated sizes of maturity are indicated by an *).

Species by functional guild	SB	TL (min–max in cm)	TL of maturity (cm)	ME Reef			ME Non-reef			NL Reef			NL Non-reef		
				Au	Sp	Su	Au	Sp	Su	Au	Sp	Su	Au	Sp	Su
Freshwater Category															
Freshwater-estuarine Opportunist															
Philypnodon grandiceps	✓	2.2–7.6	4.2	-	0.49	0.07	0.44	2.82	0.41	0.06	0.06	0.16	-	0.06	0.06
Nematalosa erebi		11.0	10*	-	-	-	-	-	-	-	-	-	-	-	-
Freshwater Straggler															
Retropinna semoni	✓	2.1–8.1	6.7*	-	0.31	0.25	-	1.31	0.06	0.25	-	0.25	0.06	-	-
Macquaria ambigua		7.2–19.7	50.7*	0.06	0.13	0.19	-	-	0.19	-	-	-	-	-	-
Hypseleotris spp.	✓	2.3–4.6	4.7*	-	-	-	0.13	-	0.31		-	-	-	-	0.06
Diadromous Category															
Catadromous															
Pseudaphritis urvillii		1.0–20.0	16.5	2.51	14.56	24.26	5.38	3.68	19.36	47.83	5.20	31.69	39.97	15.34	13.88
Semi-catadromous															
Galaxias maculatus	✓	1.8–13.5	5.0*	1.57	5.97	2.60	0.08	19.54	5.67	-	-	0.62	-	-	0.06
Estuarine Category															
Solely Estuarine															
Acanthopagrus butcheri		1.7–36.0	28.9	-	0.06	0.25	0.03	-	0.06	0.94	-	-	-	-	-
Afurcagobius tamarensis	✓	0.9–13.1	5.3	19.74	0.70	1.66	21.15	0.51	0.37	0.06	0.13	0.32	0.06	0.06	-
Atherinosoma microstoma	✓	0.9–10.8	4.5	0.74	0.17	0.14	86.09	0.47	0.16	321.13	1.32	2.00	35.28	1.86	3.95
Pseudogobius olorum	✓	1.5–7.0	3.6	0.06	0.06	-	-	-	-	5.75	1.55	0.20	1.95	0.44	0.76
Tasmanogobius lasti	✓	0.3–6.5	2.7*	0.31	2.08	2.51	0.19	0.25	0.47	1.25	-	0.06	0.31	-	0.06
Estuarine and Marine															
Arenigobius bifrenatus	✓	2.5–15.5	12.0*	0.13	0.13	-	0.44	0.13	-	1.69	0.13	4.72	0.25	0.63	0.68
Gymnapistes marmoratus		12.5–13.5	15.3*	-	-	-	-	-	0.06	0.06	-	-	-	-	-
Marine Category															
Marine-estuarine Opportunist															
Aldrichetta forsteri		2.5–37.5	25.6	2.44	1.68	2.50	10.23	0.13	0.38	-	0.63	0.06	0.06	0.38	0.69
Arripis truttaceus		4.0–13.6	55.0	-	-	0.38	0.06	-	0.06	-	0.44	0.06	-	0.06	-
Hyperlophus vittatus	✓	1.6–6.4	5.8	405.06	28.94	61.75	843.00	0.75	426.32	-	3.63	0.13	-	0.06	0.06
Rhombosolea tapirina		1.3–23.8	20.3	0.19	0.25	0.06	0.13	0.94	0.13	-	1.32	0.06	-	0.56	-
Marine Straggler															
Acanthaluteres spilomelanurus		5.9	9.3*	0.06	-	-	-	-	-	-	-	-	-	-	-
Cristiceps australis		9.0	20.0*	-	-	-	0.06	-	-	-	-	-	-	-	-
Hyporhamphus melanochir		10.4	34.0*	-	-	-	-	-	-	0.06	-	-	-	-	-
Mitotichthys tuckeri		9.2	12.7*	-	-	0.06	-	-	-	-	-	-	-		

Table S5. SIMPER results showing the main fish species contributing to differences in the community between reef and non-reef habitats sampled in the Murray Estuary during spring 2022, summer 2022 and spring 2023 (season, flow year). Values shown are the relative abundances of the species and their cumulative contributions. Highest abundances of taxa in the comparison are underlined.

Species	Reef	Non-reef	Cum. Contrib. %
Spring 2022	**Average dissimilarity= 41.49%**		
Galaxias maculatus	2.23	3.99	24.67
Pseudaphritis urvillii	1.49	0.45	37.93
Afurcagobius tamarensis	1.95	1.16	49.76
Philypnodon grandiceps	1.08	1.67	61.36
Rhombosolea tapirina	0.42	0.84	69.83
Tasmanogobius lasti	0.72	0.33	77.95
Summer 2022	**Average dissimilarity= 46.13%**		
Galaxias maculatus	1.3	2.34	14.52
Philypnodon grandiceps	0.39	1.34	27.03
Tasmanogobius lasti	1.22	0.45	39.18
Hyperlophus vittatus	0.26	0.99	49.31
Afurcagobius tamarensis	0.83	0.15	58.38
Hypseleotris spp.	0.00	0.55	65.29
Aldrichetta forsteri	0.56	0.21	70.87
Spring 2023	**Average dissimilarity= 66.49%**		
Tasmanogobius lasti	1.00	0.12	22.69
Retropinna semoni	0.29	0.49	38.4
Rhombosolea taperina	0.00	0.47	51.09
Afurcagobius tamarensis	0.58	0.25	63.65
Galaxias maculatus	0.27	0.53	75.67

Table S6. SIMPER results showing the main fish species contributing to differences in the community between reef and non-reef habitats sampled in the North Lagoon during spring 2022, summer 2022, spring 2023, summer 2023 and autumn 2023 (season, flow year). Values shown are the relative abundances of the species and their cumulative contributions. Highest abundances of taxa in the comparison are underlined.

Species	Reef	Non-reef	Cum. Contrib. %
Spring 2022	**Average dissimilarity= 50.43%**		
Arenigobius bifrenatus	0.09	0.85	32.36
Pseudogobius olorum	0.93	1.01	56.49
Afurcagobius tamarensis	0.38	0.6	75.23
Summer 2022	**Average dissimilarity= 54.48%**		
Arenigobius bifrenatus	2.56	0.7	30.39
Afurcagobius tamarensis	1.96	0.5	53.3
Pseudogobius olorum	1.46	1.62	66.63
Pseudaphritis urvillii	0.74	0.25	74.97
Spring 2023	**Average dissimilarity= 53.68%**		
Rhombosolea tapirina	1.33	0.49	27.28
Pseudogobius olorum	1.06	0.38	47.39
Arripis truttaceus	0.58	0.11	60.72
Pseudaphritis urvillii	0.95	1.42	73.19
Summer 2023	**Average dissimilarity= 43.22%**		
Afurcagobius tamarensis	0.95	0.19	27.86
Pseudaphritis urvillii	2.16	1.51	55.47
Pseudogobius olorum	0.61	0	74.94
Autumn 2023	**Average dissimilarity= 50.03%**		
Atherinosoma microstoma	1.7	0.29	23.43
Pseudaphritis urvillii	2.84	2.36	45.65
Pseudogobius olorum	1.87	0.86	64.28
Acanthopagrus butcheri	0.98	0	79.28

Appendix D. Supplementary material for Chapter 5

Table S1. Surveys for demersal macroinvertebrates and benthic macroinvertebrates (*).

Flow Year	Season	ME survey dates	NL survey dates
2022	Spring	24–26/10/22	3–5/11/22
2022	Summer	23–25/11/22	30/11–2/12/22
2022	Autumn	21–23/3/23	11–13/4/23
2023	Spring*	16–18/10/23	23–25/10/23
2023	Summer*	13–15/12/23	6–8/12/23
2023	Autumn	11–13/3/24	19–21/3/24

Table S2. Main test results from PERmutational ANalysis Of VAriance (PERMANOVA) of statistical differences in total catch-per-unit-effort (CPUE) and community structure of demersal macroinvertebrates sampled between nights (night 1 and night 2) and between habitats (reef and non-reef).

		Total CPUE		**Demersal macroinvertebrate community**	
Main test	df	Pseudo-F	$P_{(PERM)}$	Pseudo-F	$P_{(PERM)}$
Night	1	1.75	0.19	2.00	0.10
Habitat	1	22.40	**<0.01**	7.29	**<0.01**
Habitat x night	1	0.06	**0.81**	0.22	0.91
Residual	144				

Table S3. Decapod sizes (carapace width in mm) from demersal catches in the reef and non-reef habitats in the Murray Estuary (ME) and North Lagoon (NL) of the Coorong across seasons spring (Sp), summer (Su) and autumn (Au) for surveys pooled over two consecutive flow years (2022 and 2023)

Species	Carapace width in mm (min–max)	ME		NL		Season		
		Reef	Non-reef	Reef	Non-reef	Au	Sp	Su
Amarinus laevis	10–32	11.6±0.2	12.3±0.3	18.6±0.8	16.8±0.9	15.7±0.6	13.0±0.3	11.9±0.3
Halicarcinus ovatus	2–13	7.6±0.6	6.0±1.0	13.0±0.0	-	6.5±0.7	10.8±0.6	9.5±1.5
Helograpsus haswellianus	8–10	-	9.3±0.7	-	-	-	9.3±0.7	-
Paragrapsus gaimardii	5–65	18.7±0.9	21.2±0.9	26.7±4.8	24.3±1.9	17.8±1.1	21.7±0.8	21.6±2.2

Table S4. Diversity indices of **A)** Species richness (S), **B)** Shannon diversity (H') and **C)** Pielou's evenness of demersal macroinvertebrates surveyed across the Murray Estuary (ME) and North Lagoon (NL) of the Coorong in reef and non-reef habitats. Surveys include spring, summer and autumn in flow years 2022 and 2023.

	ME		NL	
Season/ Flow year	Reef	Non-reef	Reef	Non-reef
A Species richness (S)				
Spring 2022	2	4	3	2
Summer 2022	3	5	3	4
Autumn 2022	2	4	2	2
Spring 2023	5	4	4	3
Summer 2023	5	4	3	2
Autumn 2023	4	4	3	3
B Shannon Diversity (H')				
Spring 2022	0.49	0.98	0.66	0.09
Summer 2022	0.53	0.65	0.59	0.66
Autumn 2022	0.36	1.26	0.08	0.34
Spring 2023	0.40	0.94	0.45	0.50
Summer 2023	1.28	0.89	0.14	0.38
Autumn 2023	1.06	0.43	0.24	0.60
C Pielou's Evenness (J')				
Spring 2022	0.71	0.71	0.60	0.13
Summer 2022	0.49	0.40	0.54	0.48
Autumn 2022	0.52	0.91	0.11	0.49
Spring 2023	0.25	0.68	0.33	0.46
Summer 2023	0.79	0.64	0.13	0.54
Autumn 2023	0.76	0.31	0.22	0.54

Table S5. Decapod sizes (carapace width in mm) from the reef matrix of *F. enigmaticus* reefs in the Murray Estuary and North Lagoon of the Coorong during spring and summer in flow year 2023.

	Spring		Summer	
Species	Carapace width in mm (min–max)	Carapace width in mm (mean ± s.e.)	Carapace width in mm (min–max)	Carapace width in mm (mean ± s.e.)
Murray Estuary				
Amarinus laevis	1.0–7.0	4.2 ± 0.9	0.4–8.5	4.4 ± 1.0
Halicarcinus ovatus	na	4.0 ± 0.0	-	-
Helograpsus haswellianus	na	2.5 ± 0.0	-	-
Hymenosomatidae indet. (juveniles)	-	-	0.6–1.2	1.0 ± 0.1
Paragrapsus gaimardii	-	-	2.0–4.5	3.2 ± 0.3
North Lagoon			-	-
Paragrapsus gaimardii	-	-	na	5.5 ± 0.0

Table S6. Univariate PERMmutational ANalysis Of VAriance (PERMANOVA) **a)** main test results for differences in the benthic macroinvertebrate abundance of major taxa groups of A) Crustacea B) Insecta C) Annelida, D) Gastropoda and C) Bivaliva. Tests were conducted on Substrates (Su) (reef sediment, reef matrix and non-reef sediment), Regions (Re) (Murray Estuary and North Lagoon) and Seasons (Se) (spring and summer in flow year 2023). Significant values (p<0.05) are indicated in bold.

Source	df	MS	Pseudo-F	*p*	df	MS	Pseudo-F	*p*
	A) Crustacea				**B) Insecta**			
Substrate (Su)	2	11153.00	111.73	**<0.01**	2	11.37	1.23	0.31
Region (Re)	1	7208.40	72.21	**<0.01**	1	6443.40	695.26	**<0.01**
Season (Se)	1	486.29	4.87	**0.03**	1	57.62	6.22	**0.01**
Su x Re	2	4875.00	48.84	**<0.01**	2	0.60	0.06	0.94
Su x Se	2	152.63	1.53	0.23	2	96.38	10.40	**<0.01**
Re x Se	1	525.85	5.27	**0.02**	1	48.72	5.26	**0.02**
Su x Re x Se	2	291.47	2.92	0.06	2	103.13	11.13	**<0.01**
Res	84	99.83				9.27		
Total	95							
	C) Annelida				**D) Gastropoda**			
Substrate (Su)	2	237.17	46.18	**<0.01**	2	6.38	1.71	0.18
Region (Re)	1	348.77	67.92	**<0.01**	1	1.01	0.27	0.64
Season (Se)	1	9.54	1.86	0.18	1	0.01	0.00	0.97
Su x Re	2	1.82	0.35	0.71	2	10.99	2.96	**0.04**
Su x Se	2	7.20	1.40	0.25	2	4.74	1.27	0.29
Re x Se	1	17.81	3.47	0.07	1	8.06	2.17	0.14
Su x Re x Se	2	18.67	3.64	**0.03**	2	14.97	4.03	**0.01**
Res	84	5.14			84	3.72	1.71	0.18
Total	95				95			
	E) Bivalvia							
Substrate (Su)	2	97.44	58.26	**<0.01**				
Region (Re)	1	899.55	537.85	**<0.01**				
Season (Se)	1	0.69	0.41	0.53				
Su x Re	2	97.44	58.26	**<0.01**				
Su x Se	2	10.14	6.06	**<0.01**				
Re x Se	1	0.69	0.41	0.52				
Su x Re x Se	2	10.14	6.06	**<0.01**				
Res	84	1.67						
Total	95							

Table S7. Univariate PERMmutational ANalysis Of VAriance (PERMANOVA) main test results for differences in the CWM of benthic macroinvertebrates for feeding modes of **A)** sub-surface deposit feeder **B)** scavenger/opportunist **C)** predator, **D)** grazer/scraper **E)** filter/suspension feeder and **F)** Deposit feeder. Tests were conducted on Substrates (Su) (reef sediment, reef matrix and non-reef sediment), Regions (Re) (Murray Estuary and North Lagoon) and Seasons (Se) (spring and summer in flow year 2023). Significant values (p<0.05) are indicated in bold.

Source	df	MS	Pseudo-F	*p*	df	MS	Pseudo-F	*p*
	A Sub-surface deposit feeder				**B Scavenger/opportunist**			
Substrate (Su)	2	0.02	29.90	**<0.01**	2	0.05	22.80	**<0.01**
Region (Re)	1	0.01	12.02	**<0.01**	1	0.97	439.23	**<0.01**
Season (Se)	1	0.00	1.03	0.32	1	0.00	0.18	0.67
Su x Re	2	0.02	22.31	**<0.01**	2	0.07	31.91	**<0.01**
Su x Se	2	0.00	1.10	0.34	2	0.01	3.27	**0.04**
Re x Se	1	0.00	0.66	0.42	1	0.00	0.01	0.90
Su x Re x Se	2	0.00	0.92	0.41	2	0.00	1.22	0.30
Res	84	0.00			84			
Total	95				95			
	C Predator				**D Grazer/scraper**			
Substrate (Su)	2	0.01	8.24	**<0.01**	2	0.00	0.97	0.47
Region (Re)	1	0.08	134.40	**<0.01**	1	0.00	0.18	0.97
Season (Se)	1	0.00	0.64	0.43	1	0.00	1.31	0.27
Su x Re	2	0.00	8.06	**<0.01**	2	0.00	2.73	**<0.01**
Su x Se	2	0.00	4.05	**0.01**	2	0.00	0.54	0.88
Re x Se	1	0.00	0.78	0.39	1	0.00	0.14	0.98
Su x Re x Se	2	0.00	4.34	**0.01**	2	0.00	1.01	0.45
Res	84	0.00			84	0.00		
Total	95				95			
	E Filter/suspension feeder				**F Deposit feeder**			
Substrate (Su)	2	0.03	36.30	**<0.01**	2	0.00	1.43	0.25
Region (Re)	1	0.04	53.76	**<0.01**	1	0.16	138.05	**<0.01**
Season (Se)	1	0.00	0.94	0.34	1	0.00	1.24	0.27
Su x Re	2	0.02	26.96	**<0.01**	2	0.00	0.81	0.46
Su x Se	2	0.00	3.11	0.05	2	0.00	3.71	**0.03**
Re x Se	1	0.00	0.26	0.62	1	0.00	0.29	0.59
Su x Re x Se	2	0.00	0.30	0.74	2	0.00	1.79	0.17
Res	84	0.00			84	0.00		
Total	95				95			

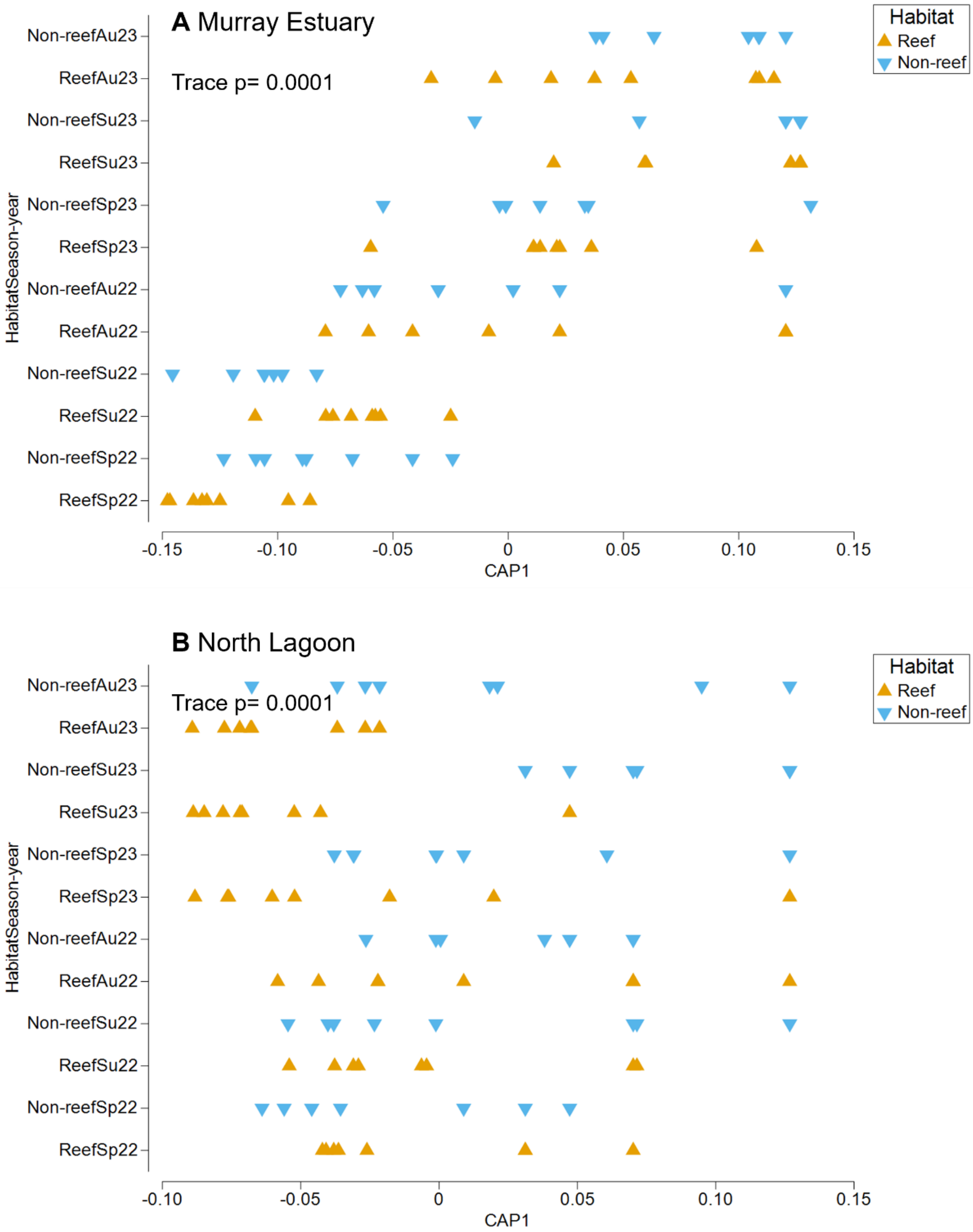

Figure S1. CAP constrained ordination plot of the demersal macroinvertebrate community showing the separation of groups by habitat (reef and non-reef) and season (spring (sp), summer (su), autumn (au) in flow years 2022 and 2023) within **A)** the Murray Estuary (m=1 axis, allocation success rate= 20.83%) and **B)** North Lagoon of the Coorong (m=1 axis, allocation success rate= 14.58%).

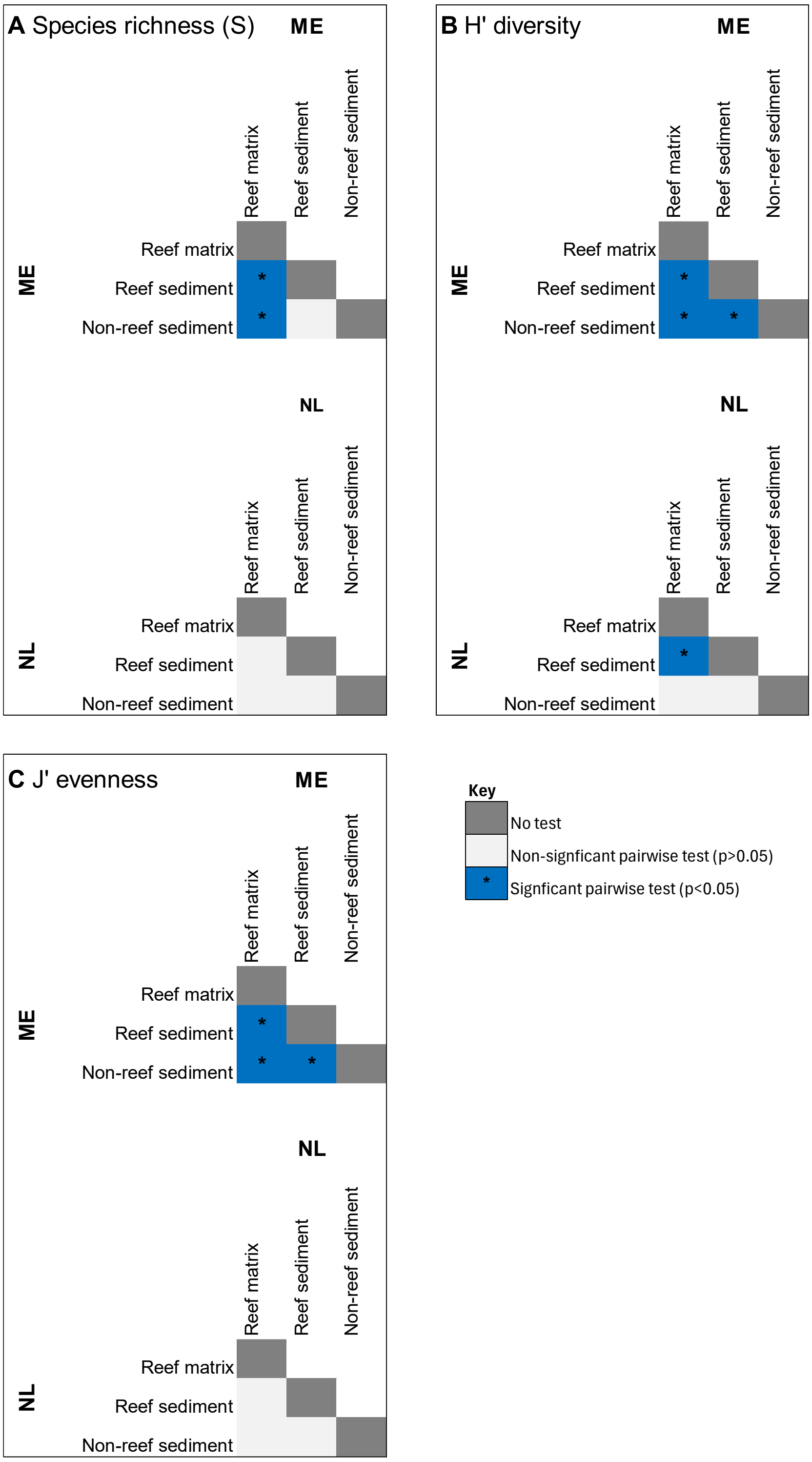

Figure S2. Visual summary of PERMANOVA pairwise test results of benthic macroinvertebrate **A)** Species richness (S) **B)** Shannon diversity (H’) **C)** Pielou’s Evenness (J’) in the Murray Estuary (ME) and North Lagoon (NL) of the Coorong. Substrate x Region interaction: *=significant difference p<0.05 between a pairwise comparison of substrate in a given region.

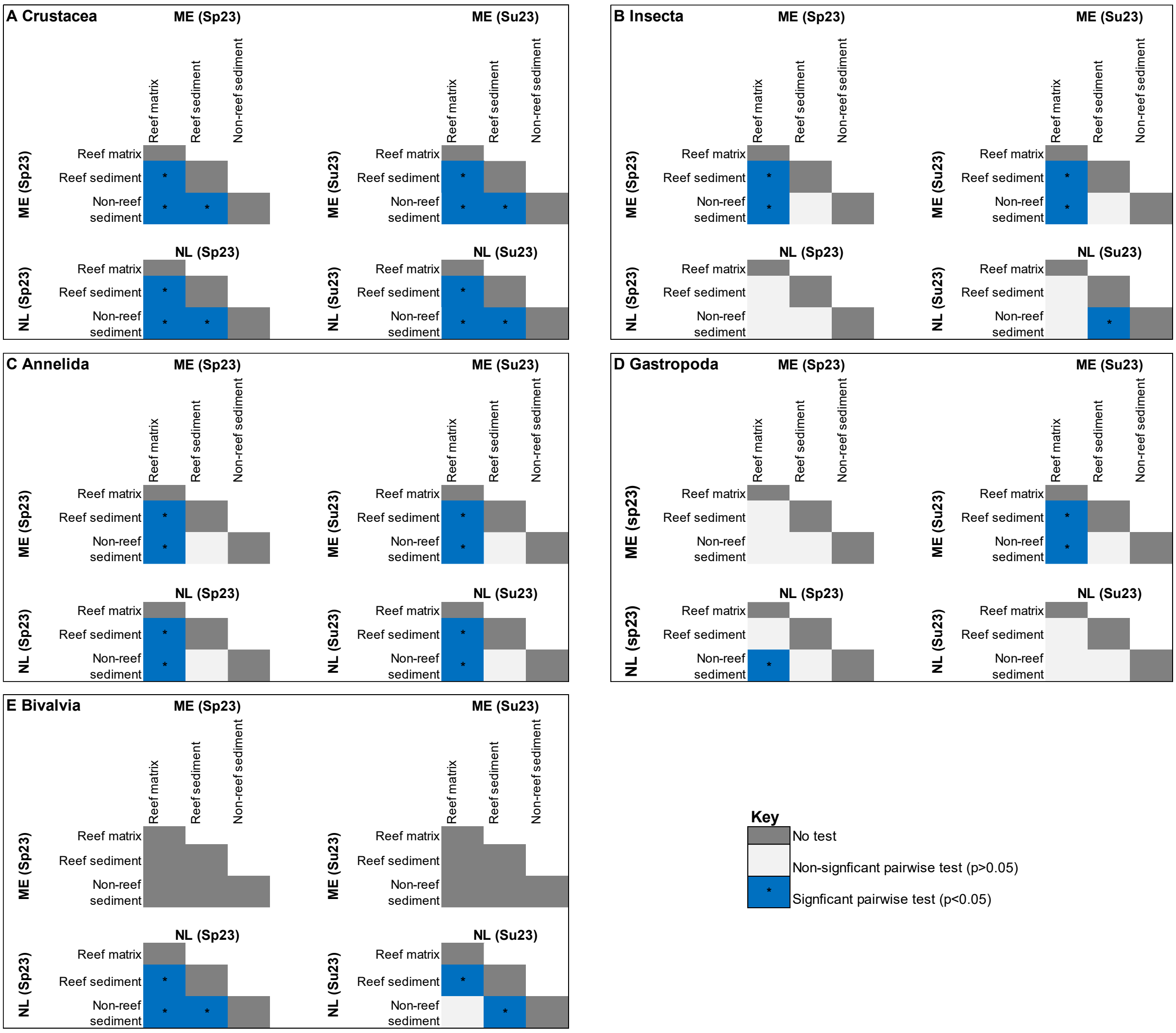

Figure S3. Visual summary of PERMANOVA pairwise test results of benthic macroinvertebrates for major taxa groups of **A)** Crustacea **B)** Insecta **C)** Annelida **D)** Gastropoda and **E)** Bivalvia in the Murray Estuary (ME) and North Lagoon (NL) of the Coorong. Substrate x Region x Season interaction: *=significant difference $p<0.05$ between a pairwise comparison of substrate in a given region and season. Labels indicate season and flow-year: spring 2023 (Sp23) and summer 2023 (Su23).