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Spatial-ecological relationships of a threatened foundation species across multiple spatial scales

Rick C. Leong

A thesis submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy



Supervised by Paul E. Gribben, Alistair G.B. Poore,

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May 2022

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Publication Details #1

Full Title:	Variation in the density and body size of a threatened foundation species across multiple spatial scales
Authors:	Rick Leong, Ana Bugnot, Ezequiel Marzinelli, Will Figueira, Katherine Erickson, Alistair Poore & Paul Gribben
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Location of the work in the thesis and/or how the work is incorporated in the thesis:	Remnant Sydney rock oyster reefs in New South Wales, Australia. The research work was conducted in the study site as part of my Ph.D. research that uses the spatial configuration of Remnant Sydney rock oyster reefs to understand the variation of oyster population characteristics (i.e. density and body size) across the spatial scales where the oyster reefs are found in.

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Rick



(Someone has been looking forward to a celebratory cake since the '90s!)

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Thesis Abstract

Foundation species such as trees, corals, kelp and seagrasses are found across multiple spatial scales (i.e., local to biogeographic scales) and provide many ecosystem services. Understanding species distributions across multiple spatial scales can inform species resilience and important spatial scales for restoration and management of threatened foundation species. However, only few studies have investigated their distribution patterns across all spatial scales they exist in. The Sydney Rock Oyster, *Saccostrea glomerata*, is a threatened, reef-building, intertidal foundation species that is found on the Australian south-eastern coast. Remnant reefs in different estuaries consist of patches of different shapes, size and distances (i.e., connectivity) from one another. In this thesis, I utilised this spatial variation to investigate how oyster population characteristics (e.g., body size and density), population processes (e.g., recruitment) and biodiversity provision by remnant *S. glomerata* reefs vary within patches (e.g., surface elevation), with patch-scale attributes (e.g., patch-area), among patches (e.g., distance between patches) and on a regional scale (i.e., among estuaries). My major finding was that variation at the largest scale (among estuaries) was the best predictor of body size and density of oysters, faunal communities and oyster recruitment. Although smaller scales (i.e., scales within estuary) relationships also occurred for all metrics, these were often in different directions (positive, negative or neutral) across estuaries. This suggests that larger scale processes are setting the context to smaller scale effects on metrics recorded. To investigate the effect of larger scale processes on oyster recruitment, I conducted a field experiment across six estuaries. The major finding was that oyster recruitment across these estuaries was negatively correlated to sedimentation loads in each estuary. In summary, my thesis highlights the need to understand ecological patterns of foundation species across multiple spatial scales and the influence of large-scale processes that may drive ecological patterns at smaller scales. From a restoration perspective, prioritising important spatial scales that maximise population characteristics and ecosystem functions, especially the recruitment of the target species can aid in efforts to promote long-term oyster reef sustainability, enhance restoration success and the services they provide.

Chapter 1

General Introduction

1.1 Introduction

A central theme in ecology is understanding patterns and drivers of species' spatial distributions. Many studies have quantified how variation in life-history (e.g., body size) and ecological processes (e.g., recruitment) vary from local scales to regional and international scales to influence distributions (MacArthur & Wilson 1967; Kareiva & Andersen 1988; Hastings & Wolin 1989; Wiens 1989). Few studies, however, have integrated across these scales to determine which scales are the most important determinants of patterns in abundance and distribution (Suárez-Castro et al. 2022). Foundation species (*sensu* Dayton 1972) such as corals, trees, seaweeds and salt marsh plants, provide ecosystem services including amelioration of abiotic and biotic stress, biodiversity provision and carbon sequestration (see review of ecosystem services and functions of foundation species by Ellison 2019). Because they are spatially dominant but can be patchily distributed across multiple spatial scales, understanding the scale at which processes control their abundance and, by extension the services they provide, is critical to their management.

Foundation species are frequently being lost. For example, ~19% global cover losses were recorded for seagrass meadows from 1880 to 2016 (Dunic et al. 2021) and losses of ~17% for tropical moist forests from 1990 to 2019 (Vancutsem et al. 2021). These losses have brought staggering declines in ecosystem functions and services leading to disruption of fundamental ecosystem processes, collapse of other ecosystems and economic loss (Ellison et al. 2005). Because of these declines, foundation species are now the target of many management and restoration strategies worldwide (Ellison et al. 2005; Castorani et al. 2018; Sarà et al. 2021). However, the success of these restoration efforts has been hindered by knowledge gaps on the spatial distribution of population characteristics, ecological processes and ecosystem functions of target species. For example, restoration is most likely to be successful for populations within spatial distributions that promote recruitment, however this information is lacking for restoration efforts that aim to increase recruitment in target sites (Coen & Luckenbach

2000; Boström et al. 2011). Understanding the spatial distributions of processes that control the abundance of a foundation species across different spatial scales can therefore inform the spatial scales that are relevant for restoration success and develop appropriate management strategies (Callicott 2002; Lindenmayer 2020).

While many studies have documented spatial variation of population characteristics and the ecological processes that influence foundation species and the biodiversity they support, there is mixed evidence to indicate which of the scales, from local, landscape and regional, is likely to be most important (see Table 1.1 for ecological patterns of foundation species at these scales). For instance, patch-size increase at local scales is predicted to increase biodiversity (*sensu* island biogeography theory by MacArthur & Wilson 1967), but this effect is less clear beyond a threshold patch-size (the small-island effect *sensu* Lomolino & Weiser 2001). Moreover, spatial-ecological processes can interact across multiple spatial scales (Angelini et al. 2015; Crotty et al. 2018; Loke et al. 2019; Bertolini et al. 2020). For example, biodiversity-patch-size relationships can be confounded by changes in patch shapes. Complex-shaped patches exhibit more edge-habitats and hence contain more edge-related species in comparison to patches with simpler shapes (Laurance & Yensen 1991; Ries et al. 2004; Ewers & Didham 2008).

Variation in large-scale environmental factors, such as climate, temperature and sedimentation rates, can drive ecological patterns across a species' distribution. For instance, greater recruitment of the mussel *Mytilus californianus* was found in the southern section of California coast that was associated to localised oceanic upwelling and larval transport in comparison to its northern counterpart (Smith et al. 2009). Despite the variation in important processes that affect foundation species at different scales, many restoration efforts are still focussed on single-spatial scales (e.g., increasing habitat patch-size at a local scale) (Callicott 2002; Lindenmayer 2020). Hence, there is a need to quantify and disentangle distribution patterns of foundation species across multi-spatial scales to implement restoration at appropriate spatial scales for cost-effective procedures in securing long-term restoration success.

Understanding multiple measures of populations, ecological processes, functions and services are essential to implement appropriate management, restoration and

conservation for foundation species. Estimating important characteristics of populations, such as density and body size, provides simplified measures of productivity of the ecosystem (Brown et al. 2004), dynamics of ecological interactions (e.g., predation) (Woodward et al. 2005; Knights & Walters 2010) and contributes to our understanding of ecological functions and services (e.g., the capacity for foundation species to support biodiversity; Crotty et al. 2018; Stelling-Wood et al. 2020). Measuring recruitment, survivorship, and growth of offspring could also identify the presence of reproduction bottlenecks in sustaining populations (Hughes 1990; Rodriguez et al. 1993; Tanner et al. 1994; Kimbro et al. 2014).

In addition to characteristics of the population, direct evaluation of ecosystem functions and services of a foundation species can inform restoration practitioners and conservation managers on the degree of habitat provision provided by the species and priority areas for restoration (Oliver et al. 2015; Ellison 2019). To date, many ecological studies amongst foundation species consist of single-study variables that have represented broad ecological processes (e.g., population body size as a proxy for ecosystem function) leading to a misleading and poor understanding of study systems (Underwood 1997; Johnson & Lidström 2018). Therefore, it is essential to have comprehensive, and multiple measurements of population characteristics, population processes and ecological functions of foundation species to provide a holistic understanding of foundation study systems prior to making decisions on their management, conservation and restoration efforts.

Table 1.1. Summary of established relationships between measured population and community estimates and spatial scales amongst literature review of foundation species. Foundation species summarised in the table consist of all marine, freshwater and terrestrial foundation species that are either mobile or sessile, either flora or fauna and occupy any trophic level in a food chain (i.e., primary producer, herbivore, omnivore or carnivore) unless stated. '+', '-', or 'Mixed' represent positive, negative, and mixed relationships respectively between a spatial scale and measured estimate respectively. 'Varies' indicates variation in community assemblages.

Spatial scale	Measured biological estimates	Literature reviewed spatial-ecological relationships	Scientific literature sources and additional notes
Regional scale	<i>Density</i>	Varied amongst regions	Reviews by Gaston & Blackburn (1996); Blackburn & Gaston (2001); Chown & Gaston (2010).
	<i>Body size</i>	Varied amongst regions	
	<i>Biodiversity</i>	<i>Species richness</i> : Varied amongst regions	Reviews by Bellwood & Hughes (2001); Vinson & Hawkins (2003).
		<i>Total abundance</i> : Varied amongst regions	
		<i>Community assemblage</i> : Varied amongst regions	
	<i>Recruitment</i>	<i>Total recruitment</i> : Varied amongst regions	Review by Edmunds (2021); other studies for Smith et al. (2009); Byers et al. (2015); Azpeitia et al. (2019).
<i>Proportion of live recruits</i> : Varied amongst regions			
Landscape-scale (Connectivity measure)	<i>Density</i>	Mixed	Review by Thornton et al. (2011).
	<i>Body size</i>	Mixed	
	<i>Biodiversity</i>	<i>Species richness</i> : +	Reviews by Lawton (1999); Tschardt et al. (2012); Fahrig (2013); Loke et al. (2019).
		<i>Total abundance</i> : +	
		<i>Community assemblage</i> : Varies	
	<i>Recruitment</i>	<i>Total recruitment</i> : +	Review by Strathmann et al. (2002).
<i>Proportion of live recruits</i> : +			
		<i>Total live cover area</i> : +	
Patch-scale	<i>Density</i>	+	Studies and reviews by MacArthur &

<i>Area</i>			Wilson (1967); Lomolino & Weiser (2001); Whittaker (1972); Chisholm et al. (2016).	
	<i>Body size</i>	+	Review by Thornton et al. (2011).	
	<i>Biodiversity</i>	<i>Species richness:</i> Mixed		Studies and reviews by Chisholm et al. (2016); MacArthur & Wilson (1967); Lomolino & Weiser (2001); Whittaker (1972).
		<i>Total abundance:</i> Mixed		
<i>Recruitment</i>	<i>Community assemblage:</i> Mixed		Studies by Bowden et al., (2001); Matias et al., (2015); Underwood & Skilleter (1996)	
	<i>Total recruitment:</i> +		Studies and reviews by Raimondi & Morse (2000); Tamburri et al. (2008); Whitman & Reidenbach (2012).	
	<i>Proportion of live recruits:</i> +			
<i>Patch-scale Shape</i>	<i>Density</i>	Mixed	Studies and reviews by Hamazaki (1996); Bender et al. (1998); McGarigal et al. (2012); Fahrig et al. (2019).	
	<i>Body size</i>	Mixed	Review by Thornton et al. (2011).	
	<i>Biodiversity</i>	<i>Species richness:</i> Mixed		Studies and reviews by Roberts & Poore (2006); Santos et al. (2010); Arellano-Rivas et al. (2017).
		<i>Total abundance:</i> Mixed		
	<i>Recruitment</i>	<i>Community assemblage:</i> Mixed		Limited to macroalgae. Study by Gee & Warwick (1994).
		<i>Total recruitment:</i> +		Limited to mussel beds. Reviews by Svane & Ompi (2012); Commito et al. (2014).
		<i>Proportion of live recruits:</i> +		
<i>Within-patch scale Distance to nearest patch edge</i>	<i>Density</i>	Mixed	Reviews by Fahrig (2003); Ewers & Didham (2006); Carroll et al. (2019).	
	<i>Body size</i>	Mixed		
	<i>Biodiversity</i>	<i>Species richness:</i> Mixed		Reviews by Fahrig (2003); Ewers & Didham (2006); Carroll et al. (2019).
		<i>Total abundance:</i> Mixed		
	<i>Recruitment</i>	<i>Total recruitment:</i> -		Limited to oyster reefs (Fodrie et al. 2014;

		<i>Proportion of live recruits: -</i>	Baillie & Grabowski 2019).
		<i>Total live cover area: -</i>	
	<i>Density</i>	-	Limited to oyster reefs (Lenihan 1999; Schulte et al. 2009; Colden et al. 2017; Baillie & Grabowski 2019).
	<i>Body size</i>	-	Limited to oyster reefs (Bartol et al. 1999; Baillie & Grabowski 2019).
Within- patch scale		<i>Species richness: Mixed</i>	
Surface elevation	<i>Biodiversity</i>	<i>Total abundance: Mixed</i>	Reviews by Keer & Zedler (2002); Turner et al. (2003).
		<i>Community assemblage: Mixed</i>	
		<i>Total recruitment: -</i>	
	<i>Recruitment</i>	<i>Proportion of live recruits: -</i>	Limited to oyster reefs (Fodrie et al. 2014; Baillie & Grabowski 2019).
		<i>Total live cover area: -</i>	

1.2 Oysters: a model foundation species for spatial-ecological studies

Oysters are marine benthic foundation species that form biogenic structures through gregarious settlement on various substrata, forming oyster reefs (= oyster complexes). These shellfish systems provide an array of ecosystem functions and services (see reviews by Grabowski & Peterson 2007; Grabowski et al. 2012). For example, the hard structures of the oyster reefs provide habitats to other molluscs, polychaetes, and crustaceans (Wells 1961; Rothschild et al. 1994; Smyth & Roberts 2010), sequester atmospheric carbon (Fodrie et al. 2017) and increase the productivity of commercially important foraging fish species in marine and estuarine ecosystems (Coen & Luckenbach 2000; Peterson et al. 2004; Grabowski et al. 2005). The physical structure of oyster reefs can also alter water flow and reduce wave action, thus providing coastal protection (Lenihan 1999; Reidenbach et al. 2013; Wiberg et al. 2019; Morris et al. 2021), stabilising nearby sediments and in their neighbouring ecosystems (e.g. salt marsh plant) (Salvador de Paiva et al. 2018). Oysters on reefs increase recycling of organic matter and nutrients (Newell 1988; Dame et al. 1991; Reiss et al. 2010; Hoellein et al. 2015) leading to increases water quality in estuarine ecosystems (zu Ermgassen et al. 2013; Rodriguez et al. 2014; Colden et al. 2017).

Over the past two centuries, roughly 85% of oyster reefs have been lost globally (Beck et al. 2011) owing to the overharvest of wild populations (Newell 1988; Rothschild et al. 1994; Jackson et al. 2001), habitat destruction via dredging and trawling (Anderson et al. 2005; Halpern et al. 2008), increase in pollution (Jackson et al. 2001), disease (Powell et al. 2012), and the introduction non-native oyster species (Ruesink et al. 2005). Large-scale degradation of oyster reefs has led to massive declines of ecosystem functions and services (Grabowski & Peterson 2007; Grabowski et al. 2012). In some areas where 99% of oyster cover has been lost (e.g., in the Wadden Sea and Australia), the remnant oyster reefs have been declared as functionally extinct, i.e., having limited information on whether these reefs can perform ecological functions and services (Beck et al. 2011). Understanding the characteristics, processes and ecological functions of remnant oyster reefs are therefore essential to inform management and restoration strategies for functionally extinct shellfish habitats.

Current research on population characteristics, ecological processes and functions of oyster reefs has reported inconsistent patterns among spatial scales

examined. For example, recruitment and densities of the Eastern oyster (*Crassostrea virginica*; Byers et al. 2015; Grabowski et al. 2020) and Pacific oyster (*Magallana gigas*; Walles et al. 2015) reefs varied on a regional scale. On a landscape-scale, relationships between oyster recruitment and landscape connectivity varied among *Ostrea lurida* (e.g., Carson 2010), *C. virginica* (e.g., Haase et al. 2012) and *M. gigas* oyster reefs (e.g., Lagarde et al. 2019). At patch scales, patch area was not correlated to oyster density and recruitment of *C. virginica* (Hanke et al. 2017b). While variation within patches, such as surface elevation were found to influence abundance of adult *C. virginica* oysters and its recruits (Lenihan 1999; Schulte et al. 2009; Baillie & Grabowski 2019; Colden et al. 2017). More in-depth research is required to ascertain spatial-ecological organisation relationships among oyster reefs and the spatial scales they exist in. Importantly, only a handful of studies have concurrently assessed the contribution of processes occurring at different spatial scales on oyster population estimates (e.g., recruitment; Knights & Walters 2010; Byers et al. 2015; Hanke et al. 2017), and their ecological functions (e.g., biodiversity provision; Hanke et al. 2017b). Therefore, more research is required to understand how population characteristics, population processes and ecological functions vary within each spatial scale and across the multiple scales they exist in.

1.3 Study region and species

The Sydney rock oyster, *Saccostrea glomerata* Gould (1850), (formerly known as *Saccostrea commercialis*) is an Australian reef-building shellfish species found along the south-eastern of Australia, including south-east Queensland and the coastline of New South Wales (Figure 1.1; Gillies et al. 2018). This species can densely aggregate on hard substrates, sand, mud banks, mangrove roots and/or on their adult conspecifics thus forming oyster reefs. Historically, reef areas ranged from tens to hundreds of thousands of square kilometres in both intertidal and subtidal zones (up to 8 meters in depth) (Ogburn et al. 2007; Gillies et al. 2018). These reefs once supported a large bulk of Australia's maritime industry where oysters and their shells were largely harvested for consumption and the production of lime for construction from 1790s to 1900s (Ogburn et al. 2007; Gillies et al. 2018). At present, vast areas of *S. glomerata* reefs have been destroyed, leaving less than 10% of the area present in Australia in the 1880s (Gillies et al. 2018). Small and isolated patches (i.e., <5000 m² patches) are now only found in the mid-intertidal zone of estuaries (Diggles 2013; Gillies et al. 2018). There is little or no

natural recovery from the reefs owing to the presence of parasitic diseases, invasive mud worms, pollution, estuary modifications, such as sedimentation burial of adult oysters, and recruitment from land-sediment runoff (Ogburn et al. 2007; Beck et al. 2011; Diggles 2013; Wilkie 2012). Hence, *S. glomerata* reefs have been declared as functionally extinct (Beck et al. 2011; Gillies et al. 2018) and are now recognised as one of Australia's most imperilled marine habitats (Gillies et al. 2018).

In New South Wales, remnant reefs are found in most estuaries along the coastline of the state (~2,137 km). In each estuary, they can be found in different positions in the estuary, including in downstream and upstream areas and as fringing reefs (i.e., a band of reef along the foreshore edge), island reefs (i.e., reef patches surrounded by sediment and water channels) or a combination of both reef types (Gillies et al. 2018; NSW Marine Estate and Authority 2021).

On landscape- and patch- scales, the spatial configuration of the remnant reefs may consist of one or more patches of various shapes (e.g., ovoid, irregular and rectangular), size and distances from each other, based upon the dimensions of the original substrate that were aggregated on and the hydrodynamic influence. The landscape settings of remnant reefs may include the surrounded presence of bare sediment and/or other marine foundation species such as *Avicennia* mangroves and seagrass meadows of *Zostera* and *Posidonia* (personal observations; McAfee et al. 2016; Gilby et al. 2018). The heights of the remnant reefs are dependent on hydrodynamics and tidal ranges that limit oyster recruitment and growth and survival (Bishop & Peterson 2006; Diggles 2017). Their heights can be categorised as high-relief (>0.15 m in height from base of substrate; Figures 1.2 A,B & F) or low-relief (0.05 - 0.15 m in height; Figures 1.2 C,D & E; NSW Marine Estate and Authority 2021).

Within patches, higher densities of *S. glomerata* adult individuals and recruits are most found at lower elevations (Lee et al. 2012). However, the distribution of *S. glomerata* relative to distance to patch-edges and habitat-complexity (e.g., surface rugosity and interstitial space) of these remnant reefs remain unknown.

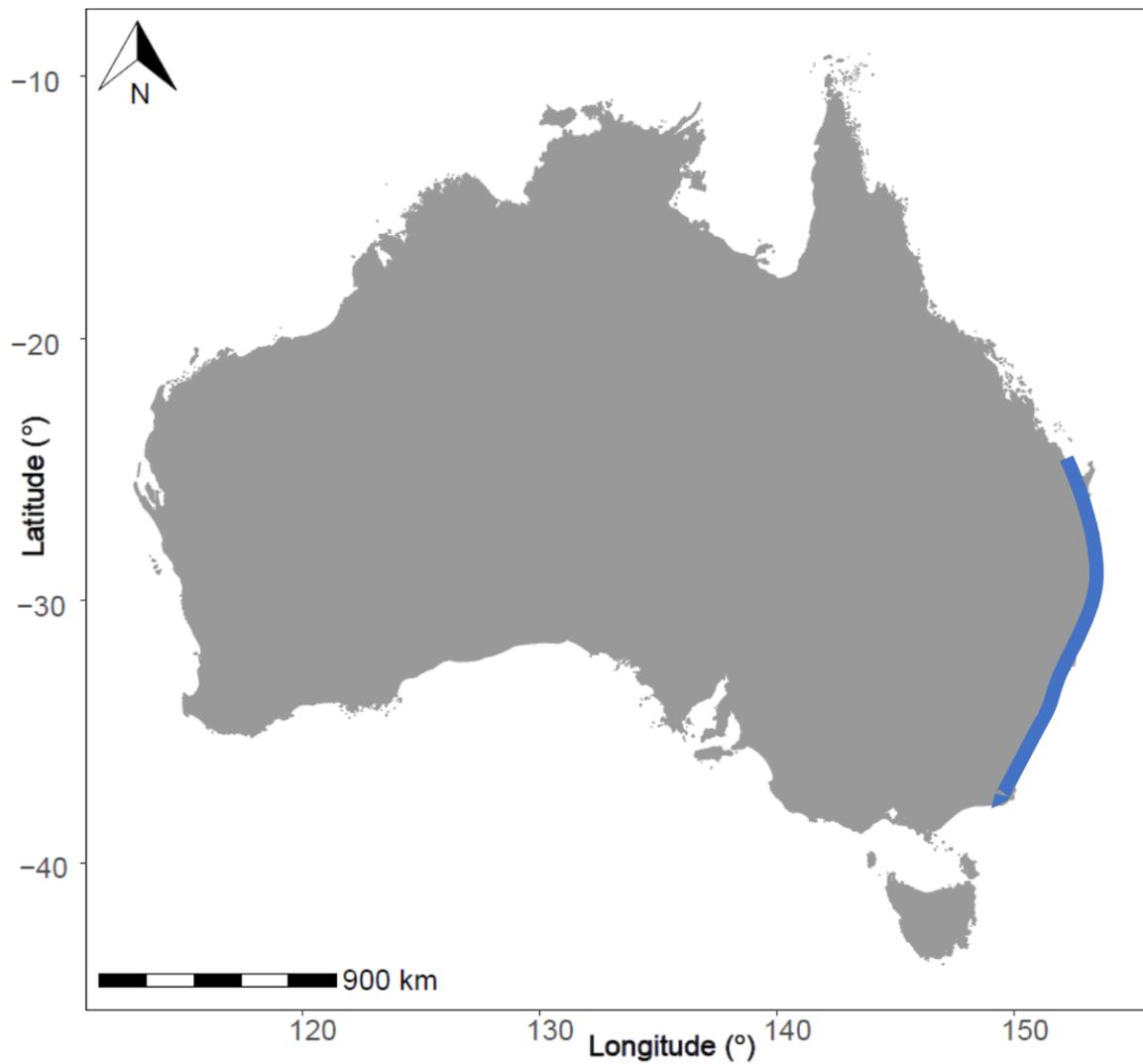


Figure 1.1. The distribution of Sydney rock oyster (*S. glomerata*) reefs following Gillies et al. (2018) in blue along the south-eastern coast of Australia.

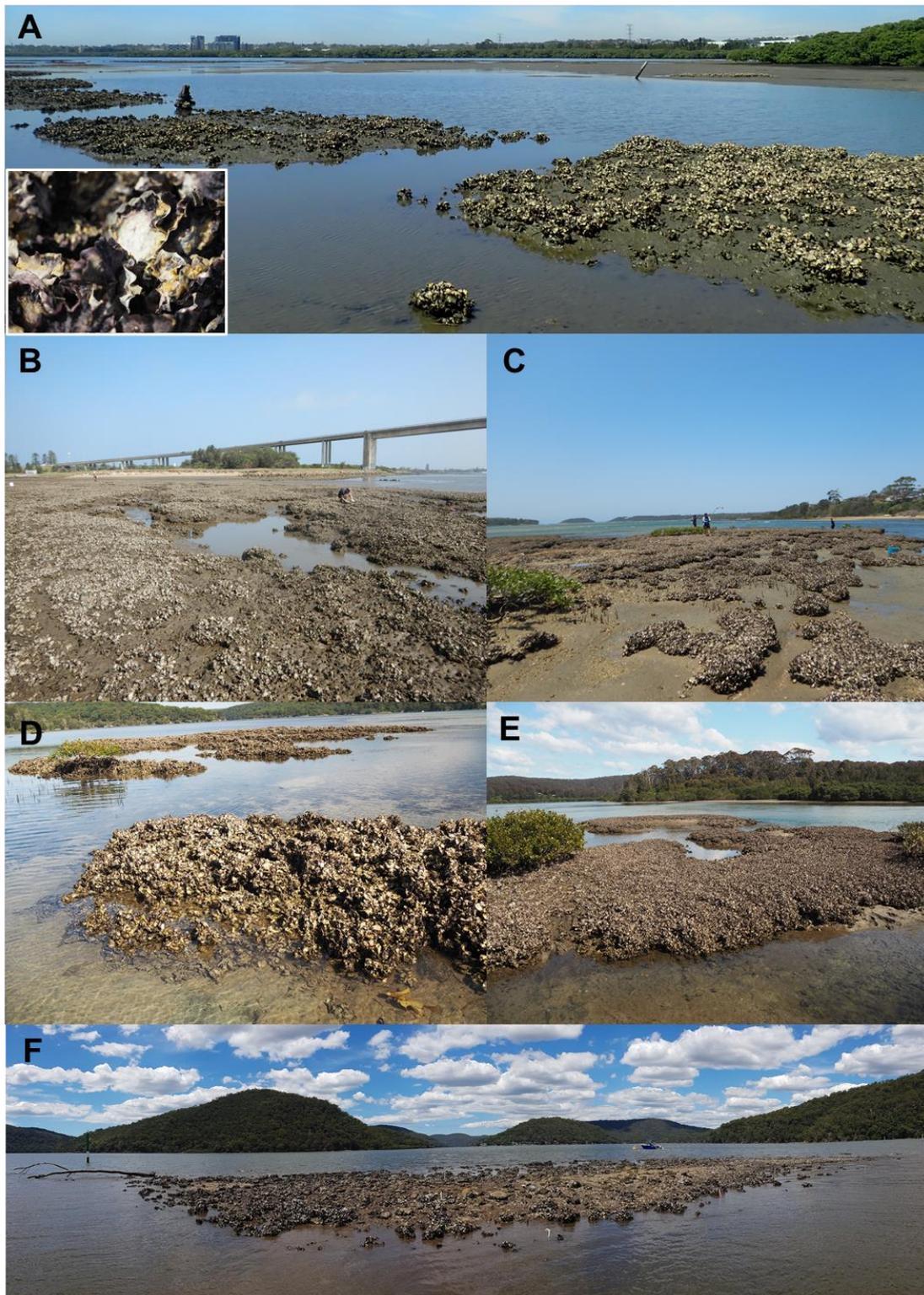


Figure 1.2. Photos of dense aggregation of *S. glomerata* (white box inset A) and remnant *S. glomerata* reefs (unscaled) amongst the estuaries of New South Wales sampled in this thesis. Muddy, compact and low-relief reefs were located in (A) Georges River (B) Hunter River and (F) Hawkesbury River. High-relief reefs were sampled in (C) Crookhaven River, (D) Port Hacking and (E) Bermagui River. All photos were taken by Rick Leong and were not scaled to view.

1.4 Thesis Outline

1.4.1 Overview of Thesis

In this thesis, I aim to understand how processes occurring at different spatial scales varying from 1 cm to 2000 km are associated with population characteristics, population processes (recruitment) and biodiversity associated with the threatened habitat-forming oyster, *S. glomerata*. My thesis comprehensively investigates the spatial-ecological relationships exhibited by *S. glomerata* reefs, from within-patches, patch-, landscape- and regional scales to test for consistency of population characteristics, population processes and ecological functions across these scales. Observational studies were conducted in Chapters 2 and 3 followed by experimental studies in Chapters 4 and 5 (see Figure 1.3 for visual framework of data chapters). All hypothesised spatial-ecological relationships in Chapters 2 – 5 were explicitly listed in the Introduction of each chapter, based upon the summarised literature review listed in Table 1.1. This is followed by a general discussion (Chapter 6) summarising outcomes of this thesis and potential applications in oyster restoration. Chapter 2 has been published as Leong et al., 2022 in *Restoration Ecology* (see Appendix A). Overlap of content in the Introduction section of each chapter are expected as selected chapters (Chapters 2, 3 and 4) were written as chapters suitable for independent publication.

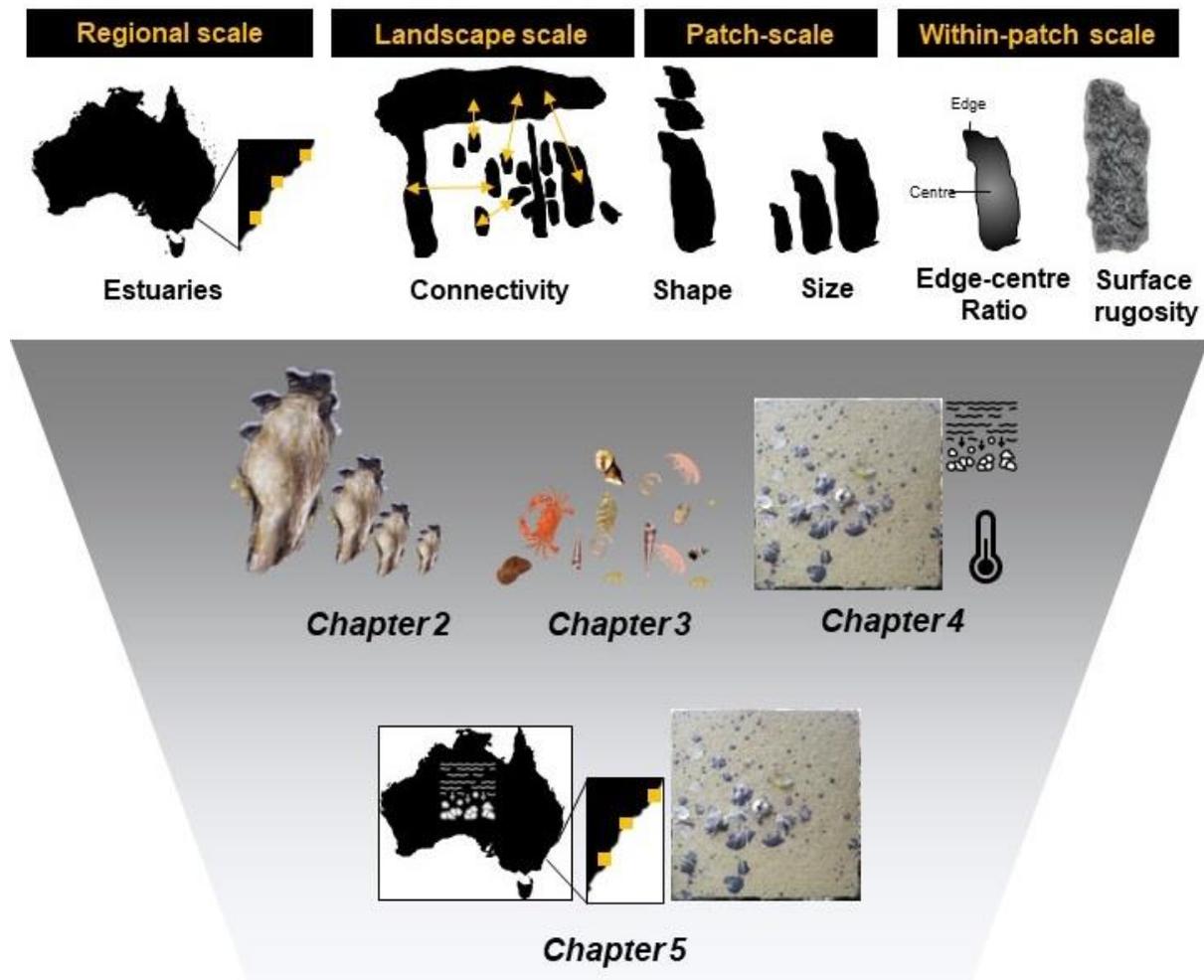


Figure 1.3. Conceptual diagram of thesis layout denoting the spatial scales and configuration of remnant *S. glomarata* reefs investigated in this thesis (horizontal diagrams on top row) against measured population characteristics (Chapter 2), ecosystem function i.e., epifaunal biodiversity (Chapter 3) and population processes i.e., oyster recruitment (Chapter 4; middle region of diagram). Chapter 5 was designed based upon the findings of Chapters 2 – 4 and focuses on regional scale sedimentation effects on oyster recruitment (bottom region of diagram).

1.4.2 Chapter 2

In the first data chapter of my thesis, I investigated the relationships between oyster population characteristics and spatial configuration of the remnant reefs. Firstly, I randomly sampled oyster cores from different shapes, sizes, and landscape-connectivity of remnant *S. glomerata* reefs at three estuaries in New South Wales. From the cores, I measured oyster population characteristics (densities, 95th percentile and median lengths of live oysters). Once the characteristics were quantified, I investigated the relationships between oyster population characteristics and spatial attributes where the remnant reefs exist in. These spatial attributes include regional (amongst the estuaries), amongst-patch (landscape-connectivity within each estuary) patch- (size and shape of reefs within each estuary) and within-patch (rugosity, distance to patch-edge and elevation in each reef). By understanding the variations of these population characteristics in each spatial scale and their habitat configuration, I aimed to inform magnitudes of ecosystem functions across different spatial scales. From a restoration perspective, my results can advise for designs of restored habitat patches that maximises ecosystem functions. This chapter has been published as Leong et al. (2022) in the journal *Restoration Ecology* (see Appendix A).

1.4.3 Chapter 3

In this chapter, I investigated variation among spatial scales in the degree to which remnant *S. glomerata* reefs support biodiversity. Using the same sampled cores from Chapter 2, I assessed the biodiversity (i.e., abundance, taxa richness, taxa evenness, Shannon's diversity index and multivariate assemblage composition) of epifauna in remnant oyster reefs. Each of the measured biodiversity variables was compared against attributes at the regional scales (amongst the estuaries), within-patches (rugosity, core interstitial space, distance to patch-edge and elevation in each reef), whole-patches (size and shape of reefs) and among-patch (connectivity) within each estuary. This information will provide an understanding on how biodiversity provision by *S. glomerata* varies across each spatial scale and identify spatial attributes that can be utilised to enhance the biodiversity supported by restored reefs in restoration projects.

1.4.4 Chapter 4

In this chapter, I investigated how oyster recruitment success differs across spatial scales on the remnant *S. glomerata* reefs. I established recruitment plates on *S. glomerata* reefs for approximately 10 months and measured recruitment success variables (i.e., total recruitment, proportions of live recruits and total live recruit cover area) from the tiles. The measured variables were then tested for associations with the same spatial attributes within the same scales mentioned in 1.4.2 and 1.4.3. I also investigated how variables associated with recruitment success relate to abiotic factors, specifically temperature and sedimentation rate on regional scales and within each estuary. Sediment traps and temperature loggers were placed on a subset of reefs and recruitment deployment periods in all estuaries. Sedimentation rate and temperature variables (i.e., 5th, percentile, 95th percentile and coefficient of variation temperatures) were then tested for significant relationships with recruitment within each estuary and on a regional scale. By understanding the variation of recruitment success of *S. glomerata* across differing habitat configurations on the spatial scales they exist in, I provide an insight into variation of population processes at multiple spatial scales. This aims to then identify the scales that are important for restoration projects with recruitment enhancement goals. Coupled with relationships between recruitment success and abiotic factors, my results inform whether abiotic factors can predict recruitment success.

1.4.5 Chapter 5

In this chapter, I designed an experiment to investigate how levels of *in situ* sedimentation on a regional scale may be associated with oyster recruitment (i.e., total recruitment, and percentage of live recruits). This experiment design was based upon the observed variation in oyster population characteristics, epifaunal biodiversity and recruitment consistently at the regional scale compared to other scales (Chapters 2, 3 and 4), and coupled with the regional differences between sedimentation rates and total recruitment found in (Chapter 4). I first measured the amount of sediment deposition on the remnant *S. glomerata* reefs in six selected estuaries and categorised the estuaries based on sedimentation levels. This was followed by the testing for significant relationships between recruitment variables and the categorised estuaries. The presence (or absence) of relationships between recruitment variables with estuarine-

sedimentation levels on a regional level will inform whether regional differences in environmental factors are associated with changes in *S. glomerata* ecosystem functions. Furthermore, results from this chapter will inform appropriate levels of an environmental factor that promote recruitment success for regional-based restoration activities.

Chapter 2

Variation in the density and body size of a threatened foundation species across multi-spatial scales

2.1 Abstract

Population characteristics (e.g., density and body sizes) of foundation species can affect their own persistence and provision of ecosystem functions. Understanding the drivers of population characteristics of foundation species at multiple spatial scales is therefore critical for maximizing ecosystem functions of restored habitats. We analyzed variation in population characteristics (densities, 95th percentile and median lengths of live oysters) of Sydney rock oysters, *Saccostrea glomerata*, on remnant oyster reefs at regional scales at three estuaries along a ~250 km of coastline in New South Wales, Australia. We then analyzed how population characteristics were further related to spatial attributes at smaller spatial scales including within-patches (rugosity, distance to patch-edge and elevation), whole-patches (size and shape) and amongst-patches (connectivity) within each estuary. The densities and body sizes of *S. glomerata* were related to spatial attributes occurring within-patch (e.g., elevation), whole-patch (e.g., shape) and landscape (i.e., connectivity) scales, but these relationships varied among estuaries. Indeed, the greatest variation in oyster density and size occurred at regional scales, suggesting that processes acting at larger spatial scales (e.g., water quality and/or climate) set the context for smaller scale influences on oyster characteristics. Our results highlight the potential importance of incorporating site-specific, spatial attributes in the design of restored oyster reefs to maximize ecosystem services and functions provided by restoration efforts.

2.2 Introduction

Marine foundation species (*sensu* Dayton 1972) such as mangroves, seagrasses, seaweeds and shellfish provide critical ecosystem functions and services, including

habitat and food provision for fish and invertebrates, nutrient cycling, water quality improvement and coastal protection (Ellison et al. 2005; Grabowski & Peterson 2007; Angelini et al. 2015; Bulleri et al. 2018; Gribben et al. 2019; Lloyd et al. 2020). Despite their importance to ecosystems, foundation species have experienced staggering losses globally. For example, oyster reefs have been globally reduced by 85% (Beck et al. 2011), mangrove forests by 35% over 50 years (Polidoro et al. 2010) and seagrass meadows by up to 29% from 1880 to 1990 (Waycott et al. 2009). Because of the critical services they provide, they are the focus of global restoration efforts (Bayraktarov et al., 2016; Lindenmayer et al., 2008; Swan et al., 2016).

The population characteristics (e.g., density and body size distribution) of foundation species have strong consequences for their own persistence and the ecosystem functions and services they provide. For example, the density and size of marine foundation species can influence their own growth, recruitment and survivorship (Gribben et al. 2020), the biodiversity they support (Stelling-Wood et al. 2020), hydrodynamics and wave attenuation (Salvador de Paiva et al. 2018) and water filtration (Green et al. 2013). From a restoration perspective, population characteristics of a target species may therefore inform the persistence and magnitude of the ecological services in areas of interest, and thus may be a fundamental yet understudied component of many restoration strategies (Baggett et al. 2015; Ladd et al. 2018).

Population characteristics of foundation species can vary across multiple spatial scales (Godron & Forman 1981; Fahrig 2003). At small spatial scales, these characteristics can vary within habitat patches, although patterns are equivocal. For example, the population density and mean body size of foundation species can be smaller at patch edges in comparison to patch centers (Hanke et al. 2017a), but the opposite pattern also occurs (Bell et al. 2001; Boström et al. 2011; Bertolini et al. 2020). Such variation may be explained by within-patch attributes (i.e., distance from patch-edge) interacting with whole-patch attributes such as patch size and shape (edge-to-area ratios), as larger patches are often associated with higher densities of foundation species and may be better at buffering abiotic and biotic stress than smaller patches (Angelini et al. 2011; Livernois et al. 2017; Crotty et al. 2018). Thus, understanding how multiple spatial scales interact to influence the population characteristics of foundation

species, and potentially their function, is critical to inform the design of restored habitat patches and maximize ecosystem functions provided and restoration outcomes.

At larger scales, habitat patches can interact with each other in the landscape by altering ecological flows of resources and progeny (Brooks 2003; Ewers & Didham 2006; Zambrano et al. 2019) and ecological interactions (e.g., predation rates; Martin et al. 2018), all of which may influence the population characteristics of foundation species. Indeed, patch configuration and their connectivity can affect population characteristics in both terrestrial (e.g., Fahrig 2017; Thompson et al. 2017) and aquatic ecosystems (Angelini et al. 2011; Crotty et al. 2018). Moreover, the density and traits of foundation species can also be determined by background environmental variation (e.g., temperature) occurring at regional scales (e.g., grassland, le Roux & McGeoch 2010; macroalgal beds; Leonard 2000). Understanding the roles of landscape and regional scales on controlling population characteristics of foundation species will help identify the configuration of restored patches and site selection that maximizes their ecological functions and resilience, improving on existing restoration strategies (Angelini et al. 2011; Gilby et al. 2018).

In estuaries in Australia, oysters once formed extensive reef complexes up to 10 ha from the intertidal to depths of ~8 m (Ogburn et al. 2007). However, more than 90% of these complexes, including those of the iconic Sydney rock oyster, *Saccostrea glomerata* (Gould 1850), have been lost through overharvesting for food and lime, disease and pollution (Ogburn et al. 2007; Gillies et al. 2018). *S. glomerata* reefs are now considered functionally extinct (Beck et al. 2011) and they are a key focus for restoration (Gillies et al. 2018). To date, global oyster restoration efforts mostly consist of substrate provision for recruitment (Westby et al. 2019). Oyster densities and size can affect their own recruitment (Knights & Walters 2010), growth (Honkoop & Bayne 2002), survival (Holliday et al. 1991; Honkoop & Bayne 2002) and filter-feeding capacity (Ozbay 2006), as well as the biodiversity they host (Wilkie et al. 2012). However, few restoration projects have considered how spatial context may influence the persistence of the restored oyster populations and the ecological functions they provide (McAfee et al. 2020). This is due, in part, to a lack of understanding about how population characteristics vary with patch attributes (e.g., edge-versus-centre, size, shape, complexity) and configuration at multiple spatial scales.

In this study, we used the natural variation of patch-size, patch-shape, and connectivity in remnant oyster reefs in three estuaries in southeast Australia to determine how spatial variation from within patches to regional scales influence population characteristics of *S. glomerata*. At each estuary, we sampled oyster densities, median and 95th percentile body size on remnant oyster reefs at local (within- and whole- patch) and landscape (amongst-patches) scales and regional (among estuaries) scales. We tested the hypotheses that oyster densities and size would be correlated to (1) distance from the patch-edge within patches, (2) area and perimeter-to-area ratios as whole-patches, and (3) proximity of patches. Additionally, we hypothesized that (4) oyster sizes and densities would vary among estuaries due to differences in background environmental conditions operating at regional scales.

2.3 Methods

2.3.1 Sampled estuaries across the regional scale

Remnant *S. glomerata* reef complexes were sampled in three estuaries across ~250 km of the coastline in New South Wales (NSW) Australia; Hunter River (32° 52' 56.5788" S, 151° 47' 20.9508" E), Port Hacking (34° 4' 22.0404" S, 151° 7' 14.5956" E) and Crookhaven River (34°54'21.04"S, 150°44'48.62"E) (Figure 2.1). Reef complexes in Hunter River, Port Hacking and Crookhaven River were characterized by *S. glomerata* aggregation on mud banks, ballast heaps and rocky boulders, respectively (Table 2.1). Each estuary contained different levels of anthropogenic disturbances, annual temperatures and turbidity measurements (NSW Office of Environment and Heritage 2016; Table 2.1). Crookhaven River reefs possessed the largest mean patch area and spatial range (i.e., maximum distance between any two reefs in the estuary) of all estuaries, followed by Hunter River and Port Hacking (Table 2.1). Hunter River contained almost twice the number of reefs compared to Crookhaven River and Port Hacking (Table 2.1). In each estuary, 9-11 reefs ranging in area from 5 m² to 4000 m² and consisting of different shapes (e.g., ovoid, elongate, irregular) were randomly selected for mapping and sampling (Appendix Table B.1). Reef contours were mapped using satellite images from NearMap Ltd (<http://maps.au.nearmap.com/>). Small reefs (<5 m²) were not mapped or sampled to avoid damage to them.

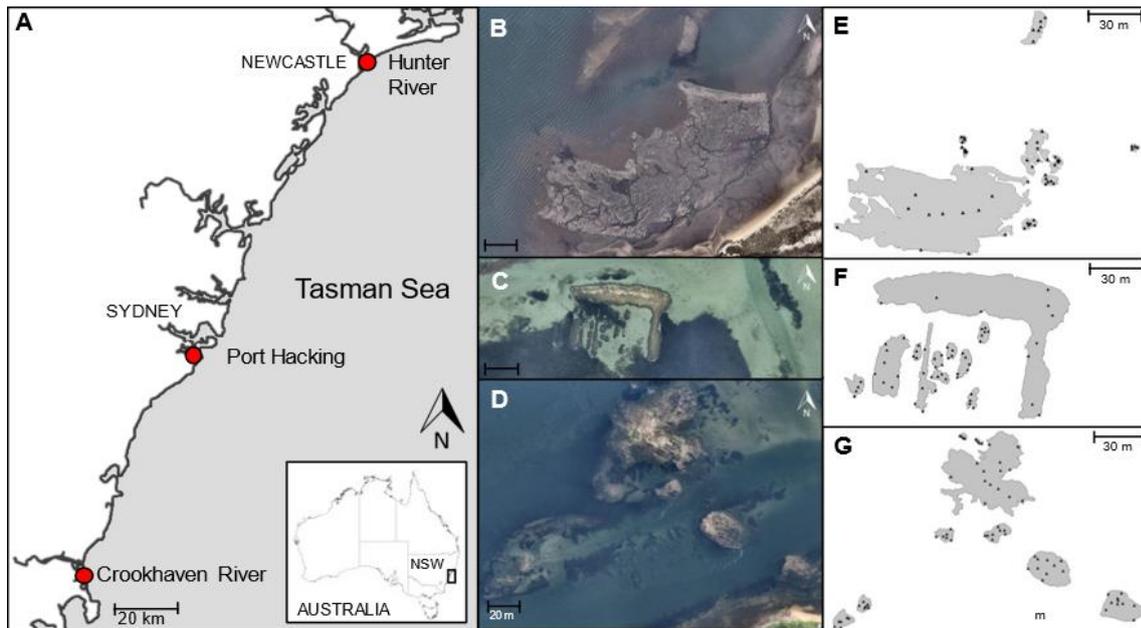


Figure 2.1. Locations of sampled *S. glomerata* oyster reefs (red dots) in estuaries in New South Wales (NSW), Australia (inset; A). Satellite imagery of the reefs (Nearmap Ltd.) during low tide and the corresponding sample locations (see triangles) on reef contours of the selected reefs in Hunter River (B & E), Port Hacking (C & F) and Crookhaven River (D & G), respectively.

Table 2.1. Characteristics of estuaries where the sampled oyster reefs are located. Observed and/or calculated characteristics of each estuary were obtained from ¹OzCoasts (2015), ²NSW Office of Environment and Heritage (2016) for periods between 2007 to 2015 and ³NearMap Ltd unless specified.

Estuary Characteristics	Estuary		
	Hunter River	Port Hacking	Crookhaven River
Estuary-type classification ¹	wave-dominated estuary	tide-dominated estuary	wave-dominated delta
Average annual summer temp. \pm SE ($^{\circ}$ C) ²	24.7 \pm 0.3	25.7 \pm 0.3	24.1 \pm 0.3
Average annual turbidity \pm SE (NTU) ²	19.1 \pm 7.2	2.4 \pm 0.6	2.3 \pm 0.2
Disturbance class ³	High	Low	Medium
Number of reefs ³	25	14	10
Base material of remnant reefs	mud banks (McLeod et al. 2020)	ballast heap (Albani & Cotis 2013)	Sand and rock boulders (pers. obs)
Approx. distance to estuary mouth (km) ³	6.5	4.3	2.2
Mean patch area (m ²) \pm SE ³	237 \pm 155	112 \pm 78	355 \pm 200
Mean distance between reefs (m) \pm SE ³	32.2 \pm 1.4	12.7 \pm 1.0	80.8 \pm 7.8

2.3.2 Quantifying oyster characteristics

On each reef, we sampled oysters by taking 10 x 10 x 10 cm cores with a hammer and chisel during mean low tide (BOM 2019). All cores were sampled in Austral spring (late October-early November 2018) outside of the recruitment period of *S. glomerata* (Diggles 2017) to focus on the oyster characteristics of post-recruitment individuals as these are likely providing the ecological functions on reefs. The number of cores sampled on each reef differed according to reef area (Appendix Table B.2), with a minimum of four cores sampled on the smallest reefs (5-25 m²) and a maximum of 14 cores on the largest reefs (≥ 2000 m²). Sampling locations were randomly selected within reef contours using function 'spsample' from package 'sp' (Pebesma & Bivand 2005) in R (v4.0.3, 2020; Figures 2.2.1E-1G) and were mapped with a Real-Time Kinematic and differential Global Positioning System (RTK-DGPS, Leica GNSS 14, vertical accuracy ± 8 mm; horizontal ± 13 mm).

Cores were fixed in 10% formalin mixed in seawater. Total volume of oysters in each core (hereafter biovolume) was estimated by displaced volume in water. The majority of live oysters were identified as *S. glomerata* (93.2% in Crookhaven River, 99.9% in Hunter River and 92.1% in Port Hacking) following dissection methods in Wilkie et al. (2012) with the remaining identified as the invasive Pacific oyster (*Magallana gigas* Thunberg 1793, formerly *Crassostrea gigas*). Although competition between both species could alter the density and body size of *S. glomerata* at low- and mid-intertidal heights on aquaculture farms (Krasoi et al. 2008), we assumed limited effects of competition, at the time of sampling, owing to small proportions (i.e., $< 8\%$ at any sampled estuary) of *M. gigas* currently present on intact *S. glomerata* reefs.

We measured the shell length of all live oysters with Vernier calipers (± 0.1 cm) along the anterior-posterior axis as this is correlated to body size for live oysters (Gribben et al. 2020). Post-measurement, we calculated the median (50th) and 95th length percentiles per core as proxies of "average" and "largest" oyster sizes in each core, respectively. We also counted all live oysters per core where individuals were categorized as either 'juvenile' (defined as settled spat < 1 cm in length and flesh attached) or 'adults' (oysters ≥ 1 cm in length). Both adult and juvenile counts were highly correlated to each other (Pearson correlation

coefficient, $r = +0.78$, $p < 0.001$) hence they were combined as total densities per core for the statistical analyses.

2.3.3 Quantifying within-patch, amongst-patches and whole-patch attributes

We defined 'patch attributes' as the spatial characteristics of reefs for all spatial measurements. We quantified within-patch attributes at each sampled core on each reef. These included surface elevations of the sampled cores, distance to the nearest patch-edge and the surface complexity around the samples. Elevation relative to sea level at each coring point was measured with the RTK-DGPS unit as height above mean sea level (MSL). The distance of each core to the nearest reef edge was calculated in ArcGIS (v10.3, ESRI, 2016) using the NEARDIST function with cores' XY coordinates and reef-contour maps.

To quantify surface complexity of reefs on each core, oyster reefs were mapped during low tide via photogrammetry prior to coring (see Figueira et al. 2015 for methods). We used this method as it is accurate (i.e., lower error and variance) than more traditional methods, such as the chain method (Friedman et al. 2012). All reefs in Port Hacking and Crookhaven River were mapped but not all in Hunter River due to time constraints. Digital elevation models (DEMs) produced from mapped reefs were created in Agisoft Metashape PhotoScan (v1.1.6, 2015), trimmed to reef edges and imported to ArcGIS (v10.3, ESRI, 2016). Resulting 3D models had an average mesh resolution (distance between vertices) of 8.2 mm and average model error of 4.7 mm, while DEMs had an average cell size of 2.5 mm. DEMs were imported into ArcGIS and sample points (based on XY coordinates) were buffered with a 20-cm radius circle. Surface rugosity independent of surface slope (hereafter 'rugosity') was calculated for each of these buffered areas (corresponding to the location of each sample core) with the arc-chord ratio (ACR) rugosity index function (Du Preez 2015) in the Benthic Terrain Modeler (BTM) plugin (v3.0; Walbridge et al. 2018) in ArcGIS (see Appendix Supplement B1 for detailed method description). Five whole-patch attributes (Table 2.2) were calculated based upon shape, area and perimeter (McGarigal et al. 2012) using the function 'calculate_lsm' in 'landscape metrics' package in R (Hesselbarth et al. 2019).

We defined the ‘oyster reef landscape’ as a mosaic of oyster reefs within an unstructured matrix (i.e., sandy and/or muddy bottom; Turner 1989). To quantify the connectivity within an oyster reef landscape, we used four metrics of habitat “isolation” (McGarigal et al. 2012; see Table 2.2) based upon reef areas and inter-reef distances (Cushman & McGarigal 2002). The metrics were obtained in R using the reef-contour maps. The nearest neighbor distance was calculated using the function in ‘gdistance’ package (van Etten 2017). The proximity index was calculated using the function ‘ProxIndex’ in package ‘spatialEco’ (Evans 2015). The mean nearest neighbor distance and the isolation index were manually calculated (see Appendix Table B.3 for formula for each metric).

Table 2.2. List of metrics used to quantify within-, whole- and amongst- patch (patch-connectivity) attributes. Formulae of metrics can be found in Appendix Table B.3.

Attributes	Description
Amongst-patches	
Nearest-neighbour Distance	The shortest Euclidean and edge-to-edge distance between a focal reef and its nearest neighbouring reef (McGarigal et al. 2012).
Mean Nearest-neighbour Distance	Average of the nearest Euclidean and edge-to-edge distances from a focal reef to all other reefs in the same landscape (McGarigal et al. 2012).
Proximity Index	Index which measures the distance of a focal reef to other reefs in relation to area of the focal patch. Index for a patch is calculated by summing ratios of focal patch-area to nearest neighbour distances from focal patch to other patches (Gustafson & Parker 1992).
Isolation Index	Index is a weighted sum of products between nearest neighbour distance from focal patch to other patches, and the ratios of focal patch area to the total patch area (Moilanen & Nieminen 2002).
Whole-patch	
Two-dimensional Fractal Dimension Index	Standardised and scale-independent measure of perimeter of a patch relative to a square perimeter and patch-area (McGarigal et al. 2012).
Circularity Index	Ratio between the patch-area and the smallest circumscribing circle of the patch (McGarigal et al. 2012).
Shape Index	Ratio of actual patch-perimeter to hypothetical patch-perimeter as a square with the same area, characterising total edges of patch (McGarigal et al. 2012).
Perimeter	Perimeter of each patch calculated from satellite image, reef contours.
Perimeter-Area Ratio	Ratio of perimeter- patch to patch-area for each patch.
Area	Area of each patch calculated from satellite image, reef contours.
Within-patch	
Distance to Edge	Shortest distance of each sampled core to the nearest reef edge.
Surface Elevation	Height of each sampled core above mean sea level.
Surface Rugosity	Surface roughness on each sampled core and 20-cm radius surrounding each core derived from photogrammetry and digital elevation models (<i>sensu</i> Figueira et al. 2015).

2.3.4 Data Analysis

2.3.4.1 Oyster characteristics across the regional scale

Because patch attributes related to population characteristics differently within each estuary (Figures 2.3 to 5, Table 2.3), we first tested for regional differences in oyster population characteristics (abundance, median length and 95th percentile length) via the comparisons amongst estuaries. We tested relationships between population characteristics and patch attributes within each estuary separately (see next subsection).

We used a generalized linear mixed model (GLMM) assuming a negative binomial distribution for oyster density and linear mixed models (LMMs) for median and 95th percentile oyster lengths as response variables, with estuaries as a fixed factor. Biovolume per core (i.e., the volume of sampled structure including live oysters and dead oyster shell) was included as a continuous co-variate in each model to account for potential differences in shell matrix in each core. Reef (hereafter 'reef_id'; i.e., unique reef complexes) was included as a random factor to account for potential non-independence between samples cores from within the same patch. The GLMM was performed using 'glmmTMB' package (Magnusson et al. 2020) and LMMs with the lme4 package (Bates et al. 2015). Statistical significance of estuary for each model was computed with likelihood ratio tests (LRTs) using the 'Anova' function in the 'car' package (Fox et al. 2013). Post-hoc tests with Tukey were performed function 'lsmeans' (Lenth 2016) in lieu of statistical significance of estuaries (see Appendix Table B.5).

2.3.4.2 Oyster characteristics across within-, whole- and amongst- patch attributes

We tested relationships between each oyster characteristic (abundance, median length and 95th percentile length) and patch attributes (within-, whole- and amongst- patches) of the remnant reefs through model fitting and selection.

For each estuary, we first tested for collinearity of patch attributes prior to model fitting (Zuur et al. 2009); where two or more variables were correlated (Pearson's correlation coefficient, $r \geq \pm 0.7$), we left one of those variables in the

model and excluded the rest (see Appendix Table B.6 for correlation matrices between attributes per estuary). We then fitted each oyster characteristic as a response variable using GLMMs and LMMs where 'biovolume' and 'reef_id' were also included in each model as a continuous co-variate and random factor, respectively. A total of nine models were fitted; one for each oyster characteristic (density, median length and 95th percentile length) repeated in each of the three estuaries (see Appendix Table B.7 for equation of each model fit). For each Hunter River model, rugosity was excluded as a co-variate due to substantial absence of data points (refer to 'Quantifying within-patch attributes' subsection) to prevent loss of precision of model estimates (Bartlett et al. 2014).

For each model, we conducted step-wise model regression with all possible combinations of patch attributes as predictors, using the 'dredge' function in 'MuMIn' package (Bartoń 2018). The most parsimonious/'best' model in each set was chosen based upon the model combination with the lowest small-sample corrected Akaike information criterion (AICc; Burnham & Anderson 2002). Selected models and their corresponding patch attributes were validated using histograms of the residuals and plots of the residuals versus the fitted values (Zuur et al. 2009). See Appendix Tables B9-11 for model selection outputs.

2.4 Results

2.4.1 Oyster characteristics across the regional scale

The abundance of oysters per core differed on a regional scale (LRT $X^2=41.7$, $df=2$, $p<0.001$; Appendix Table B.4), with lower abundances in Hunter River compared to Crookhaven River and Port Hacking (post-hoc Tukey, Crookhaven River = Port Hacking > Hunter River, Figure 2.2A). Largest oysters (i.e., 95th quantile lengths per core) also differed across all estuaries (LRT $X^2=35.5$, $df=2$, $p<0.001$; Appendix Table B.4), with shorter lengths in Hunter River compared to Crookhaven River and Port Hacking (post-hoc Tukey, Crookhaven River = Port Hacking > Hunter River, Figure 2.2B).

Median oyster lengths also differed across estuaries (LRT $X^2=7.2$, $df=2$, $p=0.027$; Appendix Table B.4); Crookhaven River had greater lengths than Port Hacking and Hunter River (post-hoc Tukey, Crookhaven River > Port Hacking = Hunter River, Figure 2.2C).

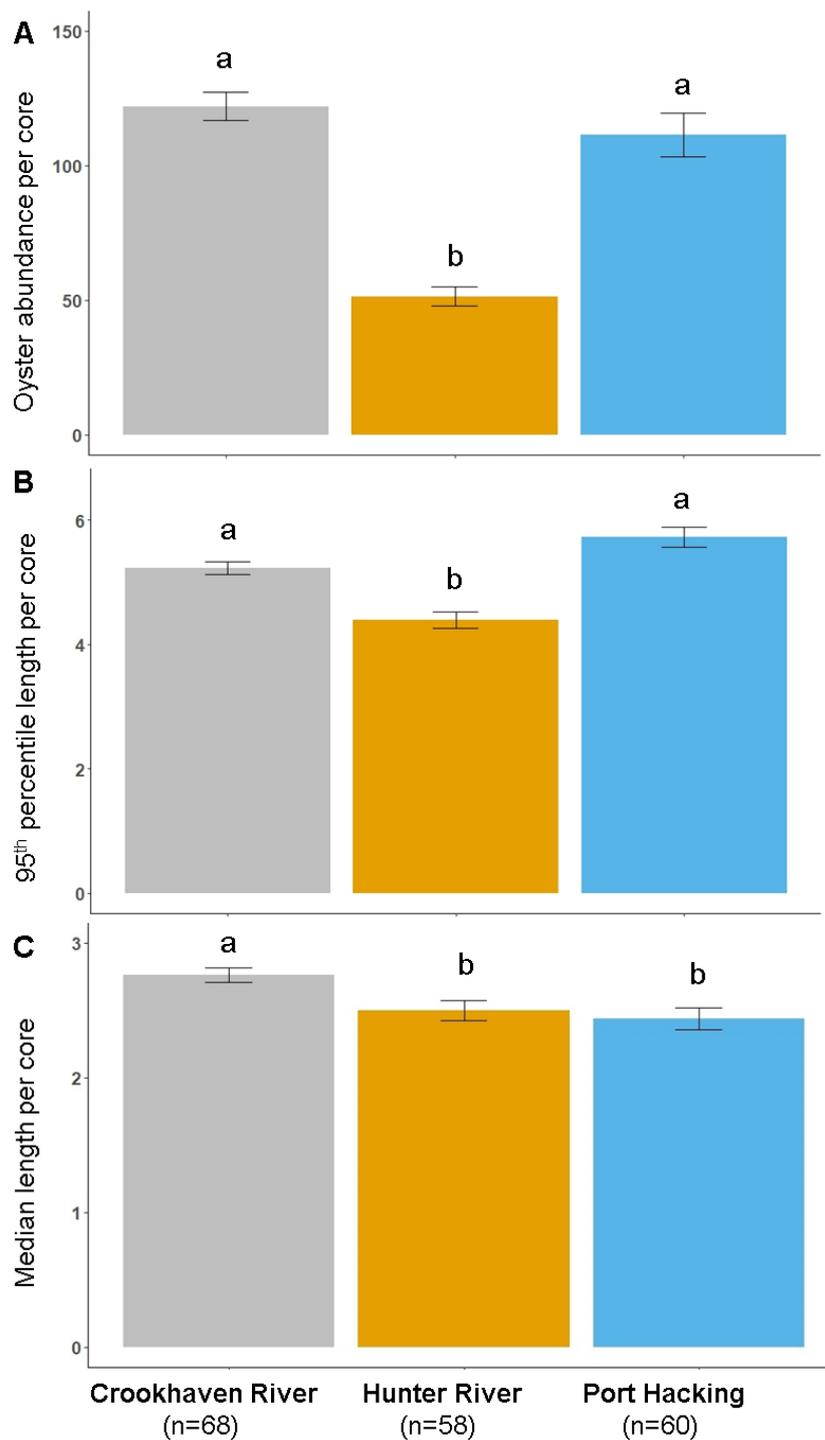


Figure 2.2. Mean (\pm SE) oyster abundance (A), 95th percentile length (B) and median length (C) of oysters sampled in Crookhaven River, Hunter River and Port Hacking. Number of sampling cores per estuary is denoted as n . Different lowercase letters represent significantly different results ($p < 0.05$) from Tukey post-hoc tests.

2.4.2 Oyster characteristics across within-, whole- and amongst- patch attributes

Among all estuaries, oyster abundances were best explained by within-patch and whole-patch attributes, with different combinations found across estuaries (Table 2.3, Figure 2.3). Surface elevation was the only attribute that was strongly related to oyster abundances at all estuaries (Table 2.3, Figure 2.3A). However, the elevational trends were not the same across the estuaries; oyster abundance significantly decreased at higher reef elevations at Crookhaven River and Hunter River but increased at Port Hacking (Figure 2.3A). Oyster abundance was highest for the least fractal and smaller reefs at Hunter River (Figures 2.3B and 2.3C). Higher reef proximities were only associated with lower abundances in Crookhaven River.

Size of the “largest” oysters per core (as measured by the 95th percentile oyster lengths) was also best explained by within-patch and whole-patch attributes, with different combinations found across each estuary (Table 2.3, Figure 2.4). Higher surface elevation of reefs was associated with smaller oysters in Crookhaven River and Hunter River (Figure 2.4A). Circle and fractal dimensionality indices of reefs were associated with large oysters in Crookhaven River and Port Hacking; the former showing positive correlation with size of large oysters and the latter showing opposing relationships in both estuaries (Figures 2.4E and 4F).

By contrast, median oyster lengths were associated with whole-patch and patch-connectivity attributes at two of three estuaries (Table 2.3, Figure 2.5). None of the within-patch attributes included explained median oyster lengths. Similar to 95th percentile lengths, oyster median lengths were associated with decreased fractal dimensionality of reefs and increased reef circle index in Crookhaven River (Figure 2.5E). At Port Hacking, median lengths were best explained by isolation index, proximity index and reef area (Figures 2.5D, 5G and 5H) where they were negatively associated with isolation index.

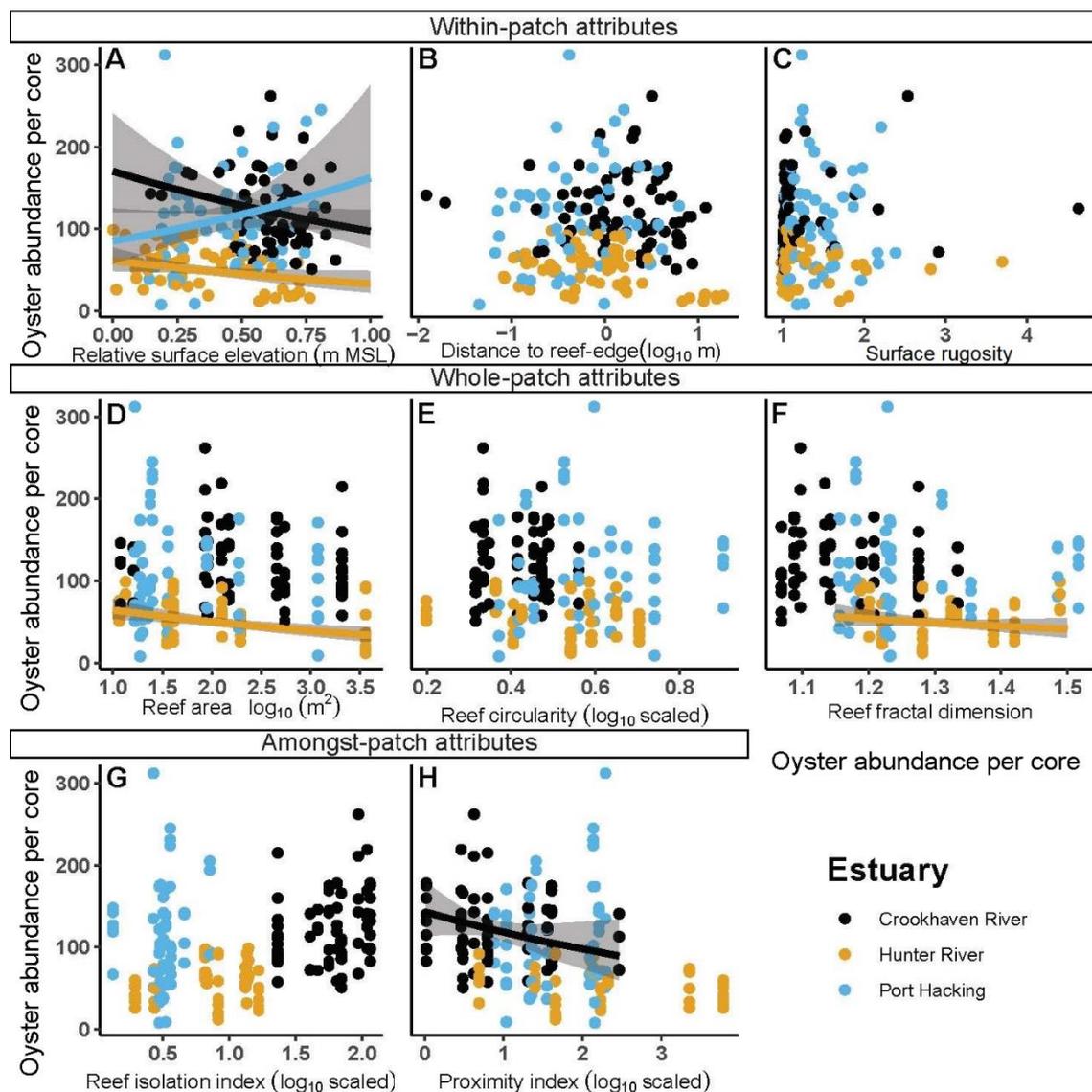


Figure 2.3. Relationships between oyster abundance and spatial attributes (A. elevation; B. distance to reef-edge; C. surface rugosity; D. area; E. circularity index; F. fractal dimension index; G. isolation index; H. proximity index) at sampled estuaries. Regression lines and 95% confidence intervals (shaded area) were plotted for selected spatial attributes from model selection (see Data Analysis section and Table 2.3).

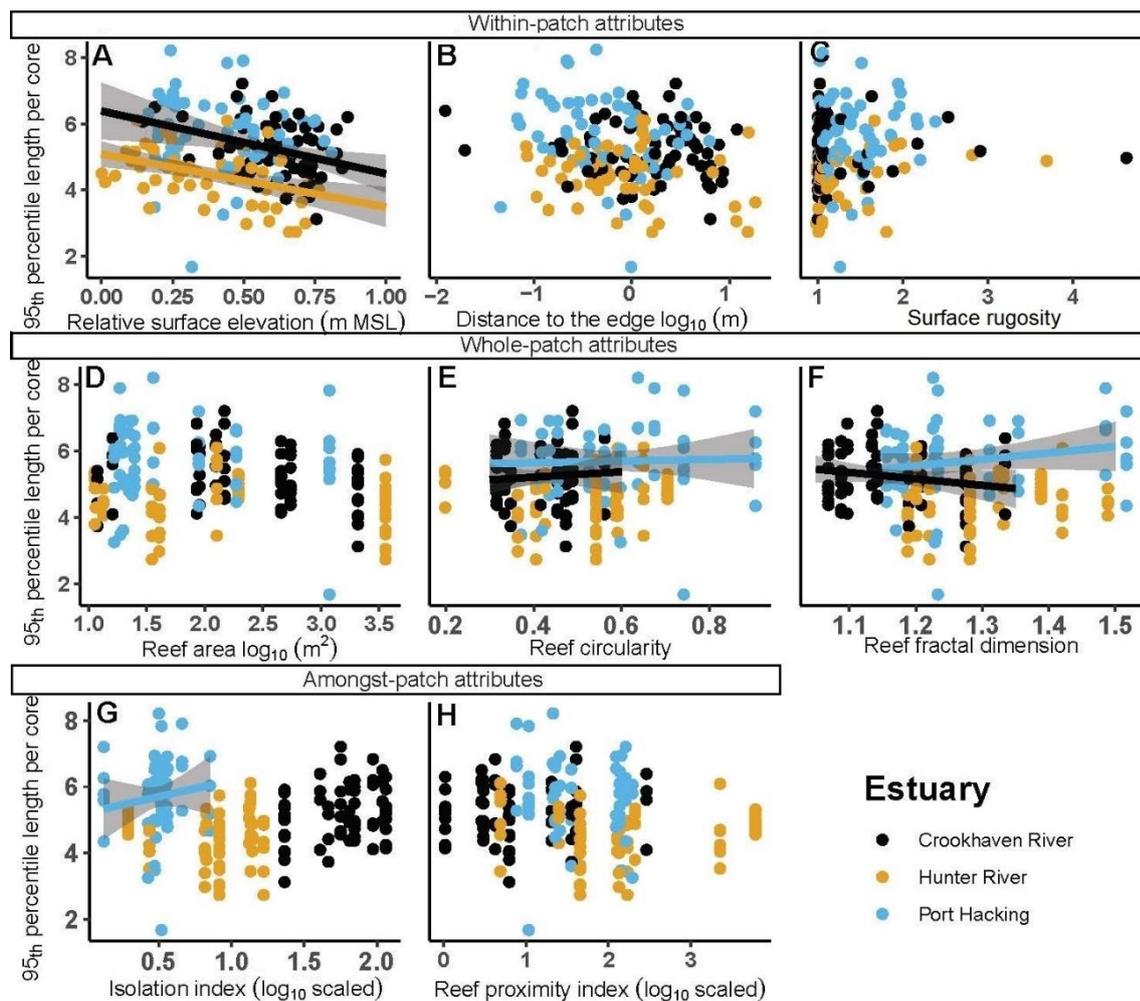


Figure 2.4. Relationships between largest oyster sizes and spatial attributes (A. elevation; B. distance to reef-edge; C. surface rugosity; D. area; E. circularity index, F. fractal dimension index; G. isolation index; H. proximity index) at sampled estuaries. Regression lines and 95% confidence intervals (shaded area) were plotted for selected spatial attributes from model selection (see Data Analysis section and Table 2.3).

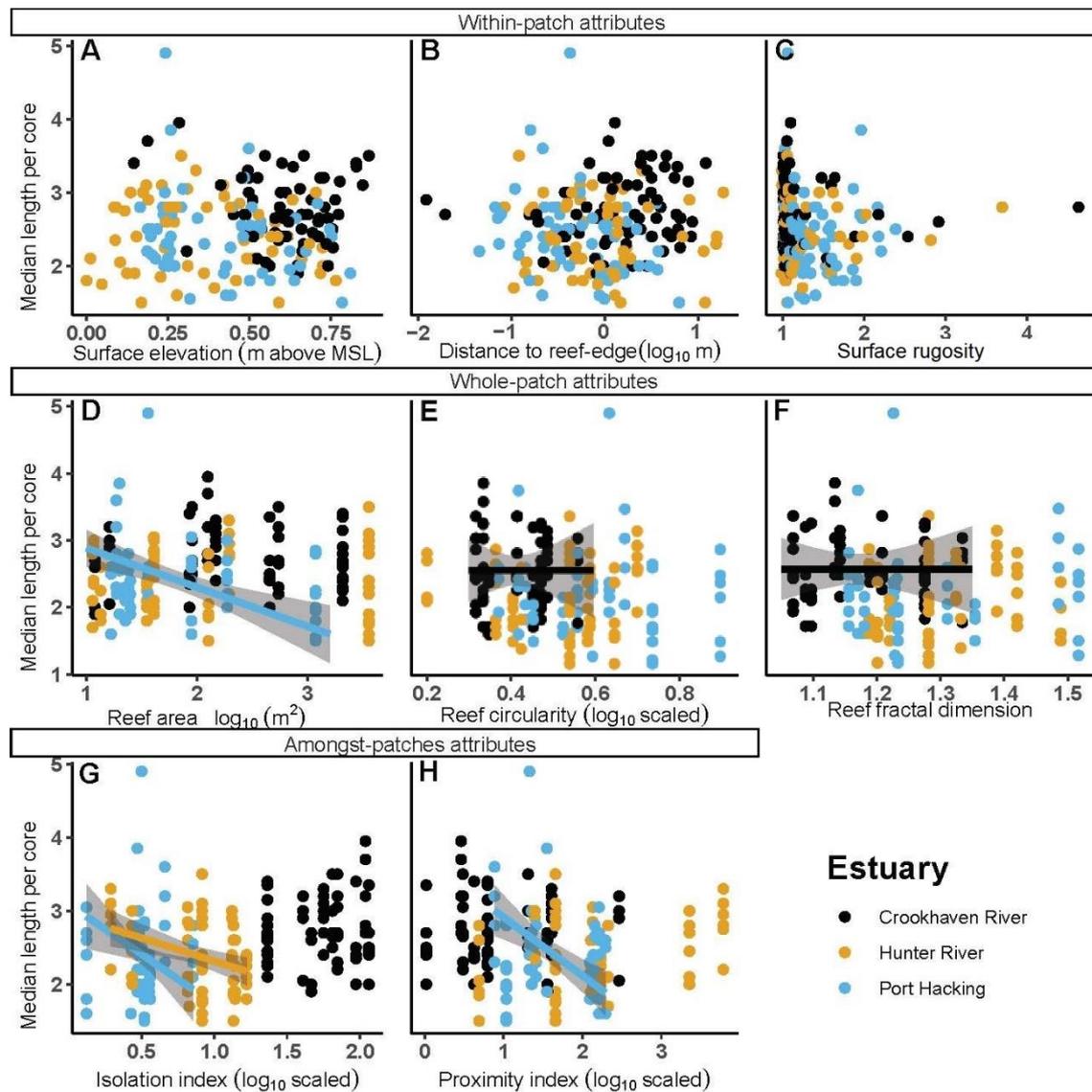


Figure 2.5. Relationships between median oyster lengths and spatial attributes (A. elevation; B. distance to reef-edge; C. surface rugosity; D. area; E. circularity index; F. fractal dimension index; G. isolation index; H. proximity index) at sampled estuaries. Regression lines and 95% confidence intervals (shaded area) were plotted for selected spatial attributes from model selection (see Data Analysis section and Table 2.3).

Table 2.3. Selected spatial attributes that relate to oyster density, 95th percentile length and median length from 'best' models obtained for Crookhaven River (CR), Hunter River (HR) and Port Hacking (PH) reefs. '+' and '-' represent positive and negative estimates respectively for selected attributes. White and black cells represent attributes were not selected and not included (due to collinearity) in best models respectively. Refer to Supplementary Tables B9-B11 for detailed model outputs.

Spatial scales & patch attributes		Population Characteristic & Estuaries								
		Abundance			95 th Percentile Length			Median Length		
		CR	HR	PH	CR	HR	PH	CR	HR	PH
Within-patch	<i>Surface Elevation</i>	-	-	+	-	-				
	<i>Distance to Edge</i>									
	<i>Surface Rugosity</i>									
Whole-patch	<i>Area</i>		-							-
	<i>Fractal dimension</i>		-		-		+	-		
	<i>Circularity Index</i>				+		+	+		
Amongst-patch	<i>Isolation Index</i>								-	-
	<i>Proximity Index</i>	-					+			-

2.5 Discussion

The population characteristics (e.g., densities and body size) of foundation species can mediate the functions they provide (e.g., habitat provisioning, water filtration). Thus, understanding the spatial processes that govern these may help inform the spatial design of restored oyster reefs and enhance the ecosystem services and functions they provide. Here, we determined how the density and body size of the reef-forming Sydney rock oyster, *S. glomerata*, varied at multiple spatial scales. Our study revealed that the density and body size of *S. glomerata* were related to reef attributes at within-patch, whole-patch, and landscape scales. However, the greatest variation in both oyster density and size was observed at regional scales, suggesting that processes operating at this scale set the context for smaller scale habitat influences on oyster population characteristics.

Our results support previous studies showing that oyster characteristics can differ amongst estuaries (Powers et al. 2009; McAfee et al. 2016; Kimbro et al. 2020). The larger oyster sizes and densities observed in Crookhaven River and Port Hacking could be linked to better water quality and greater wave action at these sites (Table 2.1), which can increase recruitment, food supply and filtration rates, driving greater survival and growth (Dove & Sammut 2007; Diggles 2013; Theuerkauf et al. 2017; Vozzo et al. 2020). Hence, the potentially poorer water quality at the most estuarine site studied, Hunter River, as evidenced by the greater turbidity that occurs in the river (Table 2.1), might explain the lower densities and body sizes found at this estuary. Differences in temperature among estuaries - such as may occur with latitudinal gradients - do not explain patterns in density and shell length as there is little difference in temperature amongst estuaries (Table 2.1) and our warmest site is in the middle so oyster lengths are not related to any latitudinal gradient in temperature that may exist over the 250 km of coastline our estuaries span. Differences in biotic interactions could also explain patterns in body size and density among estuaries. Indeed, oyster predation in Australia is driven by fish (Anderson & Connell 1999). At the same time as this study, Erickson (2019) studied fish assemblages in Port Hacking and Crookhaven River. This study found greater fish predation at Port Hacking than Crookhaven River, which is one of the sites with high density and size of oysters. Moreover, at Hunter River, we would expect predation to be low due to high turbidity at this site as has been observed in

other systems (Lunt & Smee 2014; Reustle & Smee 2020). Hence, it is unlikely that differences in rates of predation explain

differences in oyster length and density among estuaries. Studies assessing the variation in oyster population characteristics at regional scales and including estuaries with increasing levels of water quality are therefore needed to further explore these relationships.

Our models showed that factors acting at scales within estuaries also play an important role in determining oyster density and body size. Within-patch characteristics explained oyster abundances and length of the largest oysters at all estuaries, but the specific characteristics and trends varied between estuaries. For example, while densities increased with elevation at Port Hacking, as reported in previous studies (Lenihan 1999; Schulte et al. 2009; Colden et al. 2017), the opposite trends were observed in Crookhaven River and Hunter River. Interestingly, these reefs were at higher elevation relative to sea-level than Hunter River, hence they might be at the upper limit of their optimal tidal elevation and likely affected by a reduced hydroperiod resulting in lower densities and smaller sizes at their highest points (Bartol et al. 1999; Bishop & Peterson 2006, Byers et al. 2015). However, our results support the current understanding that tidal elevation is an important environmental factor to consider when restoring oyster reefs (Wallis et al. 2016).

In terms of whole-patch attributes, our results showed that patch shape explained variations in oyster size in two out of three estuaries. Specifically, increases in circle index (i.e., narrower, and elongated patches) were linked to larger oysters in Crookhaven River and Port Hacking. Meanwhile, fractal dimensionality (i.e., the geometric complexity along the edges of the patches) was positively associated with large oyster sizes at Port Hacking, but negatively at Crookhaven River. These results, although variable across estuaries, suggest that patch-shape influences oyster sizes particularly at exposed sites. Reef shape at these sites might be interacting with the local hydrodynamics, with elongate and complex reef shapes providing better protection for oysters. These results indicate that oyster restoration initiatives at exposed sites might benefit from incorporating more elongate and complex shapes, while this might not be necessary for protected sites.

Patch size and edge of foundation species have well described effects on population characteristics (Godron & Forman 1981; Kennedy & Bruno 2000; Hanke et al. 2017a). Moreover, surface rugosity can both influence and be influenced by the population characteristics of foundation species, as it can control larval settlement, recruitment and post-recruitment growth by altering water flow, food supply and predation (Scharf et al. 2006; Colden et al. 2017; Whitman & Reidenbach 2012). Somewhat surprisingly, this study found little or no relationships between population characteristics and these spatial attributes, highlighting that the spatial attributes affecting densities and size are highly variable between sites. Restoration projects should therefore be informed by knowledge of the ecological processes relevant to the areas targeted for restoration.

Patch-connectivity indices were related to oyster densities at Crookhaven River and oyster sizes at Port Hacking, while no effect on population characteristics was found at Hunter River. At Port Hacking, isolated patches had smaller median length of oysters, but tended to have the largest oysters. Meanwhile, at Crookhaven River, abundance of oysters was greater in more isolated reefs. There is a range of factors that could be explaining these patterns. For example, these differences could be driven by the different predation pressures between isolated patches, as observed by previous studies (Harwell et al. 2011; Duncan et al. 2019). In fact, lower abundances of fish were observed in more isolated patches at Crookhaven River (Erickson 2019). Moreover, differences between patches in processes such as the timing of recruitment and growth rates can also influence oyster larval and thus reef connectivity (Theuerkauf et al. 2017). Future studies are needed to disentangle these possible explanations.

Restoration strategies for oyster reefs and, by extension, the functions they perform currently rely on build-it-and-they-will-come approaches, typically putting out substrate to encourage recruitment by increasing the availability of surfaces for settlement. These efforts usually consider the material used (e.g. oyster shells, rock, concrete; Westby et al. 2019), but they seldom consider the spatial arrangement of this material (McAfee et al. 2020; Reeves et al. 2020). Restoration programs that leverage the relationships between reef configuration and oyster characteristics may significantly enhance their outcomes. Importantly, small-scale factors related to the reefs themselves (size, shape, and connectivity) had important implications for body

size and density of oysters, so integrating these aspects into reef construction - which could be easily done - should maximize the ecosystem benefits provided. Moreover, although these reef attributes were common among estuaries, often their relationships with oyster density or body size were in opposite directions. In fact, our models suggest that the reef attributes to manipulate will be dependent on the region or environmental setting, as this was the scale at which most variation in oyster body size and density occurred. These results emphasize that a 'one-size-fits-all' approach to oyster reef restoration may not be appropriate. Rather, restoration efforts need to be informed by local ecological knowledge of the remnant foundation species or pilot studies at the proposed restoration site. Whilst this adds a level of complexity to restoration efforts, our study suggests that maximizing the benefits to oyster restoration needs to consider processes acting across multiple spatial scales.

Chapter 3

Relationships between spatial scales and oyster reef epifaunal biodiversity and communities

3.1 Abstract

Species-area relationships (SARs) are primary considerations for oyster reef restoration strategies in promoting biodiversity. However, such relationships change in response to many ecological processes operating at multiple spatial scales. It is unclear whether these relationships can be employed broadly in restoration strategies, especially on Australian oyster reefs where ~90 % have been lost. This study investigated the relationships within-patch (rugosity, distance to reef-edge and elevation), whole-patch (size and shape), amongst-patch (connectivity), amongst-estuary attributes of remnant Sydney rock oyster, *Saccostrea glomerata*, reefs, and their associated epifauna communities. At each of three estuaries in New South Wales, I sampled 9-11 patches of different sizes (10 - 4000m²). In each patch, I counted and identified all sessile epifauna >1mm from replicate cores at random distances from patch-centres. I tested how univariate biodiversity indices (i.e., taxa richness, taxa abundance, Shannon's diversity index and taxa evenness), and the multivariate community structure of epifauna varied with spatial attributes. Epifaunal taxa richness and communities on reefs varied the largest on a regional scale (i.e., amongst estuaries). At smaller scales, within-patch attributes such as surface elevation and mean length-width ratios were also strong predictors of taxa richness and total abundance in these communities albeit in mixed (i.e., positive, negative or absent) relationships across the estuaries. My results suggest that spatial attributes, coupled with a broader environmental setting have important implications for oyster communities and need to be considered if oyster restoration to enhance biodiversity objectives is to be maximised for long-term reef restoration success.

3.2 Introduction

Ecosystems on Earth have been undergoing extensive degradation in the Anthropocene, leading to the current sixth mass species extinction (Ceballos et al. 2015). A major driver of the global decline of biodiversity is the loss of foundation species (*sensu* Dayton 1972), such as trees (Laurance & Yensen 1991), mangroves (Ellison et al. 2005), corals (Hughes et al. 2018) and seaweeds (Lloyd et al. 2020), which support highly diverse communities. For example, mangrove forests have declined by 35% in global cover over 50 years (Polidoro et al. 2010) and seagrass meadows have declined up to 19% in area from 1880 to 2016 (Dunic et al. 2021). Strategies to enhance biodiversity have frequently focussed on the restoration of foundation species because of the high biodiversity they support (Bayraktarov et al. 2016).

The biodiversity of organisms supported by foundation species can vary from local scales (i.e., <1km) to biogeographical scales (i.e., 10-10000 kms) (Godron & Forman 1981; Boström et al. 2011; Fahrig 2017). Attributes of habitat patches, such as area, have been considered a central paradigm in predicting how variation in the habitat structure of foundation species relates to biodiversity (e.g., Matias et al. 2010; Fahrig 2013; Loke et al. 2019). However, species–area relationships (*sensu* MacArthur & Wilson 1967) for foundational species do not always follow these relationships (Matias et al. 2011, 2014). Species richness can vary independently of habitat area for forests (e.g., Haddad et al. 2017; Torrenta & Villard 2017), grasslands (e.g., Evju & Sverdrup-Thygeson 2016), macroalgal beds (e.g., Matias et al. 2010) and seagrass meadows (e.g., Boström et al. 2006). In these cases, patterns in biodiversity might be better explained by other habitat attributes occurring at multiple spatial scales. For example, interactions between landscape-connectivity and patch-size were found to influence taxa richness scales (Fahrig 2003; Martin et al. 2018). Consequently, restoration efforts should consider how processes operating at larger spatial scales may influence predictions based on habitat-area relationships.

The communities supported by foundation species can also be affected by processes operating at smaller scales, such as edge effects and habitat complexity within habitat patches (e.g., Matias et al. 2010, 2015). Physical conditions may differ between edge and centre of patches, affecting resource distribution and species interactions, thus influencing species abundances and distributions within a patch (Laurance & Yensen

1991; Ries et al. 2004; Lanham et al. 2021). For example, edges of temperate and tropical forests exhibited lower plant diversity due to increases in light penetration, increased herbivory and reduced soil moisture (see review by Murcia 1995).

In addition, biodiversity can increase with habitat complexity metrics (e.g., rugosity) within patches of foundation species through the provision of interstitial spaces and refugia from predators. For example, the surface rugosity of foundation species was directly related to the diversity of fish in coral reefs (e.g., Nagelkerken et al. 2000) and macroinvertebrates in freshwater macrophytes (e.g., St. Pierre & Kovalenko 2014). By forming three-dimensional structures, foundation species can also occur at a range of vertical elevations within their habitat that influences ecological interactions and thus communities associated with them (see review by Turner et al. 2003). For example, in foundation species, richness increased with centimetre-scale surface elevation increases in mangrove forests (e.g., Leong et al. 2017) and salt marsh plants (e.g., Keer & Zedler 2002). Therefore, an understanding of relationships between within-habitat variation and associated communities may lead to better biodiversity predictions of the communities associated with them.

Patterns of biodiversity supported by foundation species can also emerge at large scales (i.e., regional scales; *sensu* Mittelbach et al. 2001), influenced by prevailing environmental conditions. Regional temperature gradients can drive biodiversity patterns for both terrestrial (e.g., rainforests; González-Caro et al. 2014; Brodie et al. 2016) and marine foundation species (e.g., kelp forests; Teagle & Smale 2018; Bué et al. 2020). At landscape scales (i.e., beyond patches), the connectivity among patches can also influence biodiversity patterns (Boström et al. 2011, Fahrig 2017). Multiple habitat patches may interact by exchanging resources and progeny (Brooks 2003, Ewers and Didham 2006, Zambrano et al. 2019) affecting ecological interactions thus affecting biodiversity patterns at landscape scales (e.g., predation rates; Martin et al. 2018). It is assumed that habitat patches closer to each other have greater patch connectivity (i.e., increased species dispersal between patches) and thus support greater biodiversity at a landscape scale (Dunning et al. 1992, Taylor et al. 1993). This has been observed for forests (e.g., Bailey 2007; Haddad et al. 2015), coral reefs (e.g., Ault & Johnson 1998) and mangrove forests (e.g., Roos et al. 2021).

Importantly, larger scale processes interact with those operating at smaller spatial scales to influence the biodiversity supported by foundation species (Cohen et al.

2016; Suárez-Castro et al. 2022). For example, the abundance of an invasive crab in a habitat-forming tube worm attached to the underside of rocks on boulder fields is dependent on patch-attributes (e.g., elevation) and regional processes (e.g., wave exposure; Uyà et al. 2020). However, the interactions between patch-scale, landscape and regional processes on biodiversity provision by foundation species remains poorly understood. Understanding how processes occurring at different scales affect biodiversity patterns can inform spatial scales that are essential for conservation and restoration strategies that aim to enhance biodiversity (Angelini et al. 2011; Gilby et al. 2018).

Among marine foundation species, oyster reefs have been severely degraded worldwide from overharvesting, habitat modification, water pollution and disease, with over 85% of oyster reefs globally lost since the 1880s (Beck et al. 2011). The biodiversity of epifauna on oyster reefs can increase with patch-size (e.g., Hanke et al. 2017), in patch-centres (e.g., Hanke et al. 2017) and with increased habitat-complexity (Luckenbach et al. 2005). Biodiversity can also vary among estuaries at a regional scale (McAfee et al. 2016; McLeod et al. 2020), although the role of oyster reef elevation and connectivity remain unexplored. To date, relationships between biodiversity and these spatial attributes have only been quantified individually. Studies incorporating multiple spatial scales are needed to identify the scales most important in driving biodiversity patterns on oyster reefs and to inform future restoration priorities for mitigating biodiversity loss.

In this study, I used remnant reefs of the Sydney rock oyster *Saccostrea glomerata* (Gould, 1850) to explore how biodiversity on oyster reefs may vary from small (i.e., within-patch, whole-patch) and local scales (i.e., among-patches) to large spatial scales (i.e., regional). In Australia, more than 90% of oyster reefs have been lost, including those of *S. glomerata* (Ogburn et al. 2007; Gillies et al. 2018). I sampled the biodiversity (abundance, taxa richness, taxa evenness, Shannon's diversity Index and community assemblages) of epifauna on oyster reef complexes at three estuaries in New South Wales (NSW), Australia. I hypothesised that biodiversity on *S. glomerata* reefs would (1) vary on a regional scale; (2) increase with patch-connectivity, -shape and -size; (3) increase with increasing distance to the patch edge and habitat complexity within patches, but (4) decrease with surface elevation (as a measurement of tidal height) within the patches. This study contributes to understanding the core processes

driving biodiversity in these biogenic habitats and identifies the spatial attributes that can be utilised to enhance the biodiversity supported by restored reefs.

3.3. Methods

3.3.1 Regional- scale sampling

Following methods outlined in Chapter 2 (see Section 2.3), I sampled epifauna from the sample cores that was collected from *S. glomerata* reef complexes in the same three estuaries in NSW, Australia (Figure 2.1).

3.3.2 Quantifying attributes at habitat and landscape scales

All spatial attributes at within-patch, patch- and landscape- scales that were quantified in Chapter 2 were identical to those applied in this chapter (see Sections 2.3.2 and 2.3.3 for methods). In addition to these attributes, I quantified another habitat-complexity metric, mean oyster-length to width ratio. With the measured lengths and widths of live *S. glomerata* oysters with Vernier callipers (± 0.1 cm), I calculated the shell length-to-width ratios, and their averages per core (hereafter 'mean length-width ratio') to estimate the interstitial space within each cored reef structure where larger ratios represented more uneven oyster sizes filling up a reef structure and thus increases in interstitial volumes (Hornbach et al. 2010). Biovolume and mean length-width ratio were correlated (i.e., Pearson's correlation coefficients, $r = +0.44$, $p < 0.001$) to each other but $r < \pm 0.7$, so I assumed independence of co-variates (sensu Zuur et al. 2009). All the spatial attributes studied in this chapter are listed in Table 3.1.

3.3.3 Estimating species' abundances, diversity indices and assemblage structure through core sampling

All invertebrate epifauna (≥ 1 mm) found in the sampled oyster cores were counted and identified under a dissecting microscope to the lowest morpho-species taxonomic resolution possible (see Appendix Table C.1 for taxa list). Morpho-species classification is typically used for these data sets and suitable for detecting spatial patterns (Oliver & Beattie 1996; Lloyd et al. 2020). Species richness (Whittaker 1972), Shannon's (1948) diversity index and species evenness (Pielou 1966) were calculated for each core.

Table 3.1. List of metrics used to quantify within-, whole- and amongst- patch (patch-connectivity) attributes in this chapter. Formulae of metrics, except mean length-width ratio can be found in Appendix Table B.3.

Attributes	Description
Amongst-patches	
Nearest-neighbour Distance	The shortest Euclidean and edge-to-edge distance between a focal reef and its nearest neighbouring reef (McGarigal et al. 2012).
Mean Nearest-neighbour Distance	Average of the nearest Euclidean and edge-to-edge distances from a focal reef to all other reefs in the same landscape (McGarigal et al. 2012).
Proximity Index	Index which measures the distance of a focal reef to other reefs in relation to area of the focal patch. Index for a patch is calculated by summing ratios of focal patch-area to nearest neighbour distances from focal patch to other patches (Gustafson & Parker 1992).
Isolation Index	Index is a weighted sum of products between nearest neighbour distance from focal patch to other patches, and the ratios of focal area to total patch area (Moilanen & Nieminen 2002).
Whole-patch	
Two-dimensional Fractal Dimension Index	Standardised and scale-independent measure of perimeter of a patch relative to a square perimeter and patch-area (McGarigal et al. 2012).
Circularity Index	Ratio between area and the smallest circumscribing circle of the patch (McGarigal et al. 2012).
Shape Index	Ratio of actual patch-perimeter to hypothetical patch-perimeter as a square with the same area, characterising total edges of patch (McGarigal et al. 2012).
Perimeter	Perimeter of each patch calculated from satellite image, reef contours.
Perimeter-Area Ratio	Ratio of perimeter-patch to patch-area for each patch.
Area	Area of each patch calculated from satellite image, reef contours.
Within-patch	
Distance to Edge	Shortest distance of each sampled core to the nearest reef edge.
Surface Elevation	Height of each sampled core above mean sea level.
Surface Rugosity	Surface roughness on each sampled core and 20-cm radius surrounding each core derived from photogrammetry and digital elevation models (<i>sensu</i> Figueira et al. 2015).
Mean Length-Width Ratio	Average shell length-to-width ratios per core that represents measure of volume of interstitial space

within each cores (Hornbach et al. 2010).

3.3.4 Data Analysis

3.3.4.1 Regional scale

I first tested the hypothesis that biodiversity would vary on a regional scale. The abundance and species richness of epifauna were contrasted among estuaries using generalised linear mixed models (GLMMs) assuming a negative-binomial distribution, with 'estuary' as a fixed factor and 'reefs within each estuary' (hereafter 'reef_id') as a random factor nested within 'estuary' to account for potential non-independence between sampled cores from the same reef. Shannon's diversity index and species evenness were assessed using linear mixed models (LMMs) under the same design above. Biovolume per core was also included as a co-variate in each LMM and GLMM to account for potential differences in sampling effort and baseline abundance of oysters. GLMMs and LMMs were performed using 'glmmTMB' package (Magnusson et al. 2020) and 'lme4' package (Bates et al. 2015), respectively. Models were validated using residuals versus the fitted model plots (Zuur et al. 2009). Statistical significance for the effect of estuaries were computed with likelihood ratio tests (LRTs) in the 'car' package (Fox et al. 2013), while post-hoc tests in lieu of statistical significance was computed with function and package 'lsmeans' (Lenth 2016).

To assess variation in epifaunal assemblages among estuaries, I used multivariate generalised linear models with a negative binomial distribution using the 'manyglm' function ('mvabund' package; Wang et al. 2012). Biovolume was added to the models as co-variate as described above. To account for the random factor i.e. 'reef_id' in the models, 'reef_id' was placed as a blocking factor in the models and all observations within each level of 'reef_id' were sampled using case resampling method (*sensu* Davison & Hinkley 1997). Statistical significance of estuary, and the pair-wise comparison between estuaries for the multivariate models were computed with likelihood ratio tests (LRTs) using the function 'anova' in the same package with 1000 iterations. To determine which taxa contributed most to the differences amongst the estuaries, I calculated the proportional contribution of LRTs for each taxon to the sum of LRTs over all taxa (Warton et al. 2012). Significance of taxa-specific GLMs were then determined by

their LRTs and their respective adjusted p-values. I visualised the differences in community assemblages amongst estuaries using a non-metric multidimensional scaling (NMDS) plot and Bray-Curtis dissimilarity matrices with square root transformation in the 'vegan' package (Oksanen et al. 2015).

3.3.4.2 Within-, whole- and amongst-patch attributes

I fitted mixed models and conducted step-wise model selection to test the hypotheses that biodiversity will increase in tandem with increases in patch-area, patch-shape, patch-connectivity, distance to the patch edge, and rugosity but decrease with surface elevation. Twelve model sets were fitted, one for each response variable (abundance, species richness, Shannon's diversity Index and species evenness) in each of the three estuaries. I tested for multi-collinearity of patch attributes within each estuary's dataset and excluded any that were strongly correlated (i.e., Pearson's correlation coefficient, $r \geq \pm 0.7$) prior to model fitting (Zuur et al. 2009) (see Appendix Table C.2). Response variables were then fitted using GLMMs and LMMs (as per Section 3.2.4.2, where 'biovolume' and 'reef_id' were also included in each model). Rugosity was also excluded as a co-variate in Hunter River models due to a lack of data points (refer to Chapter 2). I conducted step-wise model selection starting with full models and eliminating/adding predictors until the best model (lowest corrected Akaike information criterion) using 'dredge' function (package 'MuMIn'; Bartoń 2009). The selected model and their corresponding patch attributes were validated using residuals versus the fitted plot values (Zuur et al. 2009).

The relationships between epifaunal assemblages and spatial attributes of oyster reefs were also analysed separately for each estuary as multivariate GLMs with the inclusion of biovolume and 'reef_id' as structured in Section 3.2.4.1. Co-linear patch attributes were excluded as described above. Model selection was done as described above using step-wise model regression ('step' function) with the lowest Akaike information criterion (AIC) values (Burnham & Anderson 2002). Models containing selected attributes were then refitted and validated using plots of the residuals versus the fitted values (Zuur et al. 2009). For each assemblage, and a selected attribute for each model, the contribution of each taxon was then determined by their LRTs and their respective adjusted p-values.

3.4. Results

3.4.1 Regional scale

Across all estuaries, I identified 82 taxa and counted a total of 46,249 individuals of invertebrates associated with the oyster reefs sampled (see Appendix Table C1). All measures of biodiversity varied among regions in the univariate analyses. The reefs at Port Hacking estuary had almost twice the mean abundance of epifauna per core ($341 \pm \text{SE } 11$ individuals) in comparison to Crookhaven River ($221 \pm \text{SE } 11$ individuals) and Hunter River reefs ($185 \pm \text{SE } 17$ individuals; LRT $X^2 = 38.1$, $df = 2$, $p < 0.001$, Figure 3.1A). Mean taxon richness was highest at Crookhaven River ($11 \pm \text{SE } 0$ taxa), followed by Port Hacking ($11 \pm \text{SE } 0$ taxa) and Hunter River reefs ($8 \pm \text{SE } 0$ taxa; LRT $X^2 = 63.0$, $df = 2$, $p < 0.001$, Figure 3.1B). Mean Shannon's Diversity Index was highest in reefs at Crookhaven River ($1.87 \pm \text{SE } 0.03$), followed by Hunter River ($1.39 \pm \text{SE } 0.04$) and Port Hacking ($0.4 \pm \text{SE } 0.04$; LRT $X^2 = 294.5$, $df = 2$, $p < 0.001$, Figure 3.1C). Epifaunal evenness was similar at both Crookhaven River ($0.69 \pm \text{SE } 0.01$) and Hunter River ($0.68 \pm \text{SE } 0.02$) and higher when both estuaries were compared to Port Hacking's reefs ($0.40 \pm \text{SE } 0.01$; LRT $X^2 = 428.4$, $df = 2$, $p < 0.001$, Figure 3.1D).

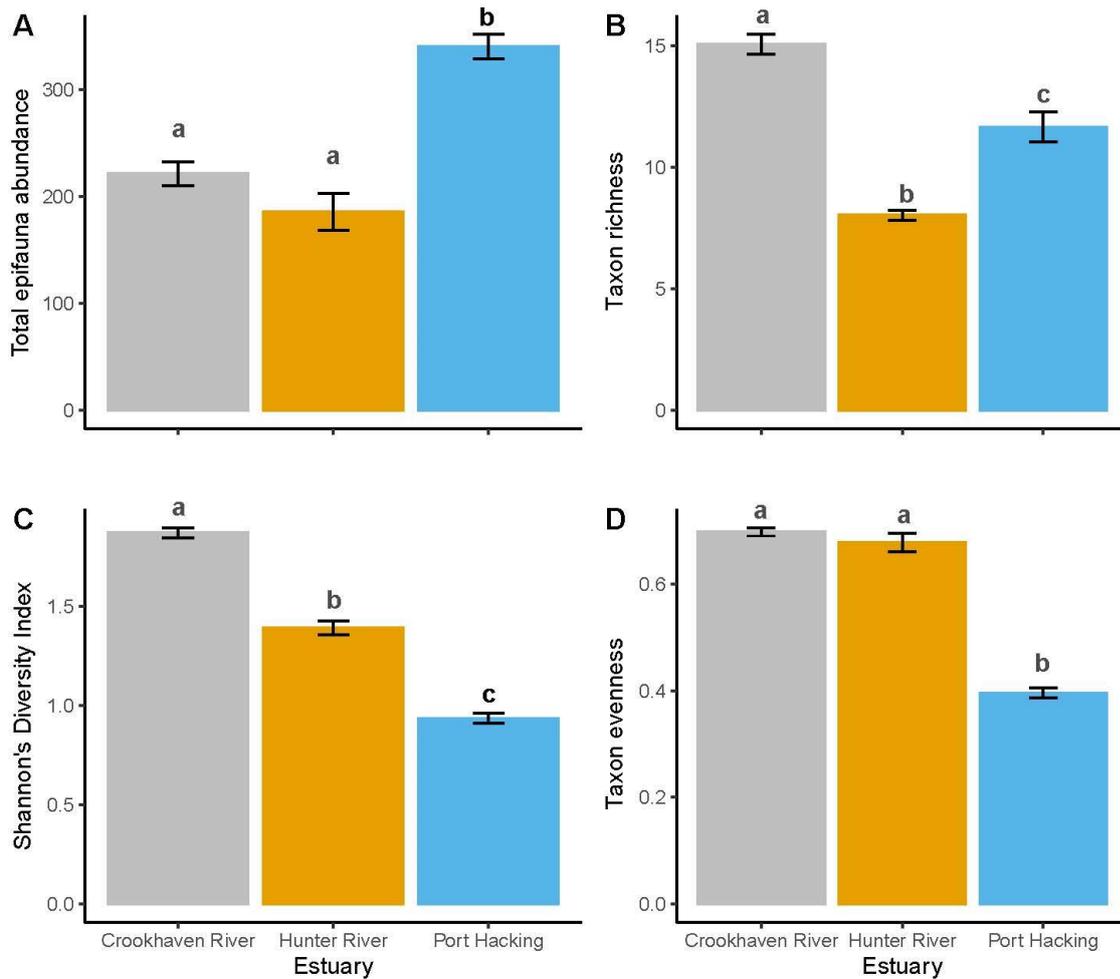


Figure 3.1. Mean (\pm SE) total abundance (A), taxon richness (B), Shannon Diversity index (C) and taxon evenness (D) of epifaunal in cores taken from oyster reefs in Crookhaven River, Hunter River and Port Hacking. Number of sampling cores per estuary is denoted as n . Different lowercase letters represent significantly different pair-wise groups (with p -adjusted < 0.05) from Tukey post-hoc tests for each index.

The structure of epifaunal communities, consisting of different taxonomic resolutions (i.e., species, genera, family and phyla) varied among estuaries (LRT $X^2 = 2357.3$, $df = 182$, $p=0.002$), with different assemblages at each estuary (post-hoc *mvabund* bootstrapping: Crookhaven River \neq Port Hacking \neq Hunter River, adjusted p-value <0.05 , Figure 3.2). A total of 27 taxa contributed to the differences in assemblages amongst the estuaries (see Appendix Table C.5). Of these taxa, anemones (Actinaria), barnacles (Cirripedia), amphipod (Corophiidae), and the gastropods *Lasaea australis* and *Patelloida mimula* were the five taxa that cumulatively contributed to 43.7% of variation in assemblages (sum of LRTs) amongst the estuaries (see Figure 3.3). Actinaria and Corophiidae were only present in Crookhaven River and Hunter River respectively (Figures 3.3A-C respectively). Cirripedia (barnacles) were the most abundant at Port Hacking, followed by Hunter River and the least abundant in Crookhaven River (Figure 3.3B). In contrast, *P. mimula* and *L. australis*, were highest in abundance at Crookhaven River, and lower at Port Hacking and Hunter River respectively (Figures 3.3D-E).

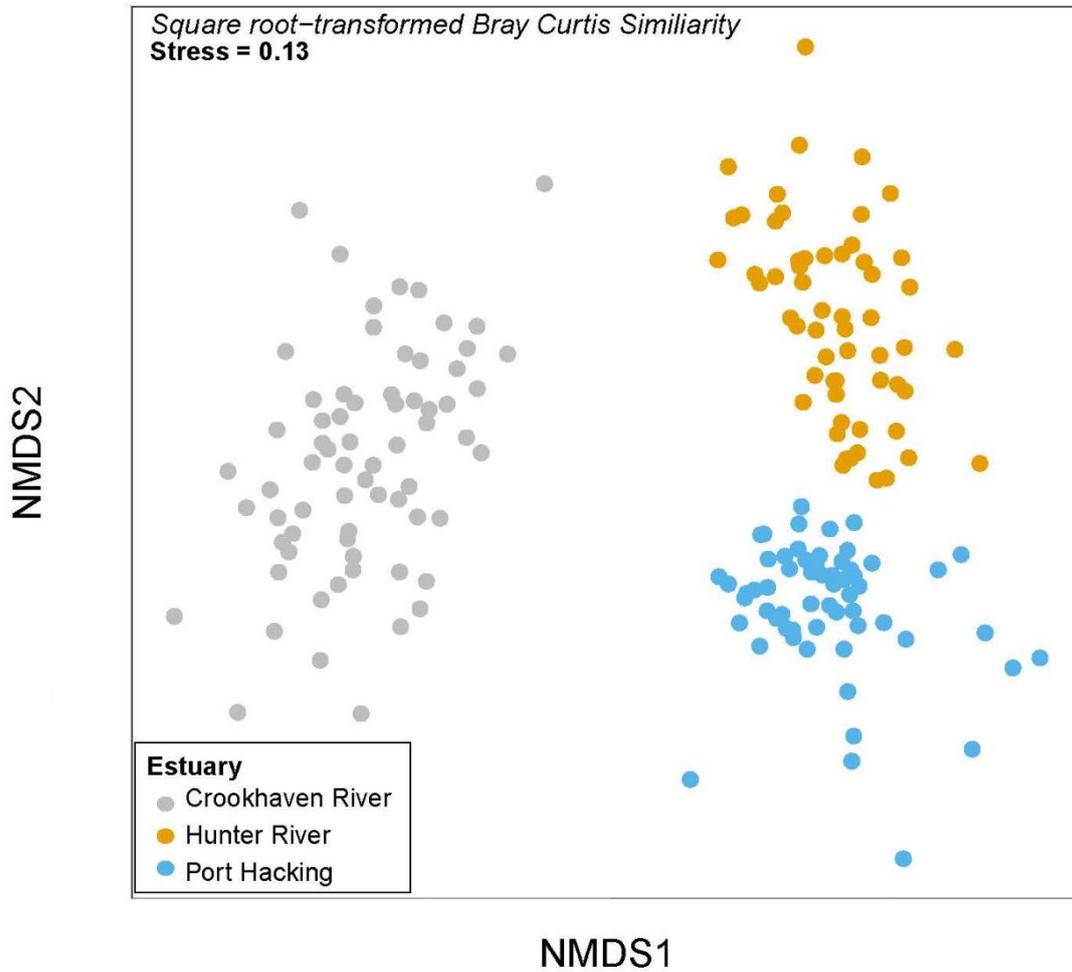


Figure 3.2. A non-metric multi-dimensional scaling (nMDS) ordination based on Bray Curtis similarities on square-root transformed abundances of epifauna across estuaries (Crookhaven River, Hunter River and Port Hacking).

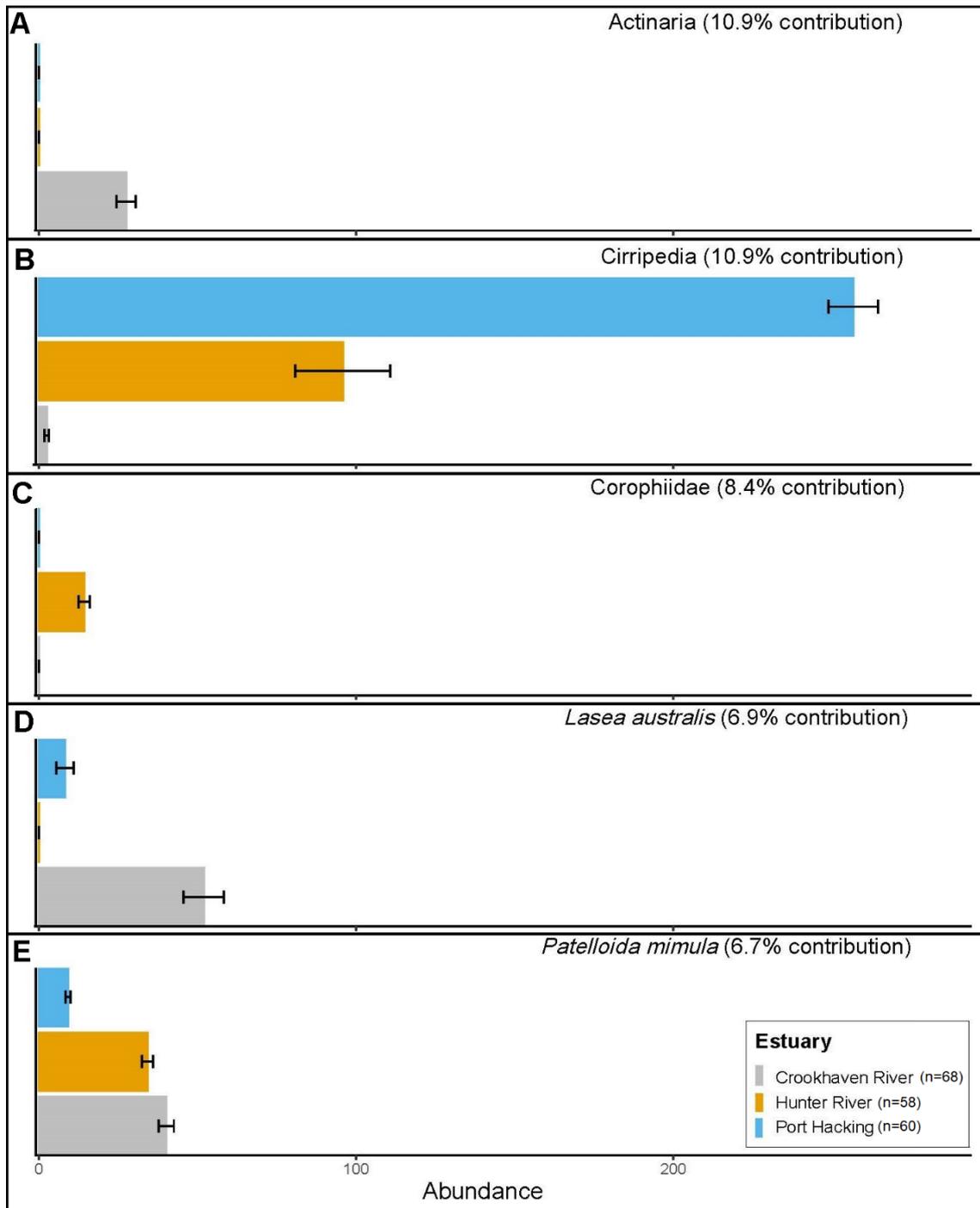


Figure 3.3. Mean (\pm SE) abundance of (A) Actinaria, (B) Cirripedia, (C) Corophiidae, (D) *L. australis* and (E) *P. mimula* i.e., the five taxa that contributed to the most variation of the epifaunal assemblage amongst the estuaries. Number of sampling cores per estuary is denoted as *n*. Contribution of each taxon is stated on the top right of each taxa plot, respectively.

3.4.2 Within-, whole- and amongst-patch attributes

Within estuaries, total abundance of epifauna varied across all spatial-scales, but within- and whole-patch attributes were the most important at explaining this variation (Table 3.2). Higher surface elevation was related to greater total epifaunal abundances at Port Hacking and Hunter River reefs (Figure 3.4A). There was a decrease in total epifaunal abundance when surface rugosity increased at Port Hacking (Figure 3.4C). Meanwhile, epifauna increased with reef area at Port Hacking, but the opposite pattern was observed in reefs at Crookhaven River (Figure 3.4D). Isolation and proximity indices were negatively related to epifaunal abundance at Crookhaven River (Figures 3.4G-H).

Within-patch attributes consistently affected taxon richness of oyster reefs at all sites (Table 3.2). Surface elevation and mean length-width ratio were consistently associated with taxon richness in reefs at all estuaries, although the direction of the relationship varied among estuaries (Figure 3.5A, H). At the whole-patch level, reefs with more edges (e.g., increasing fractal dimensionality) had less diversity at Port Hacking and Hunter River (Figure 3.5F). A positive relationship between species diversity and reef area occurred at Port Hacking only (Figure 3.5D). A decreasing Isolation Index was associated with an increase in taxon richness at Port Hacking and Crookhaven River (Figure 3.5G).

An increase in edginess from fractal dimensionality was associated to increases in Shannon Diversity Index in reefs at Hunter River (Figure 3.6A). Meanwhile, Shannon Diversity Index increased with patch area at reefs in Port Hacking (Figure 3.6B). Taxon evenness was directly related to reef fractionality in reefs at Hunter River (Figure 3.6C) and with surface elevation in reefs at Port Hacking (Figure 3.6D).

The models best explaining assemblage composition at each estuary included surface elevation in reefs at Crookhaven River and Port Hacking, while no patch attribute was selected for Hunter River (null model was the best model, Table 3.2, see Appendix Table C.6). The relationship between surface elevation and multivariate assemblage in reefs at Port Hacking was potentially explained by the lower densities of the microgastropod *Pseudoliotia micans* at higher surface elevation (Pearson's correlation coefficient, $r = -0.23$, adjusted p-value = 0.053). At

Crookhaven River, abundances of the mussel *Trichomya hirsuta* were negatively correlated with surface elevation (Pearson's correlation coefficient, $r = -0.45$, adjusted p-value = 0.024); there was a non-significant positive correlation with *L. australis* (Pearson's correlation coefficient, $r = +0.36$, adjusted p-value = 0.087).

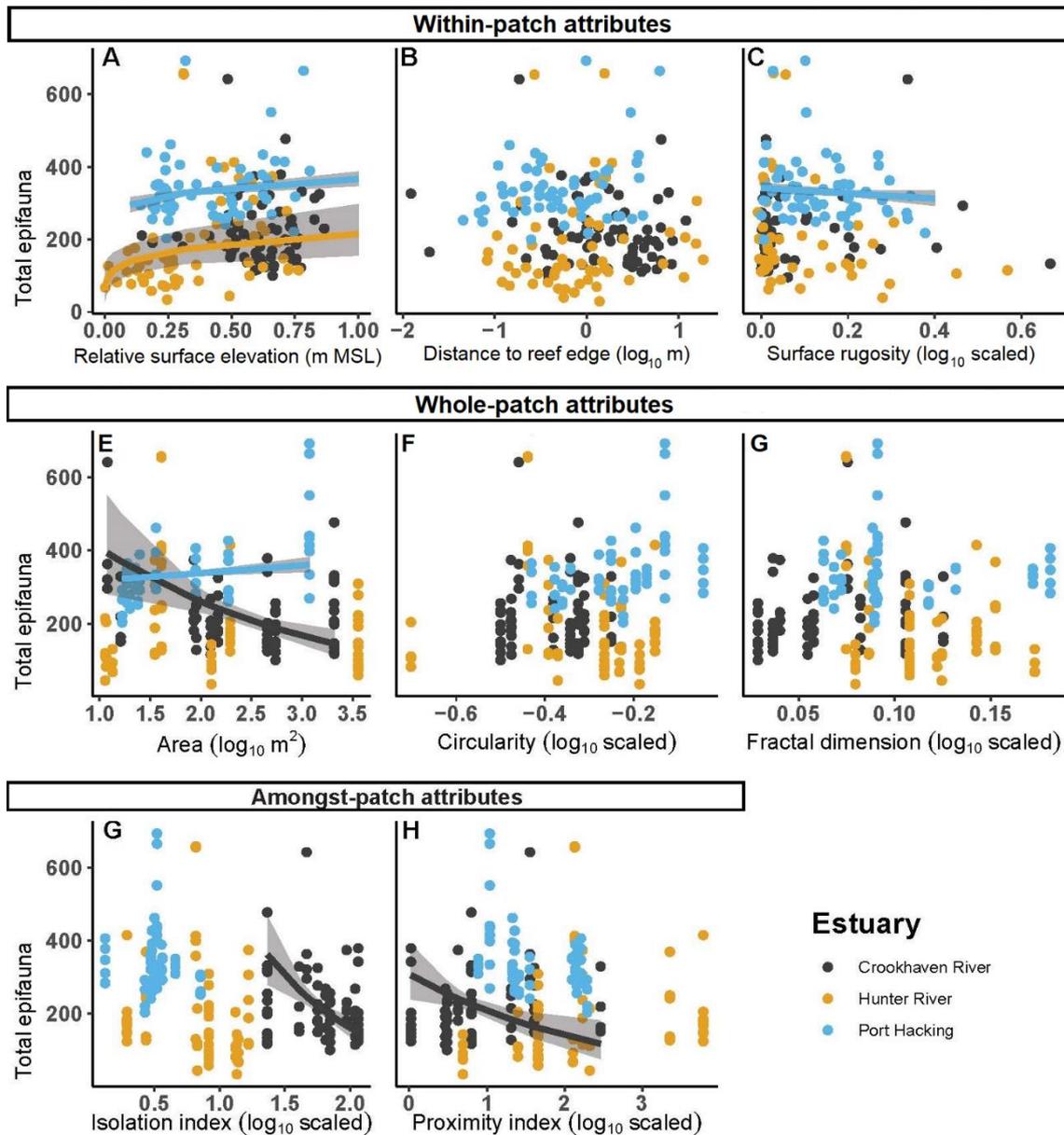


Figure 3.4. Relationships between total epifaunal abundance and within-patch (A. elevation; B. distance to reef-edge; C. surface rugosity), whole-patch (D. Area; E: Circle, F: fractal dimension) and amongst-patch (G. Isolation Index; H: Proximity) attributes of oyster reefs at Crookhaven River, Hunter River and Port Hacking. Regression lines and standard errors (shaded area) were obtained for significant terms from best models.

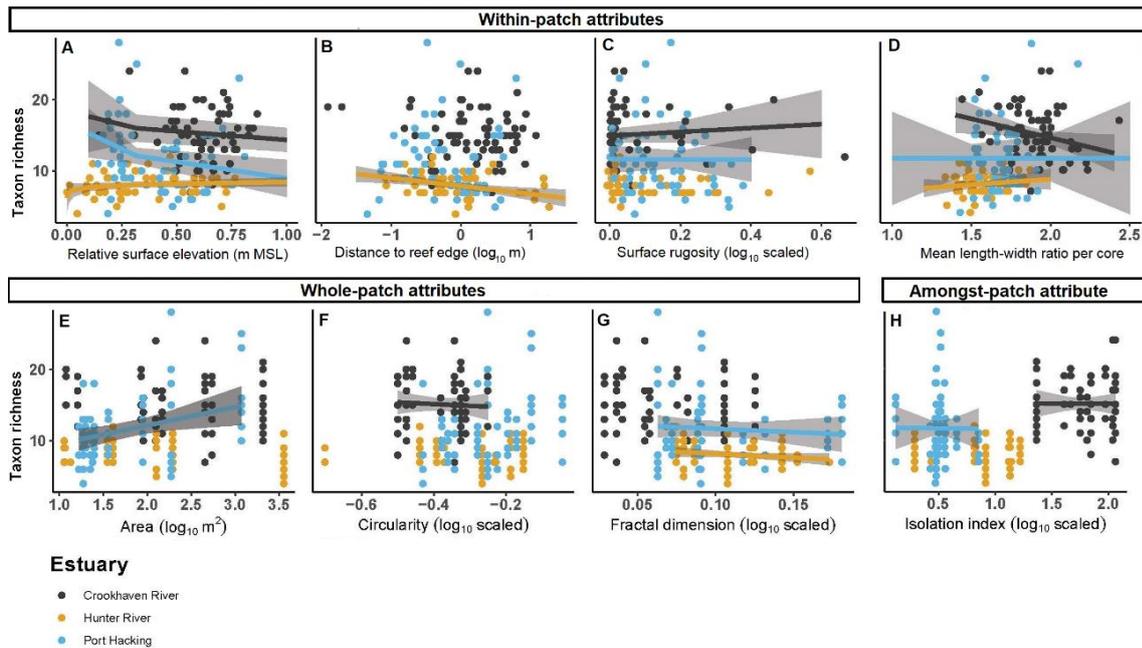


Figure 3.5. Relationships between taxon richness and within-patch (A. elevation; B. distance to reef-edge; C. surface rugosity and D. mean shell length-width ratio), whole-patch (E. area; F. circle, G. fractal dimension) and amongst-patches (H. Isolation Index) attributes of oyster reefs at Crookhaven River, Hunter River and Port Hacking. Regression lines and standard errors (shaded area) were obtained for significant terms from best models. Proximity index was omitted due to lack of space and significance across all estuaries.

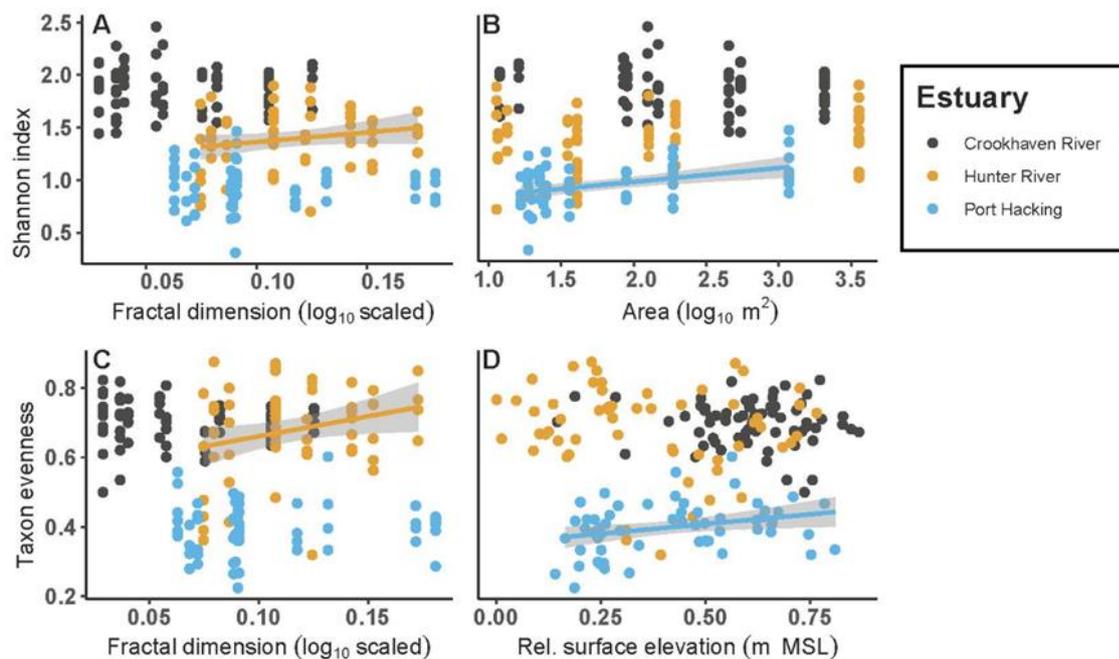


Figure 3.6. Relationships between (A-B) Shannon's Index and (C-D) taxon evenness with selected patch attributes in Crookhaven River, Hunter River and Port Hacking. Regression lines and standard errors (shaded area) were obtained for significant terms from best models.

3.5. Discussion

A key challenge in ecology and restoration is determining which spatial scales contribute to habitat-biodiversity relationships, especially when the configuration of foundation species can vary across landscapes (Fahrig 2003, 2017) and on regional scales (Angelini et al. 2011; Byers et al. 2015). In this study, I found support for the hypothesis that biodiversity on remnant oyster reefs would vary on a regional scale (i.e., amongst estuaries in New South Wales). In contrast, I found less support for the hypothesis that biodiversity would increase with patch-connectivity, -shape and -size; The epifaunal taxa richness had opposite or inconsistent trends with patch-connectivity, -shape and -area among the estuaries. Within the oyster patches, I found little support for the hypothesis that increasing distance to the patch edge and habitat complexity where the distance to the patch edge and habitat-complexity were negatively correlated to epifaunal taxa richness in most estuaries. I had more support for the hypothesis that biodiversity increases with surface elevation; epifaunal taxa richness decreased and epifaunal abundance increased at higher elevations, albeit only in two of three sampled estuaries. As a whole, my study suggests that the largest variations in biodiversity and assemblage structure were explained by processes on regional scales and scales occurring within habitat patches, such as surface elevation and habitat-complexity.

3.5.1 Role of regional processes

Across regional scales, large variation in taxon richness and assemblage composition of epifauna were observed on *S. glomerata* reefs, which align with the variation observed in mean epifauna richness and assemblages for *S. glomerata* reefs across four estuaries in a previous study (McLeod et al. 2020). Strong effects of regional scales were also observed in other foundation species such the seagrass *Zostera* (Pinnell et al. 2021) and kelp beds (Wernberg et al. 2003). Differences in communities among reefs may be due to the presence of other neighbouring, foundation species such as seagrass meadows and mangrove forests in the estuaries, as connectivity to these can increase the epifaunal diversity on oyster reef complexes through increased habitat-availability for common invertebrate taxa (Bishop et al. 2012; Reeves et al. 2020). This could explain the greater epifauna diversity observed in Crookhaven River, where *Avicennia* mangroves and *Posidonia* and *Zostera* seagrasses were spatially interspersed amongst the reefs (pers. obs.; see satellite images of Figure 2.1).

Abiotic factors (e.g., sedimentation, temperature, water quality and wave action) and stressors (e.g., eutrophication and bottom-water hypoxia; habitat modification), can also influence biodiversity patterns of communities in foundation species such as oysters at regional scales (thesis Chapters 4 and 5; Colden et al. 2017; McAfee & Bishop 2019; Scanes et al. 2016). The high sedimentation rates (refer to Chapters 4 and 5) and the low water quality (NSW Office of Environment and Heritage 2016) recorded in Hunter River in comparison to the other two estuaries may have contributed to the lower epifauna diversity observed in the estuary. For example, the high sedimentation setting might explain the presence of sediment-tolerant and deposit-feeding organisms, such as amphipods from the family Corophiidae found in the estuary (see Figure 3.3B; Meadows & Reid 1966; Thompson et al. 2002).

The higher taxa richness of epifauna recorded in Crookhaven River might be explained by the site's proximity to the estuary mouth (Table 2.1). These reefs received a greater oceanic influence, likely resulting in greater salinity and wave exposure. Coupled with the high water quality (NSW Office of Environment and Heritage 2016), oyster reefs in Crookhaven River likely hosted a combination of estuarine and marine species. Given its location, the epifaunal composition on the Crookhaven River reefs are likely similar to rocky shore assemblages. This is supported by the presence of high wave-energy tolerant species (e.g. sea anemones (Actinaria, Figure 3), *Plebidonax* sp. Appendix Table C.1; King 1976); and *Patelloida latistrigata* (Appendix Table C.1; Creese 1982) that are only present on Crookhaven River. This is consistent with previous research that shows that geographical setting of oyster reefs can influence the biodiversity on foundation species (Byers et al. 2015; McAfee et al. 2016).

Whilst patterns in species distributions in space can be influenced by their functional mode (e.g., mobility or feeding guild; Bruno et al. 2003, Wisz et al. 2013, D'Amen et al. 2015), only five taxa contributed to almost 44% of variation in communities among estuaries. Moreover, the same functional mode was dominant at different estuaries, but by different species suggesting that regional scale-processes on communities are operating at a species level, not a functional level.

3.5.2 Role of within-reef habitat structure and connectivity among reefs

Spatial attributes of oyster reefs also played an important role in predicting biodiversity at each estuary. All univariate indices of community structure, except for Shannon

Diversity index, were associated to within-patch attributes but the specific attributes and trends were variable between estuaries. In particular, surface elevation was associated with taxon richness at all estuaries, although relationships varied with biodiversity, with lower diversity observed at higher elevation at Port Hacking and Crookhaven River, with the opposite pattern observed at Hunter River. These biodiversity patterns observed at Port Hacking and Crookhaven River reefs corroborate with findings of higher epifaunal diversity observed on *S. glomerata* individuals at lower tidal elevation (Wilkie et al. 2012), with the inverse relationship observed at Hunter River could be related to relief-height of the reefs. Port Hacking and Crookhaven River reefs have a high-relief (>0.15 m in height compared to surrounding substrate) in comparison to Hunter River reefs (0.05 - 0.15 m in height compared to surrounding substrate) (NSW Marine Estate and Authority 2021). Therefore, the elevational increases on the high-relief reefs may approach the upper tidal limit, a zone of greater aerial exposure and therefore environmental stress for the epifauna at higher elevations (Byers et al. 2015).

Surface elevation also related to changes in assemblage at both estuaries. For example, the abundance of *P. micans* was negatively associated with surface elevation in Port Hacking, while *T. hirscuta* and *L. australis* were associated at opposing trends to each other with surface elevation at Crookhaven River. While there might be limited evidence between surface elevation and taxon richness on shellfish reefs, an experimental study by Wilkie et al. (2012) with live *S. glomerata* oyster on plates at lower tidal elevation possessed higher epifaunal richness and different epifaunal assemblages in comparison to plates at higher tidal elevation. My results also align with the species richness observed at different elevations in many intertidal rocky shores (e.g., Watt & Scrosati 2013) and across different regional scales (Harley & Helmuth 2003; Chappuis et al. 2014).

Habitat complexity can also have important implications within patches in structuring biodiversity patterns. Habitat-complexity of oyster reefs, either on the surface (measured as surface rugosity) and below the surface (estimated based on mean length-width oyster ratios), were related to epifauna taxon richness at all sites. While studies often show positive relationships between rugosity and biodiversity (Luckenbach et al. 2005), this pattern was only evident in reefs at Crookhaven River,

and the opposite relationship was found at Port Hacking. This was likely due to the lower structural integrity (i.e., looseness) of the surface of the reef structure at Port Hacking compared to Crookhaven River (pers. obs.). The reduced integrity of oyster reef matrix in Port Hacking would likely lead to the dislodgment of oyster shells on the top-surface of the reef structure during wave action and increasing abrasion between the epifauna and oyster shells thus reducing taxon richness and abundances (Luckenbach et al. 1999).

Below the surface, greater interstitial spaces were related to increases in taxon richness in Port Hacking and Hunter River oyster reefs. This increase in biodiversity could be due to increasing habitat availability and refuge from predators, as observed in rocky reefs and other foundation species systems (Lenihan 1999; Grabowski et al. 2005; Summerhayes et al. 2009; Callaway 2018). In contrast, Crookhaven River showed reduced taxon richness with increasing interstitial space. As length-ratios were substantially higher in Crookhaven River (mean $1.89 \pm \text{SE } 0.02$) compared to the other estuaries (Port Hacking; mean $1.68 \pm \text{SE } 0.02$ and Hunter River; $1.57 \pm \text{SE } 0.02$), the larger interstitial spaces are likely more accessible to nekton and other mobile predators, thus reducing the epifaunal biodiversity. The interstitial space-biodiversity patterns observed in this study is somewhat corroborated by studies in *Crassostrea virginica* reefs where reef complexes with larger interstitial spaces had higher predation rates on oyster epifauna (Hill & Weissburg 2013; Heoutsterberg et al. 2017). Interestingly, my results also highlight the potential complementary relationships between surface rugosity and interstitial space in predicting epifaunal biodiversity on oyster reefs. This was exemplified by the significant and inverse relationships between both habitat-complexity metrics in Crookhaven River and Port Hacking oyster reefs. These results suggest that complexity above and below the surface of the oyster reefs can provide different functional niches to epifaunal communities, and both types of habitat complexity should be measured to account for robust biodiversity provision in oyster reefs and other three-dimensional, biogenic foundation species.

In terms of whole-patch attributes, I only observed a positive species-patch area on Port Hacking reefs relationship despite the abundance of literature supporting increased diversity in larger habitat patches (e.g., Newmark 1986; Lawton 1999; Fahrig 2013). This suggests that species-area relationships alone may not be good predictors

of taxon richness, especially in patchy and fragmented habitat-forming ecosystems (Fahrig et al. 2019; Loke et al. 2019). In terms of edge-to-centre ratios, my results agree with studies on other shellfish foundation species that showed edge effects on epifaunal richness (Cole 2010; Hanke et al. 2017a; Carroll et al. 2019).

In support of other studies (Dunning et al. 1992; Taylor et al. 1993), patch-connectivity increased epifaunal taxa in patches at two of the three sites (Port Hacking and Crookhaven River). By contrast, epifaunal abundance had opposing relationships to proximity and isolation indices in reefs at Crookhaven River. This relationship may be explained by landscape configuration of the reefs in relation to environmental factors. The reefs with higher proximity and less isolation in Crookhaven River were clumped together in the windward facing side of the reef complex and relatively closer to the estuary mouth (refer to Table 2.1). These reefs may have experienced stronger stress reducing due to wind waves, reducing epifaunal abundance (pers. obs.).

3.5.3 Future applications for oyster reef restoration

My findings demonstrate the need to incorporate variation of biodiversity measures in multiple and specific spatial attributes in planning restoration strategies. My study provides evidence against an overreliance on general or single spatial attribute metrics, such as species-area relationships to predict biodiversity patterns on oyster reefs. Whilst biodiversity supported on reefs was strongly associated to regional scale processes, my study illustrated that the patch and landscape scales can also influence biodiversity supported by foundation species. Within estuaries, restoration strategies may benefit from increasing connectivity both to other biogenic habitats and amongst patches, although further research is required to determine under what environmental circumstances connectivity enhances biodiversity to foundation species. Efforts aiming to enhancing biodiversity may also benefit from simultaneously manipulating within-patch attributes by, for example, constructing artificial reefs with higher surface elevations and increasing interstitial space in a target estuary.

My study highlights the interactive nature of the spatial scales exhibited by foundation species for biodiversity provision. However, further research is needed to experimentally determine the processes explaining spatial patterns of biodiversity on oyster reefs. With an increasing prioritisation on restoration efforts in oyster reefs in Australia and within NSW (Gillies et al. 2018), my results advocate for developing *S.*

glomerata restoration strategies based upon the observed biodiversity-spatial scale relationships.

Chapter 4

Relationships between spatial scales and oyster reef recruitment

4.1 Abstract

Recruitment of foundation species is essential for population maintenance with strong implications for long-term restoration success. While recruitment can vary at many different scales, few studies have determined which spatial scale best predicts recruitment. Such information is critical to understanding where restoration efforts for foundation species may be most effective. In this chapter, I investigated how the recruitment of the Sydney rock oyster, *Saccostrea glomerata*, to remnant reefs varied across multiple scales from meters to 100s of kilometres. At each of three estuaries in New South Wales, I measured total recruitment, proportion of live recruits, total live cover of oysters (a proxy for oyster productivity) on settlement tiles at the 5-7 reef patches per estuary. Tiles were in the field for a minimum of 10 months. These measured variables were then tested for associations with the spatial attributes of the sampled reef complexes. I also correlated recruitment to abiotic factors such as temperature and sedimentation. Total recruitment, proportion of live recruits and total live cover of oysters varied across the estuaries. Across all estuaries, all recruitment variables increased with patch-area and complexity of patch-shapes. However, for the spatial attributes, mixed relationships (i.e., positive, negative, or absent) were observed with the recruitment variables amongst the estuaries. Total recruitment was unexpectedly positively associated with sedimentation rate but there was no clear pattern related to temperature. My results add to more evidence that population processes are strongly influenced on a regional scale and this variation may be linked to abiotic processes on a regional scale, such as sedimentation rates. My results suggest that oyster reef restoration efforts aiming to promote oyster recruitment should consider the influence of regional scales and abiotic factors to maximise success of restoration efforts.

4.2 Introduction

Recruitment is a fundamental process influencing population maintenance and resilience, and it has important implications for long-term restoration success (Connell 1985; Roughgarden et al. 1985; Raimondi 1988; Strathmann et al. 2002). Recruitment is defined as the cumulative result of settlement, survivorship, and growth of the offspring after a specific period of time (*sensu* Hunt & Scheibling 1997). For marine benthic foundation species such as corals, mussels and oysters that occur over several biogeographic, landscape and habitat scales, their recruitment can be limited by a range of bottlenecks (Godron & Forman 1981; Blanchette & Gaines 2007; Broitman et al. 2008). These bottlenecks include larval supply (Underwood & Fairweather 1989; Raimondi 1990), availability of substrate (Tamburri et al. 2008; Arnold et al. 2010), larval behaviour (Tamburri et al. 2008; Arnold et al. 2010) and settlement and post-settlement mortality events (Connell 1985; Walters & Wethey 1996; Taylor & Bushek 2008) all of which operate differently at multiple spatial scales.

At regional scales (i.e., 10s to 100s of kilometres), recruitment success of marine benthic species can vary based upon localised environmental drivers and biotic processes (e.g., temperature, predation and tidal inundation), as observed amongst coral reefs (e.g., Edmunds 2021), oyster reefs (e.g., Byers et al. 2015) and mussel beds (e.g., Azpeitia et al. 2019; Smith et al. 2009). For example, greater recruitment of mussel *Mytilus californianus* was found in southern California coast in comparison to its northern counterpart likely driven by localised oceanic upwelling that affected larval transport and temperature (Smith et al. 2009). At patch- and landscape-scales (i.e., meters to kilometres), recruitment patterns can also differ based upon patch area and patch shapes. Increases in patch area likely increases probability for recruitment and settlement within the same patch owing to increased chemical settlement cues and settling area from adult conspecifics (Raimondi & Morse 2000; Tamburri et al. 2008; Whitman & Reidenbach 2012). For example, a small decrease in spatial area of coral (0.25 m²) led to a 46% decrease in coral recruitment (Vermeij 2005). Meanwhile, patch-shapes can promote recruitment, as irregularly shaped mussel-bed patches have been observed to have greater recruitment due to more gaps and surface area for settlement (Svane & Ompi 1993; Commito et al. 2014). Additionally, spatial connectivity of habitat patches may also influence recruitment rates at landscape scales. Less distanced habitat-patches may exhibit higher recruitment rates through reduced dispersal

distances and larger landscape area for settlement (Strathmann et al. 2002). For example, recruitment of corals were significantly higher at distances ≤ 300 m from a coral reef in the central Great Barrier Reef compared to distances > 300 m (Sammarco & Andrews 1989).

Within patches, changes in elevation and relative positions from edges can influence settlement, growth, and survivorship of recruits. At lower elevations and at edges, total recruitment and recruitment survivorship were higher in comparison to higher elevations and centres of patches in intertidal oyster reefs (Baillie & Grabowski 2019; Fodrie et al. 2014). These observations were likely due to increased periods of submergence at lower elevations and reef-edges closer to flux of seston during incoming tides (Roegner & Mann 1995; Bartol et al. 1999). Despite these findings, there is still limited knowledge on how the spatial configuration of marine foundation species contribute to the recruitment success.

Recruitment patterns are also governed by processes across multiple spatial scales, recruitment patterns can be For instance, the settlement of recruits can still be governed by small-scale (i.e., habitat complexity) variation in substrate (e.g., presence or absence of crevices) despite sufficient larval supply at large spatial scales (i.e., habitat and landscape-scales) determining overall potential number of recruits (Underwood & Anderson 1994; Pineda et al. 2010). Thus, understanding the spatial scales that explain the most variation in recruitment is critical to maximise restoration efforts for marine benthic foundation species.

Abiotic conditions can also drive recruitment patterns over multiple spatial scales. Temperature, for example, strongly influences larval development, settlement and growth thus recruitment at landscape- and patch-scales (Mittelbach et al. 2001; Dove & O'Connor 2007; Edmunds et al. 2010). For instance, increases in mortality of coral recruits were associated with elevated temperatures via premature larval metamorphosis across landscapes of coral reefs (Edmunds et al. 2001; Edmunds 2021). Within patches, for example, the presence of interstitial space on oyster reef provides temperature refuge which promotes recruit survivorship (Bartol et al. 1999). Lower surface elevation in oyster reefs is associated with lower temperatures and can promote recruit survival (Lenihan 1999). In addition to temperature changes, suspended sediments in the water column can reduce settlement at different spatial scales. Moreover, habitat-structure, such as the amount of interstitial space may limit

predation on recruits (Gregor and Anderson 2016). Sediment may provide ephemeral substratum in the water column and smother settled recruits as observed amongst corals (e.g., Birrell et al. 2005), oysters (e.g., Kimbro et al. 2014) and mussels (e.g., Österling et al. 2010). For example, a $2.5 \text{ mg cm}^{-2} \text{ d}^{-1}$ increase of sedimentation reduced *ex-situ* settlement rates of *Acropora millepora* by approximately 75 % (Babcock & Davies 1991). On the other hand, sediments can nourish growth of post-settled filter-feeding recruits such as corals and bivalves (Dodge et al. 1974). Thus, understanding the various influences of abiotic conditions on recruitment success of marine species is also essential in planning restoration strategies.

Reef-building oysters, including Sydney rock oysters (*S. glomerata*) are target species for many marine restoration efforts for the many reasons discussed in Chapters 1 and 2. While most oyster reef restoration plans have focussed on seeding oyster juveniles on artificial reef structures (Luckenbach et al. 1999; Brumbaugh & Coen 2009; Fitzsimons et al. 2020), there is a limited understanding on the spatial (e.g., area available for seeding) and abiotic factors (e.g., sedimentation) requirements to sustain long-term oyster populations on targeted habitats. Previous studies with artificial three-dimensional concrete spat collection units found that *S. glomerata* recruitment and post-settlement survivorship in estuaries of New South Wales were highest in subtidal locations and sediment-free substrates (Lee et al. 2012; Diggles 2017; Esquivel-Muelbert et al. 2022), but differed amongst estuaries on a regional scale (Esquivel-Muelbert et al. 2022). In addition, *S. glomerata* recruitment was negatively associated with abiotic factors i.e. increased temperatures and turbidity (Esquivel-Muelbert et al. 2022). Understanding the spatial-recruitment patterns of *S. glomerata* recruitment on reefs, how it is affected by abiotic conditions, can inform the functional role of the remnant reefs as larval sources. From a restoration perspective, this study will inform baseline recruitment bottlenecks and restoration priorities, and aid in the selection of restoration sites (Gillies et al. 2018; Reeves et al. 2020).

In this chapter, I investigated how recruitment success (here, comprised of cumulative outcomes of propagule supply, settlement, and post settlement events) may be affected by processes at different the spatial scales on remnant *Saccostrea glomerata* reef complexes, and the association of abiotic factors with recruitment success on these complexes. I hypothesised that all recruitment success variables measured in this study (i.e., total recruitment, percentage of live oysters and cover area of oyster recruits)

would (1) vary amongst the regional scale, (2) increase with patch-connectivity, -shape and -size in each estuary, and (3) decrease with higher surface elevation and away from patch-edges. I further hypothesised that recruitment success will be (4) negatively associated to abiotic factors measured in this study (i.e., sedimentation rate and reef temperature) across all spatial scales.

4.3 Methods

4.3.1 Quantifying total recruitment, percentage live recruitment and cover area

To quantify recruitment success of *S. glomerata*, I deployed settlement tiles (dimensions 110 x 110 x 5 mm) made from prefabricated cement-fibre sheets. While rocks and oyster shells have previously been deployed to capture oyster recruitment (e.g., Taylor & Bushek 2008; George et al. 2015; McAfee & Connell 2020), I opted to standardise the surface rugosity and available area for settlement by using standardised settlement tiles. I chose cement-fibre tiles as the settlement material as it has been found to recruit more *S. glomerata* than other material (e.g., plywood, fibreglass and aluminium; Anderson & Underwood 1994). I assessed recruitment on oyster reefs in the same estuaries as described in Chapters 2 and 3 of this thesis i.e., Crookhaven River, Hunter River and Port Hacking (GPS coordinates of estuaries in Chapter 2). Within each estuary, I randomly chose a subset of reefs to place the settlement tiles on (refer to Figures 4.1B-D).

The number of settlement tiles on each reef differed according to reef area, with a minimum of four tiles sampled on the smallest reefs (5-10 m²) and a maximum of 48 tiles on the largest reefs (≥ 4000 m²) (see Appendix Table D.1). The location of each tile (XY coordinates) on the reefs were pre-determined and randomised prior to deployment using 'spsample' package in R (v.4.0.3). Tiles were attached to the reefs using wooden stakes (0.02m x 0.02m x 1m) driven into the base of the reefs. Tiles, one per stake, were secured to the stakes with stainless steel screws at the centres and secured to the stakes perpendicular to the reef surface (see Figure 4.1B). The tiles were orientated as such to reduce sedimentation impact on smothering recruits and maximising recruitment success (Colden et al. 2017). Tiles were established ≤ 5 cm above the reef complexes. The elevation of each tile (locations as red dots in Figures 4.1C-E) was mapped with a Real-Time Kinematic and differential Global Positioning System unit (RTK-dGPS, Leica GNSS 14, vertical accuracy ± 8 mm; horizontal accuracy ± 13 mm).

I aimed to measure the number of live, dead and total abundance of oyster recruits over the entire *S. glomerata* recruitment period, which spans several recruitment events over an extended time period of approximately seven months

(Underwood & Anderson 1994; Lee et al. 2012; Diggles 2017). Hence, tiles were deployed by January 2020, just prior to the estimated start (February 2020) to the end of the recruitment period (August-September 2020) without replacing any missing tiles during this period (refer to tile deployment dates for each estuary in Table 4.1). At the end of the recruitment period, I took photos of the front-side of the tiles in the field with a camera (Olympus TG-6; 12 mega-pixel) and counted the number of live and dead recruits on each tile using Image J software (v. 153; Schneider et al. 2012). Following methods of Taylor (2008), live recruits were defined as recruits with both valves attached and non-gaping, while dead recruits included individuals with empty valves, single valves, gaped valves containing oyster tissue and scars (marks left from recently detached oysters). I did not count any recruits on the screws owing to differences in settlement material and surface rugosity in comparison to the tiles. From these counts, I quantified total recruitment per tile (i.e., the total abundance of live and dead oyster recruits) as an estimate of total recruits during throughout *S. glomerata* recruitment period.

To quantify cover area of the live oyster recruits, I allowed the tiles to remain *in-situ* for three additional months (i.e., end of October-early November 2020) after the recruitment period. While measuring the growth rate of oyster recruits may have been attainable with sampling intervals and cohort analysis during the recruitment period (e.g., Munroe et al. 2017), I only aimed to quantify the net recruitment success at the end of the recruitment period including cumulative effects of post-settlement growth processes such as growth in multiple recruitment events (Knights et al. 2012) and intra- and inter-species competition (Krassoi et al. 2008; Knights & Walters 2010). Therefore, I used total cover area of recruits per tile after collection of plates (see Table 4.1 for collection dates) as a proxy for oyster productivity at the level of the plate. Tiles were retrieved and fronts photographed where the total cover area of live oysters (mm^2) were also quantified in Image J software. Cover area on screws was not measured. At the same time, I determined the cover of other organisms (i.e., turf algae, barnacle, and crustose coralline algae). The average percentage cover area occupied by other species on the tiles was $17.4 \pm \text{SE } 1.6 \%$, and there was limited evidence of interspecies competition on tiles as live oysters were not strongly correlated to total area occupied by other groups of organisms (pair-wise Pearson's correlation coefficients, $r < \pm 0.7$ refer to Appendix Table D.2).

Table 4.1. Dates and number of replicates for setup and retrieval of recruitment, cover area and sedimentation rate for each estuary.

Recruitment tiles						
Estuary	Date of Setup	No. of tiles setup	End-date for recruitment count	No. of tiles for recruitment count	Date of Retrieval	No. of tiles retrieved for cover area
Crookhaven River	22 January 2020	108	1 September 2020	66	10 November 2020	39
Hunter River	27 January 2020	103	31 August 2020	96	16 October 2020	95
Port Hacking	10 January 2020	101	21 August 2020	91	13 October 2020	90
Sediment traps						
Estuary	Date of Setup	No. of traps setup	Date of Retrieval	No. of traps retrieved		
Crookhaven River	17 March 2020	26	16 June 2020	12		
Hunter River	7 March 2020	28	20 June 2020	26		
Port Hacking	6 March 2020	18	31 May 2020	8		

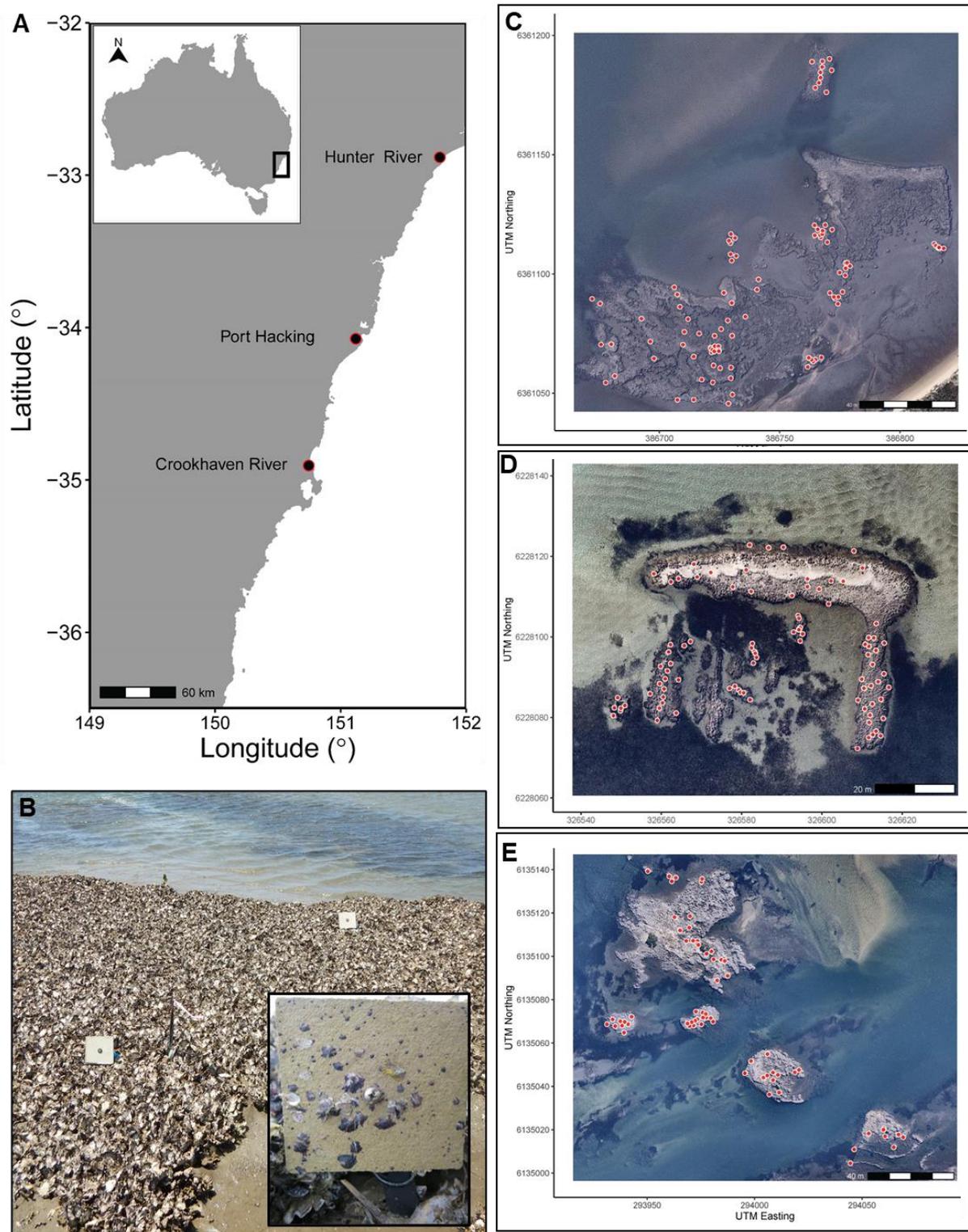


Figure 4.1. A. Location of the sampled estuaries (black dots encircled in red) along the coast of New South Wales, Australia (black box in inset), and the remaining tile replicates in August 2020 (red dots) on selected reef complexes in the sampled estuaries i.e., C. Hunter River, D. Port Hacking and E. Crookhaven River. B. *In-situ* settlement plates setup on a reef complex with a close-up and front-facing photo of a settlement tile with recruitment (inset). Aerial imagery were obtained from NearMap Ltd (<https://www.nearmap.com/au/en>).

4.3.2 Quantifying patch-connectivity, patch- and within patch-attributes

For each tile, I quantified within-patch attributes i.e., (i) surface elevation and (ii) distance to the nearest reef edge. I acquired the surface elevation values from the RTK-dGPS measurements while the distances to patch-edges were acquired with XY coordinates of tiles and mapped reef contours (obtained with NearMap) using 'NEARDIST' function (v10.3, ESRI, 2016). Whole-patch and landscape attributes were calculated described in Chapter 2. In this chapter, however, I only chose to use 'isolation index' as a measure of patch-connectivity as this index showed more consistent associations to ecological attributes in Chapters 2 and 3.

4.3.3 Quantifying abiotic variation on reefs

4.3.3.1 Temperature

I deployed nine temperature loggers (Hobo Pendant® Loggers UA-002-08, accuracy $\pm 0.2^{\circ}\text{C}$) next to a subset of randomly selected tiles (see location of loggers in each estuary in Appendix Figure D.1). Loggers were on the surface of 1-3 reefs that were randomly chosen and were attached to the base of tile stakes and to surface of reef the complex with cable ties. Loggers were calibrated to $\pm 0.2^{\circ}\text{C}$ prior to deployment and recorded air and submerged temperatures continuously at 10-minute intervals for two weeks (28th January to 11th February 2020; dates inclusive) during the estimated peak recruitment period of *S. glomerata* (*sensu* Diggles 2017). There were no extreme weather events (i.e., storms, rainfall and/or floods) at the sites during the logging period, as confirmed from the monthly weather reports from Australian Bureau of Meteorology (<http://www.bom.gov.au/climate/mwr/>). XY coordinates and surface elevations of the loggers were obtained from the GPS locations of the tiles (refer to section 4.3.1 collection methods).

To separate data logger temperatures into air and water temperatures, I filtered out temperatures during the change of incoming tides (*sensu* Harley & Helmuth 2003). These temperatures were determined by estimating the effective shore level (ESL) temperature and time points, which are the time points with rapid decreases in temperature (i.e., at least 3°C drop within 20 minutes during an incoming tide). The ESL temperatures were then omitted from the dataset. To increase the reliability of logged temperatures, I further excluded temperatures 0.15 m below above and 0.15 m below each ESL (Lathlean et al. 2011). This was carried out by matching ESL time points with

tidal heights (in metres) obtained from the nearest tidal buoy station to each estuary (Harley & Helmuth 2003; Gilman et al. 2006). Tidal heights were obtained from Manly Hydraulics Laboratory, Department of Planning, Industry and Environment (<https://www.mhl.nsw.gov.au/>) for tidal stations Bundeena (34°04'57.7"S 151°09'03.2"E; 2.98 km away from Port Hacking reefs), Stockton Bridge (32°53'05.6"S 151°47'01.7"E; 0.25 km from Hunter River reefs) and Crookhaven Heads (34°54'19.2"S 150°45'33.8"E; 1.36 km away from Crookhaven River reefs). I assumed negligible variation of day-to-night and night-to-day temperatures from the short-period (two-week) of temperature logging. From the filtered dataset, I calculated the 5th ('p5temp', as a proxy of highest-tides, submerged water temperatures) and 95th percentile temperature ('p95temp', as a proxy of lowest-tides, exposed aerial temperatures) for each logger. I also calculated the temperature coefficient of variation (CoV) for each logger to represent the dispersion of temperatures surrounding the mean temperature for each logger.

4.3.3.2 Sedimentation rate

The relationships between sedimentation and oyster recruitment, mortality and productivity were investigated using sediment traps consisting of open-lid cylindrical specimen jars (5.0 cm diameter x 10.0 cm height for Crookhaven River and Hunter River; 3.0 cm diameter x 11.5 cm height for Port Hacking). A total of 65 traps were attached to the stakes of a random subset of tiles for a period of 2-3 months (refer to Table 4.1 for number of stakes and deployment period in each estuary). Post-deployment, a total of 47 sediment-traps remained (see Appendix Figure D.1 for locations and Table 4.1 for number of traps retrieved per estuary). There were no extreme weather events (i.e., storms, rainfall and/or floods) during the sediment trapping period, as confirmed from monthly weather reports from Australian Bureau of Meteorology (<http://www.bom.gov.au/climate/mwr/>).

Upon retrieval, I rinsed the contents of the sediment traps with fresh water. Any living organism and large shell grit within the traps were then removed using a 10mm-sieve tray. Filtered sediment was then dried in an oven until constant weight at 60°C. Final, dry sediment was weighed on an electrical balance (Australian Scientific GX-224AE; maximum capacity: 200.0 g precision: ±0.0001g) and converted to sedimentation rate i.e., dry weight per number of deployment days (g day⁻¹) and therefore, it is independent of the total volume of the sediment in the traps.

4.3.4 Data Analysis

4.3.4.1 Total recruitment, percentage live recruitment and cover area across spatial attributes

I fitted generalised linear mixed models (GLMMs) and conducted step-wise model selection to test for the hypotheses about relationships between spatial attributes and the total recruitment and percentage live recruitment on tiles. In these models, total recruitment and percentage live recruitment were modelled with negative binomial and binomial error distributions, respectively. Meanwhile, total cover area was modelled as a general linear mixed model (LMM). The LMM and GLMMs were performed using 'lme4' package (Bates et al. 2015) and 'glmmTMB' package (Magnusson et al. 2020) respectively. 'Estuary' was assigned as a fixed factor to assess regional differences. Each spatial attribute (i.e., 'area', 'distance to edge', 'elevation', 'frac', 'circle index' and 'isolation index') was fitted as an independent co-variate, and also as an interaction term with 'estuary' in the models. Spatial-attributes were not strongly correlated to each other (i.e., Pearson's correlation coefficients, $r < \pm 0.7$) prior to model-fitting, so I assumed independence of co-variates (*sensu* Zuur et al. 2009). Reef (hereafter 'reef_id') was also included as a random intercept to account for potential non-independence between sampled tiles from the same reef. LMM and GLMMs therefore were analysed with the following model equation:

$$\text{Response variable} \sim \text{estuary} + \text{estuary:isolation index} + \text{isolation index} + \text{estuary:area} + \text{area} + \text{estuary:circle} + \text{circle} + \text{estuary:frac} + \text{frac} + \text{estuary:dist.to.edge} + \text{dist.to.edge} + \text{estuary:elevation} + \text{elevation} + (1|\text{reef_id})$$

where ':' represents an interaction term between estuary and a patch attribute. After fitting each model, I conducted step-wise model selection starting with full models and eliminating predictors until the best model (lowest corrected Akaike information criterion (AIC) using 'dredge' function (package 'MuMIn'; Bartoń 2009)). Selected model and their corresponding patch attributes were validated using residuals versus the fitted plot values (Zuur et al. 2009). For those selected attributes that did not have an interaction with estuary (referred to 'Attr' in the results table), I acquired the estimated regression slopes for selected attributes for all estuaries combined from the 'model.summary' function of each model. For selected attributes with an interaction

with 'estuary' ('Attr:Es' in the results table), I estimated the post-hoc regression slopes and its statistical significance for each estuary term using 'emmeans' (package "emmeans", Lenth 2016). When 'estuary' only was selected ('Es' in the results table), in absence of any selected interaction term, pair-wise post-hoc Tukey tests was conducted on the sampled estuaries using function and package 'lsmeans' (Lenth 2016).

4.3.4.2 Relationships between oyster response variables and abiotic factors at regional scale

Similar to 4.3.4.1, I performed model selection on models assessing the relationships between each response variable (i.e., total recruitment, live recruit proportions and cover area) and the abiotic variables (i.e., sedimentation rate, temperature coefficient of variation ('CoV'), 5th percentile temperature ('p5temp') and 95th percentile temperature ('p95temp')). Abiotic variables were fitted against response variables as interaction terms with 'estuary'. Each model, either LMM or GLMM as explained in 4.3.4.1, contained 'reef_id' as a random intercept. Sedimentation rate and temperature variables were modelled separately for each response variable. This was because there were insufficient replicates that had both temperature logger and sediment traps, based upon random deployments (n=6 for joint-sediment trap and temperature logger datasets). A total of six models therefore were analysed with the following model equations for each response variable:

Response variable ~ estuary + sedimentation rate:estuary + sedimentation rate + (1|reef_id)

Response variable ~ estuary + CoV:estuary + CoV + p5temp:estuary + p5temp+ p95temp:estuary + p95temp + (1|reef_id)

where ':' represents an interaction term between estuary and an abiotic variable. Model selection and validation was carried with the same procedures and packages outlined in section 4.3.4.1. Linear regression estimates, post-hoc regression estimates per estuary and pair-wise Tukey tests were conducted and/or obtained for selected abiotic variables ('Abio' in results table), interaction terms with estuary ('Abio:Es' in results table) and 'estuary' only ('Es' in results table) respectively, whenever applicable. The same statistical functions and packages used were identical to those in section 4.3.4.1.

4.4 Results

4.4.1 Total recruitment, percentage live recruitment and cover area across spatial attributes

The total recruitment, percentage of live oyster recruits and cover area of live oysters differed among estuaries (Figures 4.2a-c; Table 4.2). Port Hacking recorded the most recruits per tile ($52 \pm \text{SE } 3$ recruits), followed by Hunter River ($47 \pm \text{SE } 3$ recruits) and Crookhaven River tile ($2 \pm \text{SE } 1$ recruits; Figure 4.2a). A similar trend was found for the percentage live recruits amongst the estuaries (Figure 4.2b). Port Hacking had the highest proportion of live recruits per tile ($65.7 \pm \text{SE } 2.1$ %), followed by Hunter River ($62.6 \pm \text{SE } 2.1$ %) and Crookhaven River ($46.1 \pm \text{SE } 9.9$ %). Cover area of live recruits also differed amongst the estuaries (Figure 4.2c), where Hunter River had higher cover area ($1643 \pm \text{SE } 209 \text{ mm}^2$) in comparison to recruits from Port Hacking ($938 \pm \text{SE } 134 \text{ mm}^2$) and Crookhaven River ($668 \pm \text{SE } 322 \text{ mm}^2$).

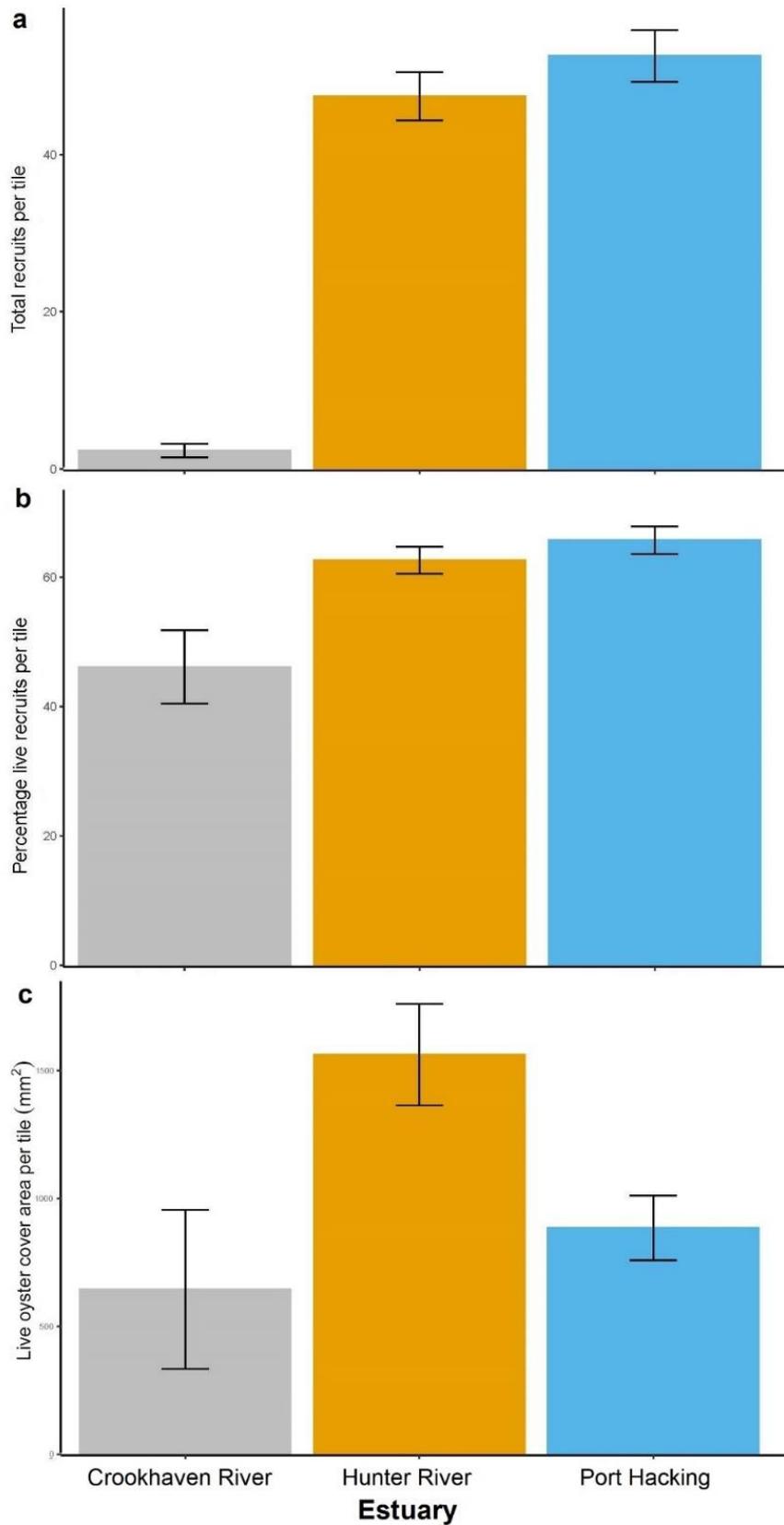


Figure 4.2. Average and SE of (a) total number of recruits per tile, (b) percentage of live recruits per tile, and (c) cover area of live oysters across Crookhaven River, Hunter River and Port Hacking.

Within-patches, I found total recruits were negatively correlated to increasing surface elevation in all estuaries (Table 4.2, Figure 4.3a). Meanwhile, there was a positive correlation between the total number of recruits and reef area (Table 4.2, Figure 4.3c). In contrast, trends between patch-connectivity and total recruits differed between estuaries; there was an increase in recruits in Hunter River and Crookhaven River with the increase of isolation of reefs, but the opposite trend for reefs in Port Hacking (Table 4.2, Figure 4.3f).

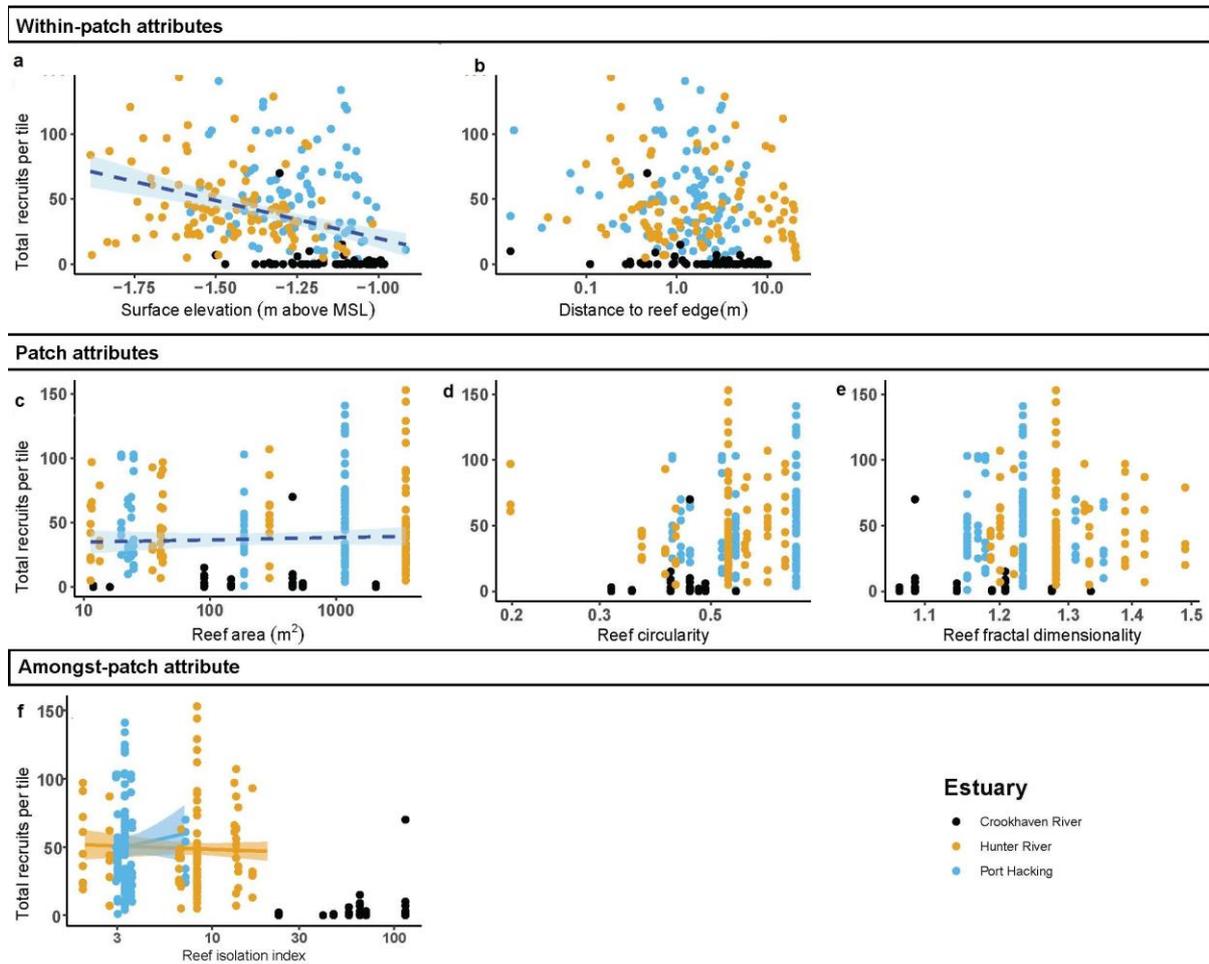


Figure 4.3. Relationships between total recruits and within-patch (A. elevation, B. distance to reef-edge), whole-patch (C. area, D. circularity, E. fractal dimension) and amongst-patches (F. Isolation Index) attributes at Crookhaven River, Hunter River and Port Hacking. Full regression lines and standard errors (shaded areas) represent significant interaction terms between estuaries and attributes ('Attr:Es' in Table 4.2). Dashed regression line and standard errors (shaded areas) in blue represent selected attribute-only terms ('Attr' in Table 4.2) from the models. All x-axes except for surface elevation are logarithmic-scaled.

The percentages of live recruits varied with patch-attributes such as reef area, two-dimensional reef fractional dimensionality and reef circularity, although the relationships varied amongst the estuaries. The percentages of live recruits decreased with increasing reef fractal dimensionality in all estuaries (Table 4.2, Figure 4.4e). Increases in reef area were associated to lower percentages of live recruits in all estuaries, by which Crookhaven River had a stronger negative relationship (i.e., larger slope estimate) compared to Hunter River and Port Hacking (Table 4.2, Figure 4.4c). The percentages of live recruits increased with reef circularity in Crookhaven River and Hunter River, but the opposite relationship was found in Port Hacking (Table 4.2, Figure 4.4d). Within-patches, the percentages of live recruits decreased further away from patch-edges in all estuaries. The negative relationship between the percentages and distances to the edge was stronger in Crookhaven River and Hunter River compared to Port Hacking (Table 4.2, Figure 4.4b). Patch-connectivity had different relationships with the percentages of live recruits in all estuaries. There was an increase in live recruit percentages in Hunter River and Crookhaven River with the increase of isolation of reefs, but the opposite trend was observed for reefs in Port Hacking (Table 4.2, Figure 4.4f).

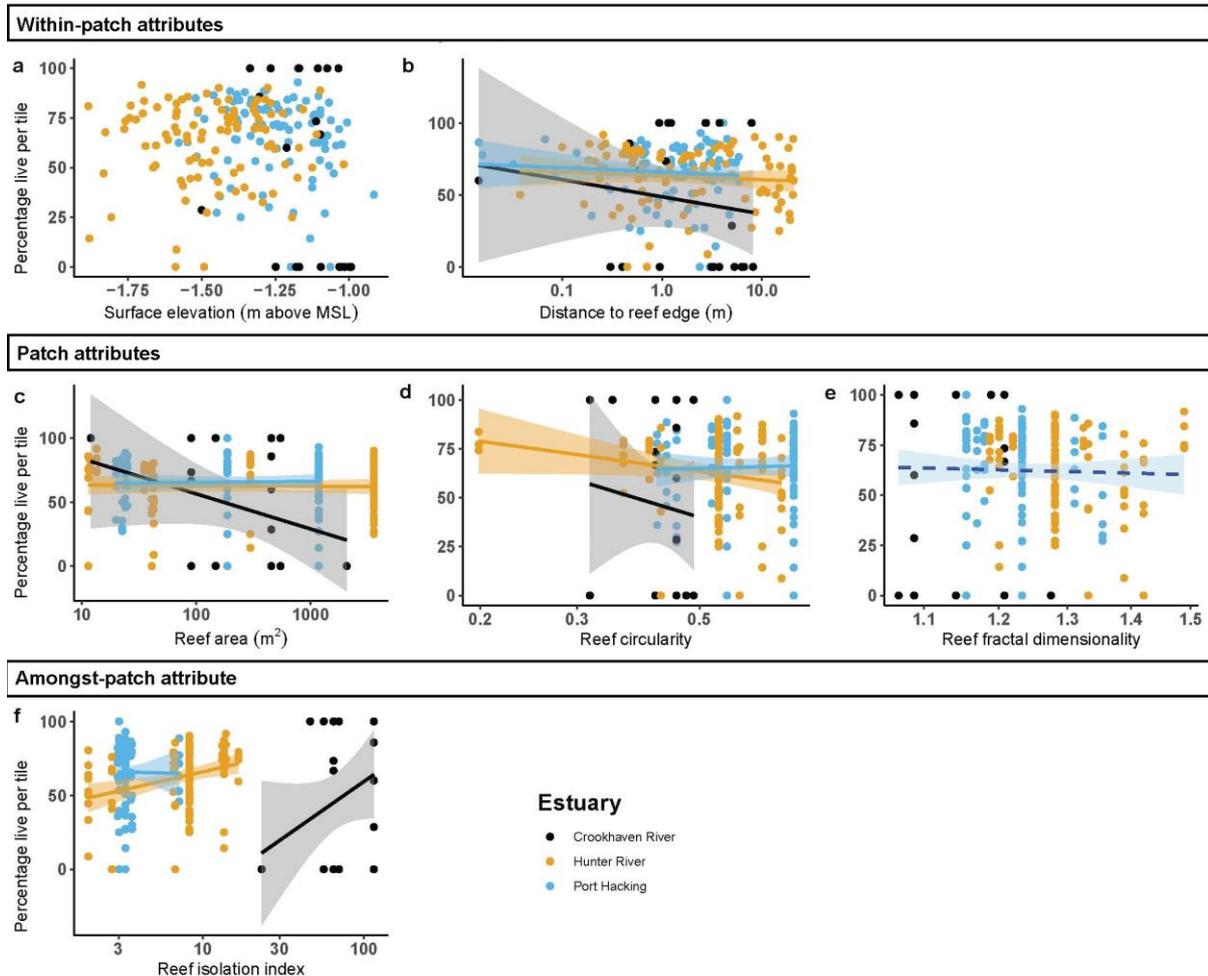


Figure 4.4. Relationships between percentile live recruits and within-patch (A. elevation, B. distance to reef-edge), whole-patch (C. area, D. circularity, E. fractal dimension) and amongst-patches (F. Isolation Index) attributes at Crookhaven River, Hunter River and Port Hacking. Full regression lines and standard errors (shaded areas) represent significant interaction terms between estuaries and attributes ('Attr:Es' in Table 4.2). Dashed regression line and standard errors (shaded areas) in blue represent selected attribute-only terms ('Attr' in Table 4.2) from the models. All x-axes except for surface elevation are logarithmic-scaled.

Within-patch and patch attributes contributed to the most changes in cover area in all estuaries. At higher surface elevations, oyster cover area on tiles decreased in all estuaries, however the trend was only significant in Hunter River and Port Hacking reefs (Table 4.2, Figure 4.5a). Amongst patch-attributes, oyster cover area decreased with increasing reef size in all estuaries (Table 4.2, Figure 4.5c). Hunter River was the only estuary that had significant relationships with reef fractal dimension and circularity, both of which were negative relationships (Table 4.2, Figure 4.5d-e). In terms of reef-connectivity, cover area rates were positively correlated to reef isolation in all estuaries. However, Crookhaven River recorded a stronger positive relationship compared to the other estuaries (Table 4.2, Figure 4.5f).

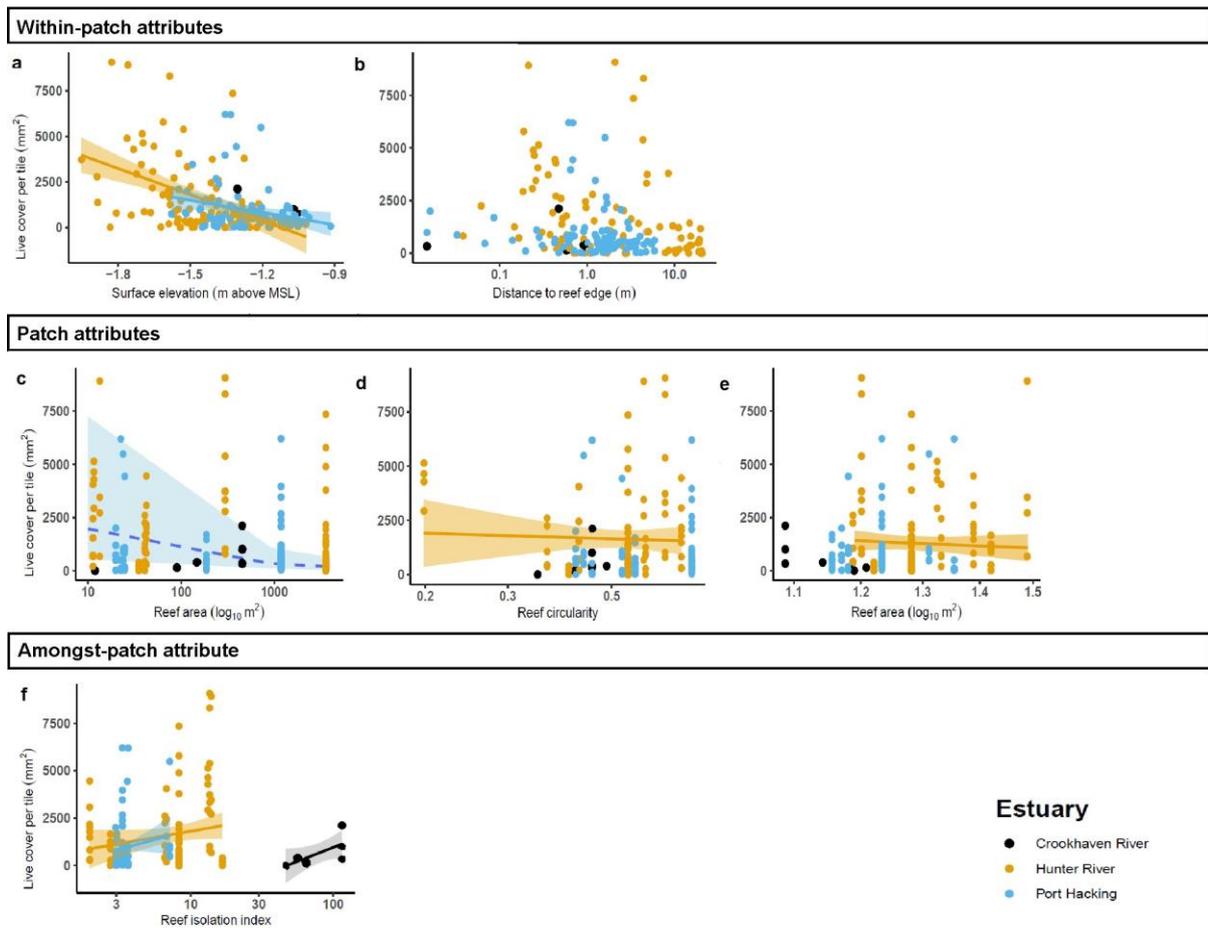


Figure 4.5. Relationships between cover area rate of live recruits and within-patch (A. elevation, B. distance to reef-edge), whole-patch (C. area, D. circularity, E. fractal dimension) and amongst-patches (F. Isolation Index) attributes at Crookhaven River, Hunter River and Port Hacking. Full regression lines and standard errors (shaded areas) represent significant interaction terms between estuaries and attributes ('Attr:Es' in Table 4.2). Dashed regression line and standard errors (shaded areas) in blue represent selected attribute-only ('Attr' in Table 4.2) terms from the models. All x-axes except for surface elevation are logarithmic-scaled.

1

Table 4.2. Selected terms of patch attribute-only (Attr), estuary-only (Es) and the interaction between estuaries and attributes (Attr:Es) from response variables (live recruits per tile, percentage live recruits per tile and cover area rate) after model selection. Unmarked cells represent terms not selected in the best model. Selected 'Attr's are denoted with post-hoc regression slope estimates where '+' or '-' representing positive or negative estimates and their standard errors (denoted as \pm) from the best model. Selected 'Attr:Es' are also denoted with post-hoc regression slope estimates with directions '+' or '-' for each estuary i.e. Crookhaven River (CR), Hunter River (HR) and Port Hacking (PH) where '*' denote significant regression estimates. 'Es' estimates were omitted since each model contained selected 'Attr:Es' term).

Spatial scales & patch attributes		Response variables					
		Total recruits		Percentage live recruits		Cover area	
		Attr	Attr:Es	Attr	Attr:Es	Attr	Attr:Es
Within-patch	<i>Surface Elevation</i>	-0.79 \pm 0.25					CR: -1.0 \pm 7.5 HR: -2.9 \pm 0.8* PH: -1.5 \pm 1.1*
	<i>Distance to Edge</i>			CR: -0.32 \pm 0.38* HR: -0.27 \pm 0.06* PH: -0.04 \pm 0.07*			
Whole-patch	<i>Circularity Index</i>			CR: -11.66 \pm 6.32* HR: +0.42 \pm 0.35* PH: +3.40 \pm 1.56			CR: +10.8 \pm 8.4 HR: -0.4 \pm 1.1* PH: +4.1 \pm 1.9
	<i>Fractal dimension</i>			-2.44 \pm 1.50			CR: +7.7 \pm 35.0 HR: -2.2 \pm 2.4* PH: -1.3 \pm 3.3
	<i>Area</i>	+0.09 \pm 0.05			CR: -3.78 \pm 1.34* HR: -0.02 \pm 0.04* PH: -0.34 \pm 0.19*	-0.39 \pm 0.16	
Amongst-patch	<i>Isolation Index</i>		CR: +3.51 \pm 1.10 HR: -0.03 \pm 0.24* PH: +0.22 \pm 0.69*	CR: +13.13 \pm 3.94* HR: +0.97 \pm 0.17* PH: +0.23 \pm 1.47*			CR: +0.29 \pm 0.73* HR: +0.01 \pm 0.03* PH: +0.10 \pm 0.12*

4.4.2 Relationships between oyster response variables and abiotic factors on a regional scale

Increases in sedimentation rates were associated to increases in total recruits in all estuaries (Table 4.3). However, at a regional scale, the relationship was stronger in Hunter River and Port Hacking compared to Crookhaven River (Figure 4.6a; Table 4.3). Sedimentation rates were also positively correlated with the total cover area of recruits (Figure 4.6c; Table 4.3). Increases in percentages of live recruits were associated to higher coefficient of temperature variation (Figure 4.6e; Table 4.3) and fifth-percentile temperatures (Figure 4.6k: Table 4.3) irrespective of estuaries. Meanwhile, higher 95th percentile temperatures were associated to lower proportions of live recruits in all estuaries (Figure 4.6h; Table 4.3).

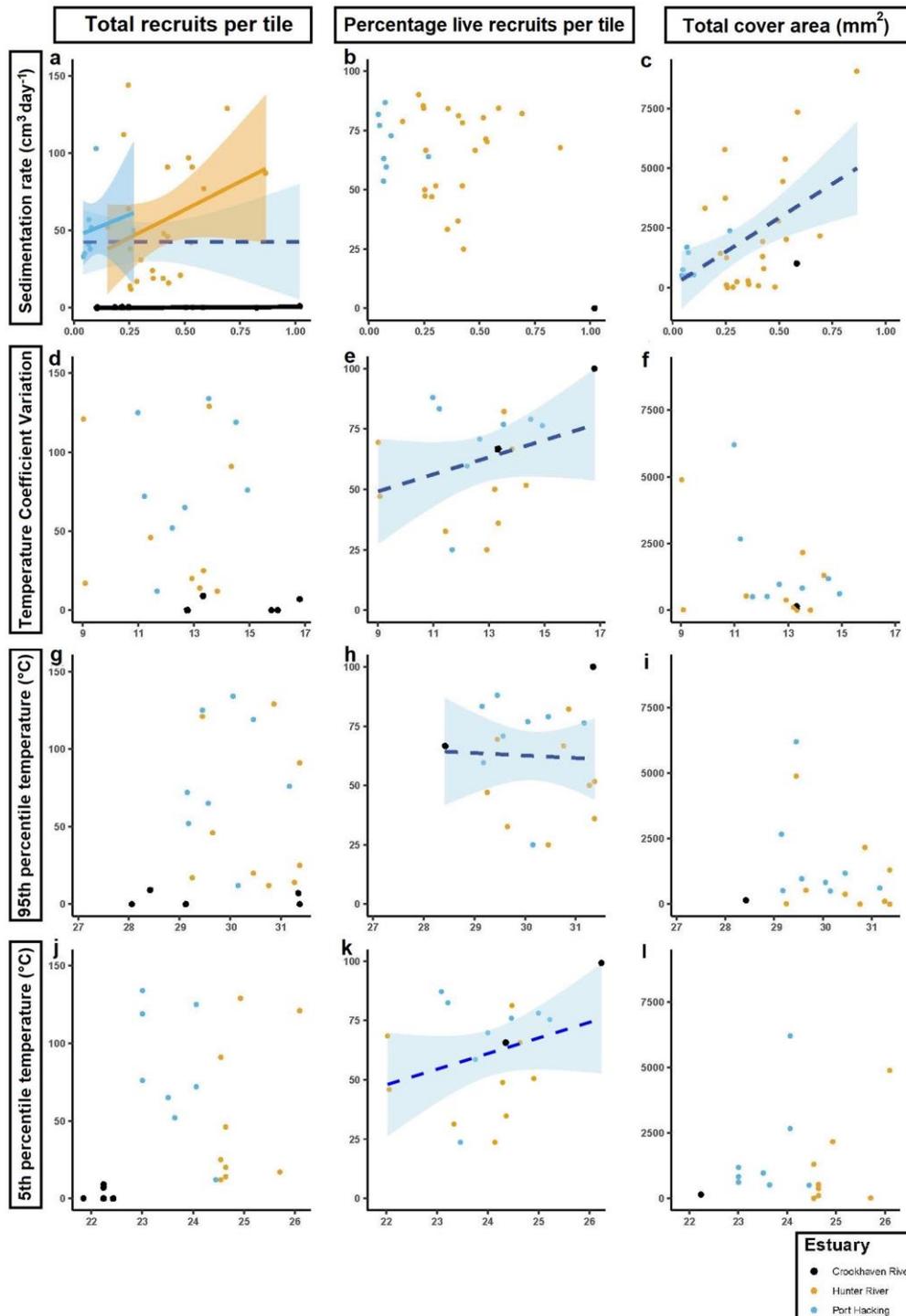


Figure 4.6. Relationships between oyster (biotic) variables (*left panel*: total recruits; *centre panel*: percentage of live recruits; and *right panel*: cover area) with other abiotic factors (i.e., a-c: sedimentation rate; d-f: temperature coefficient of variation; g-h: 95th percentile temperature and j-l: 5th percentile temperature). Full regression lines and standard errors (shaded areas) for each estuary represent significant estuary-only term ('Es' in Table 4.2). Dashed regression line and standard errors (shaded areas) in blue represent selected abiotic variable terms ('Abio' in Table 4.2) from the models.

Table 4.3. Selected terms of abiotic-only (Abio), estuary-only selected (Es) and the interaction between estuaries and abiotic variable (Abio:Es) from response variables (live recruits per tile, percentage live recruits per tile and cover area rate) after model selection. Unmarked cells represent terms not selected in the best model. Selected 'Abio's are denoted with post-hoc regression slope estimates where '+' or '-' representing positive or negative estimates and their standard errors (denoted as \pm) from the best model. Selected 'Es' was denoted with post-hoc regression slope estimates with directions '+' or '-' for each estuary i.e., Crookhaven River (CR), Hunter River (HR) and Port Hacking (PH). 'Abio:Es' was not selected in each model and therefore omitted from the table.

Abiotic variables	Response variables					
	Total recruits		Percentage live recruits		Cover area	
	Abio	Es	Abio	Es	Abio	Es
<i>Coefficient of Variation</i>			+0.88 \pm 0.19			
<i>Temperature</i>						
<i>5th percentile temperature</i>			+2.21 \pm 0.37			
<i>95th percentile temperature</i>			-0.85 \pm 0.30			
<i>Sedimentation rate</i>	+1.68 \pm 0.61	CR: +0.49 \pm 0.51 PH: +47.92 \pm 6.42 HR: +87.27 \pm 21.32 PH=HR >CR			+2.19 \pm 1.08	

4.5 Discussion

Understanding which spatial scale determines recruitment is paramount for managing and restoring habitats of foundation species (Fahrig 2003, 2017), particularly those that have broad distributions (Angelini et al. 2011, Byers et al. 2015). I found support for my first hypothesis; recruitment success varied amongst the estuaries in New South Wales. I did not find support for hypothesis 2; there were increases in recruitment with patch-size and connectivity but decreases with patch-shapes. I did however find support for hypothesis 3, as lower recruitment success was found at higher elevations and away from reef edges. Recruitment was unexpectedly positively associated with sedimentation rate, but inconsistent in trends with temperature, thus ultimately rejecting hypothesis 4.

On a regional scale, total recruits, percentages of live recruits and total cover area varied largely on tiles on *S. glomerata* reefs. While no study to date has assessed recruitment patterns on *S. glomerata* reefs themselves, numerous *in-situ* studies close to the studied reefs in this chapter or in estuaries where reefs were historically present also found regional differences on recruitment of *S. glomerata* (Esquivel-Muelbert et al. 2022). My study corroborates the high recruitment rates in Port Hacking observed by Esquivel-Muelbert et al. (2022), but opposes the higher recruitment rates previously observed in the Shoalhaven-Crookhaven River estuary complex. These findings are also consistent across other species of reef-building oysters such as *Crassostrea virginica* (Hanke et al. 2017b; Knights & Walters 2010; Byers et al. 2015; Puckett & Eggleston 2012) and *Magallana (Crassostrea) gigas* (Walles et al. 2015). The observed regional differences in recruitment can be linked to many factors including variation in density of adult oyster populations (e.g., Schulte et al. 2009) and biotic processes (e.g., interspecies competition; Krassoi et al. 2008 and predation; Kimbro et al. 2020) and larval supply (Brumbaugh & Coen 2009). Nevertheless, in my study, I found that recruitment patterns were density-independent on a regional scale as there was no relationship between density (observed in Chapter 2) and recruitment observed in this study. The absence of this relationship is corroborated by the observation amongst *C. virginica* recruits by Knights & Walters (2010).

More importantly, regional differences in abiotic factors (e.g., turbidity, hydrodynamic forces, sedimentation, temperature) can also drive regional recruitment patterns on oyster reefs (Byers et al. 2015; Whitman & Reidenbach 2012; Baillie & Grabowski 2019; Esquivel-Muelbert et al. 2022). In my study, the significant lower recruit abundance in Crookhaven River reefs compared to Port Hacking and Hunter Reef reefs could possibly be linked to higher water turbulence and rapid fluxes experienced by the reefs (personal observation). This is likely linked to the position of the reefs being relatively close to the mouth of the estuary (see Table 2.1 of Chapter 2) and thus likely experience more turbulence and reduction in oyster settlement (Crimaldi et al. 2002). The position of the reefs were not representative of the entire estuary and thus likely also explain the fewer *S. glomerata* recruits observed in comparison to Esquivel-Muelbert et al. (2022)'s higher recruit abundance obtained from the entire estuary complex.

In addition, regional differences in turbidity and sedimentation can also support the observed regional differences in recruitment patterns. Notwithstanding the low recruits observed in Crookhaven River, the observed recruitment patterns observed in Port Hacking and Hunter River likely corresponded to their annual turbidity measures (see Table 2.1). I found total recruitment and proportion of live recruits observed in both estuaries in this chapter are negatively associated with their average turbidity measured in Chapter 2. Sedimentation, on the other hand, was unexpectedly positively associated to total recruitment across all the estuaries. However, the relationship is not maintained on a localised scale (i.e., in each estuary). For example, I found that both Port Hacking and Hunter River had stronger positive relationships between sedimentation rates and total recruitment compared to Crookhaven River. The positive relationship between sedimentation and recruitment observed in all estuaries is likely linked to high larval and sediment deposition on reefs during low flow speed. Rates of sediment deposition were found to be generally higher on oyster reefs where flow speed was lowest (Lenihan 1999). Coupled with the vertical orientation of recruitment tiles that prevents sediment burial of recruits (Soniati et al. 2004), high recruitment was therefore captured during low flow speed. This is supported by the fact that greater correlations between sedimentation rate and recruitment were observed in Port Hacking and Crookhaven River reefs which exhibited lower flow speed (personal

observation) compared to Crookhaven River reefs that exhibits higher flow speed. More importantly, I found that the positive sedimentation-recruitment relationship is not maintained at a regional scale. This is exemplified with the lower average of recruits observed in Hunter River compared to Port Hacking, despite possessing the highest sedimentation rate amongst all the estuaries. This suggests potential effects of varying levels of sedimentation at regional scales on recruitment, which I will investigate the effect in the next chapter.

Within patches, recruitment success was associated with changes in surface elevation and distances to the reef edges. Total recruits and cover area of live recruits were negatively associated to surface elevation in all estuaries and in two of three estuaries respectively. Results of my study concur with my findings in Chapter 2 and other studies which found abundances, growth and survivorships of recruits were associated with lower surface elevation (Lenihan 1999; Bishop & Peterson 2006; Lee et al. 2012; Fodrie et al. 2014; Baillie & Grabowski 2019). At lower elevations, settled recruits are submerged for a longer period thus prolonging feeding and reducing desiccation stress (Bahr & Lanier 1981; Roegner & Mann 1995; Bartol et al. 1999). My study also found higher proportions of live recruits closer to reef edges. The trend is supported by high densities of recruits observed at edges of *C. virginica* reefs (Hanke et al. 2017b). Recruits at intertidal reef edges experience more volume fluxes of water, seston and oxygen with incoming tides thus promoting their growth and survivorship (Lenihan 1999; Grabowski et al. 2005; Fodrie et al. 2014).

On a landscape scale, I found that connectivity of reefs can influence recruitment patterns. Increases in reef isolation were associated to higher proportions of live oysters and cover area in all estuaries. However, between reef isolation and total recruitment, the relationship was negative in Hunter River, positive in Port Hacking and indifferent in Crookhaven River. These overall trends suggest that reef connectivity, at landscape-level is not consistently associated with settlement processes but are consistent with post-settlement processes. The observed mixed patterns in recruitment abundance at landscape-level connectivity concurs with the findings of non-consistent landscape-recruitment connectivity found in *Ostrea lurida* (e.g., Carson 2010), *C. virginica* (e.g., Haase et al. 2012) and *M. gigas* oyster reefs (e.g. Lagarde et al. 2019). In fact, these studies aforementioned have found that oyster settlement-connectivity

pattern were driven by environmental factors larger than landscape-scales (e.g., regional hydrodynamic circulation) supporting larval settlement patterns observed in many marine invertebrate systems, including oyster reefs (Cowen & Sponaugle 2009; Becker et al. 2007; Levin 2006). Meanwhile, the observed increases in live recruit proportions and cover area with increases in reef isolation suggest that oyster post-settlement processes are linked to landscape-scale connectivity. Predation, for example could have likely explained the observed post-settlement mortality patterns where reduced predation rates have been observed in more isolated oyster reefs (Harwell et al. 2011; Duncan et al. 2019). My result is further supported by a study showing fewer fish predators in more isolated patches in Crookhaven River (Erickson 2019).

In terms of whole-patch attributes, recruitment success was inconsistent across size and shapes of the remnant reefs. Larger reefs were associated to more recruits but to lower proportions of live recruits and decreases in cover area. This mixed response is likely linked to the trade-offs between settlement and post-settlement processes. Larger reefs provide more surface area for settlement, and increases in settlement cues from existing adults (Raimondi 1988; Tamburri et al. 2008; Whitman & Reidenbach 2012). However, settled recruits in larger reefs may experience increased mortality and/or reduced growth through reduced food sources from the weaker tidal fluxes over the larger reefs (Hanke et al. 2017b). This explanation also strongly corroborates with my findings of higher recruit abundances and survivorship at reef edges as aforementioned. Changes in patch shape, specifically circularity and two-dimensional fractal dimensional, were again mixed with recruitment variables. For example, increases in fractal dimension (i.e., increases the geometric complexity along the patch edges) were associated with lower live proportions of recruits and lower recruit cover area, but only in Hunter River. Meanwhile, changes to reef circularity index also had mixed relationships to live recruit proportions and cover area at all estuaries. Increases in circularity index, (i.e., increases in reef elongation and decreases in width of reefs) were associated with greater proportions of live recruits in Hunter River, the opposite for Crookhaven River and indifferent in Port Hacking. The lack of consistency in patch shape-recruitment trends observed amongst the estuaries could likely be linked to localised (i.e., regional) differences in predation pressure (Anderson & Connell 1999) and abiotic stressors (Byers et al. 2015; Whitman & Reidenbach 2012) specific to each

estuary. My findings reiterate the likelihood of strong regional differences on whole-patch attributes-recruitment patterns and such differences should be considered for restoration purposes.

Alongside sedimentation, my study also found that temperature can affect oyster recruitment success. Temperature changes were indeed associated with recruitment success across all estuaries. Specifically, I found the proportions of live recruits increased with higher high-tide temperatures (i.e., 5th percentile temperatures) but decreased with higher low-tide temperatures (i.e., 95th percentile temperatures). My results concurred that *S. glomerata* survivorship can increase with elevated water temperatures (Pereira et al. 2020) but are also negatively impacted by higher temperatures during aerial exposure (Bishop & Peterson 2006; Dove & Sammut 2007). With higher live proportions of recruits observed at the upper ranges of 5th percentile (~ 25-26°C) and lower range of the 95th percentile (~28-29°C) temperatures, my results also add to evidence of a thermal optimal survivorship spectrum for *S. glomerata* recruits ranging between 23 to 30°C (Dove & O'Connor 2007). Interestingly, a larger temperature coefficient of variation (i.e., a larger range between high-tide and low-tide temperature) was correlated to higher survivorship of recruits. While this relationship was unexpected, the larger variations in temperature could be linked to larger tidal ranges and fluxes which increases seston and oxygen fluxes and promotes sediment movement, all of which linked to increased oyster growth and survivorship (Lenihan et al. 1996; Grabowski et al. 2005; Fodrie et al. 2014).

As only a handful of studies have concurrently assessed the contribution of each spatial scale on oyster recruitment success (e.g., Hanke et al. 2017; Knights & Walters 2010; Byers et al. 2015). My study, together with these studies collectively highlight the importance of evaluating spatial variation of recruitment and abiotic factors in remnant oyster reefs for restoration science and marine larval ecology. This chapter illustrates that recruitment success has the largest variation on a regional-scale and are associated with sedimentation rate and temperature as abiotic factors. At smaller scales, recruitment success was more consistent in patterns (trends) in landscape-scales i.e., reef isolation and within-patches (e.g., surface elevation). Given that the largest variation in recruitment patterns were found on regional scales, further research is required to elucidate the roles of abiotic factors driving ecosystems.

Chapter 5

Regional-scale patterns of recruitment and sedimentation

5.1 Abstract

Regional scale processes seem to be more important drivers of recruitment patterns on oyster reefs than local processes, as observed in Chapter 4. These results also indicated that regional recruitment patterns might be related to the degree of sedimentation at each estuary, and the associated environmental characteristics, such as turbidity and salinity, all indicative of the influence of catchment runoff in the estuary. However, the relationship between sedimentation and oyster recruitment on oyster reefs has not been assessed at large spatial scales, i.e. across estuaries. As a follow-up of results from Chapter 4, I explicitly tested whether recruitment of *Saccostrea glomerata* at six estuaries in New South Wales was related to differences in rates of sedimentation among estuaries. To achieve this, I assessed oyster recruitment among three estuaries with high and three estuaries with low sedimentation rates. I deployed settlement plates on oyster reefs for 6-7 months to assess total recruitment and the percentage of live recruits per plate. The regional variation in total recruitment was strongly associated with the differences in sedimentation levels on the same scale. Specifically, reefs with typically low and high sedimentation had high and low rates to recruitment, respectively. However, there was no difference in the percentages of live recruits across the estuaries with the sedimentation levels. My results suggest that regional differences of abiotic factors can have important implications on oyster recruitment, but do not appear to influence oyster mortality in the short term. This information can help inform site suitability models necessary to plan large-scale restoration efforts.

5.2 Introduction

In recent years, regional-scale (i.e., tens to hundreds of kilometres) restoration initiatives have been prioritised in order to achieve target goals of United Nation's '2021–2030 Decade of Ecosystem Restoration' (e.g., Diefenderfer et al. 2021). This aligns with efforts to restore marine foundation species such as salt marsh plants, seagrass meadows and kelp beds which are distributed at such a scale (Godron and Forman 1981, Anderson et al. 2005, Boström et al. 2011, Fahrig 2017). However, not all restoration efforts have been successful, likely due to variation in population characteristics and processes amongst marine foundation species at regional scales (Kojis and Quinn 2001, Bible and Sanford 2016, Brasseur et al. 2018).

In Chapter 4, I explicitly sought to determine which spatial attribute may explain oyster recruitment, and how those relationship are maintained among estuaries. My results showed that the largest variation in recruitment of *S. glomerata* was among estuaries, which was more important than local spatial attributes of oyster reefs. This has also been observed for other shellfish species such as *Crassostrea virginica* (Byers et al. 2015, Hanke et al. 2017) and *Magallana gigas* (Wallis et al. 2015). Nevertheless, it is still unclear which processes (e.g., abiotic or biotic factors) may drive these patterns in oyster recruitment. Elucidating these processes is essential to improve planning of large-scale oyster reef restoration efforts, as it is fundamental to inform site suitability models (Grabowski et al. 2020, Howie and Bishop 2021).

In terms of environmental factors, temperature regimes and hydrodynamic circulation have been found to drive differences in recruitment patterns on oyster reefs on a regional scale (Lenihan 1999, Byers et al. 2015, Bible and Sanford 2016). In Chapter 4, data suggested that total recruitment on oyster reefs may vary with sedimentation rate amongst the sampled estuaries (Chapter 4). Sedimentation rates can directly impact oyster recruitment (Diggles 2013; Grabowski et al. 2020), or they can be a proxy for other environmental factors, such as a greater influence of catchment runoff in the estuary, resulting in greater turbidity, sedimentation and lower salinity. However, whether oyster populations respond similarly to variation in sedimentation and associated environmental conditions that occurs over a broad geographic range (e.g., Byers et al. 2015) remains untested.

Building on the results from Chapter 4, here, I conducted a large-scale experiment across 6 estuaries to test the prediction that differences in oyster recruitment among estuaries is associated to differences in environmental conditions, of which I used sedimentation rates as a proxy. Specifically, I aimed to understand how differences in sedimentation levels among estuaries were associated with *S. glomerata* recruitment at the same scale. I deployed settlement plates in six estuaries with nominally “low” and “high” sedimentation-levels (as ascertained by the sediment weight from sediment traps in the same estuaries) to investigate how sedimentation related to the oyster recruitment (i.e., total recruitment, and percentage of live recruits) on a regional scale. I hypothesised that (1) total recruitment and (2) percentage of live recruits would be negatively related to higher-sedimentation levels on a regional scale.

5.3 Methods

5.3.1 Sampled Estuaries

To test for the effect of sedimentation levels (“high” and “low”) on oyster recruitment on a regional scale, I conducted an experiment across six estuaries containing remnant *S. glomerata* reefs. These estuaries include the three estuaries (Crookhaven River, Port Hacking and Hunter River) sampled in Chapters 2 – 4, and three new estuaries (Georges River, Bermagui River and Hawkesbury River; see Figure 5.1 and refer to Table 5.1 for GPS locations of all estuaries). The estuaries span a coastline distance of ~530 km along the state of New South Wales. Newly selected estuaries were determined through reconnaissance trips with the following criteria: containing at least one *S. glomerata* reef with 1000 m², were 200m away from active oyster leases and existing annual turbidity within the range of the pre-existing turbidity (see average turbidity values in Table 5.2). *S. glomerata* reefs at new estuaries i.e., Georges River, Hawkesbury River and Bermagui River were attached to remnant oyster aquaculture leases, ballast heap and natural rocks, respectively.

5.3.2 Estimating total recruitment and proportion of live recruits amongst estuaries

Similar to Chapter 4, I used prefabricated cement-fibre sheets as settlement tiles (each with dimensions 110 x 110 x 5 mm) on the reef complexes. In contrast to the vertical orientation of tiles set up in Chapter 4, tiles in this chapter were attached horizontally to assess the influence of sedimentation on recruitment. Tiles were attached to the reef complexes via 2 cm x 2 cm x 100 cm garden stakes that were embedded ≤ 5cm above the reef complexes. Tiles were attached to stakes at the centres with stainless steel screws and rubber washers. Two *S. glomerata* shells were glued on the top-surface on each tile to mimic recruitment on oyster reef complexes (*sensu* Soniat et al. 2004) (see Figure 5.2A&C). Shells were similar in shape (water-drop shaped i.e., tapered at the umbo and ventrally ovoid), length (i.e., 40 ± 5 mm) and width (i.e., 20 ± 5 mm). Shells were attached to the tiles with a marine-based epoxy (Megapoxy® HT, Vivacity Engineering Pty Ltd). Shells were glued on 25-35 mm diagonally and ventral-facing to each other at the centre of the traps (Figure 5.2A&B). Shells used were decade-long abandoned shells on terrestrial ground from aquaculture leases. These shells were cleaned and disinfected following aquatic biosecurity protocols (INT11/7170 POMS

procedure) of NSW Department of Primary Industries (2018) to remove any encrusting and/or living organisms on the shells to prevent transmission of pest-diseases (e.g.. QX disease parasite *Marteilia sydneyi*; Wilkie 2012) prior to deployment.

I deployed 15 tiles in each estuary where each tile was established on reef surfaces. The tile locations were randomised across reefs given the recruitment patterns were inconsistent with patch configuration (i.e., reef size, shape and distances from each other) in the previous chapter (Chapter 4). Randomisation on the tile locations was conducted pre-deployment using 'spsample' package in R (v.4.0.3). Tiles were deployed just prior to the recruitment *S. glomerata* period (Anderson & Underwood 1994; Lee et al. 2012; Diggles 2017) in December 2020 (see deployment dates of tile per estuary in Table 5.1). I retrieved the tiles prior to end of the recruitment period in all estuaries (i.e., end of June-early July 2021) except for Bermagui River. Tiles from Bermagui River were retrieved later (i.e., in September 2021) due to COVID-19 movement restrictions in New South Wales, Australia (see the retrieval dates of tiles for each estuary).

Upon the retrieval of tiles, I counted the number of live and dead recruits (definitions aforementioned in Chapter 4 and Taylor & Bushek (2008) on top surface types of the tile (including tile and shell). From these counts, I quantified total recruitment per tile (i.e., the total abundance of live and dead oyster recruits) and proportion of live recruits to total recruitment.

5.3.3 Estimating and categorising sedimentation levels amongst estuaries

To estimate the levels of sedimentation on *S. glomerata* reefs in the selected estuaries, I placed sediment traps on reef surfaces. Each sediment trap was made of a 3mm thick, open-ended, flat-bottomed polyvinyl chloride (PVC) cylinder lid. Each trap had a low diameter-to-height aspect ratio i.e., 100mm in internal diameter and 25mm in height to capture sediment resuspension and maximum net deposition in intertidal areas (Flower 1991). To mimic surface rugosity of oyster shells on oyster reefs and taking account of the potential artefacts of shells on sedimentation rates on reef surface, I attached dead cupped-valve shells of *S. glomerata* oyster to the base of each trap. I followed the same protocol for the pre-attachment and attachment of shells in sediment traps (see Section 5.3.2) where the shapes, sizes, locations of shells were consistent on tiles and shells

were void of encrusting organisms and disease. Traps with epoxy were allowed to dry and cure for at least 24 hours prior to deployment.

I deployed 15 sediment traps on reef complexes adjacent to recruitment tiles (i.e., ≤ 10 cm radial distance from a tile) and at comparable surface elevations (i.e., ± 3 cm deviation from surface elevation of traps; Figure 5.2A). Traps were secured on the reef surface with cable ties attached to 1m, 10mm-diameter PVC pipe staked into the complexes. XY and surface elevation of each trap location was measured with a Real-Time Kinematic and differential Global Positioning System unit (RTK-dGPS, Leica GNSS 14, vertical accuracy ± 8 mm; horizontal accuracy ± 13 mm). During the sediment trapping period, there were no extreme weather events (i.e., storms, rainfall and/or floods), as confirmed from monthly weather reports from Australian Bureau of Meteorology (<http://www.bom.gov.au/climate/mwr/>). Traps were deployed for ~ 30 days (see Table 5.1 for deployment and retrieval dates). Intact non-overtuned traps (see Table 5.1 number of remaining of traps per estuary) from the estuaries were returned to the laboratory for laboratory processing. Similar to Chapter 4 (see Section 4.2.3.2), I rinsed the contents of the sediment traps with fresh water and removed any living organisms and large shell grit with a 1mm-sieve tray. Sediment was then dried in an oven until constant weight at 60°C. Final dry sediment weighed on an electrical balance (Australian Scientific GX-224AE; maximum capacity: 200.0 g precision: ± 0.0001 g).

Based on the measured dry sediment weight (see Figure 5.3C), I categorised the estuaries into 'estuary types' (a fixed factor) based upon the mean sediment weight per trap per estuary. Each estuary was either classified as "low-sediment" or "high-sediment". "Low-sediment" estuaries consisted of Bermagui River (mean weight $1.7 \pm$ SE 0.5 g), Port Hacking ($1.4 \pm$ SE 0.4 g) and Crookhaven River ($2.0 \pm$ SE 1.6 g) with recorded sediment weights below the average 2.00g. Meanwhile, "high-sediment" estuaries consisted of Hunter River ($20.8 \pm$ SE 3.7 g), Hawkesbury River ($25.9 \pm$ SE 7.0 g) and George's River ($25.5 \pm$ SE 5.0 g) (Figure 5.3C).

5.3.4 Data Analysis

I fitted generalised linear mixed models (GLMMs) to test for the effect of regional sedimentation levels (i.e., 'estuary type'; "high-sediment" and "low-sediment" levels) to the total recruitment and percentage live recruitment on the top surface of the tiles. In

these models, total recruitment and percentage live recruitment were modelled with negative binomial and binomial error distributions, respectively. GLMMs were performed using 'glmmTMB' package (Magnusson et al. 2020). 'Estuary type' was assigned as a fixed factor to assess regional differences in sedimentation rates. I included surface elevation ('elevation') as continuous co-variate in each model to account for its influence on recruitment (see in Chapter 4 and Figure 5.3B) and on sedimentation rates (Colden et al. 2017; Baillie & Grabowski 2019;). I also included 'estuary' as a nested random factor within 'estuary type' to account for different estuaries found within each level of the 'estuary type'. GLMMs therefore were analysed with the following model equation:

Response variable ~ elevation + estuary type + (1|estuary type/estuary)

Statistical significance of 'estuary type' in each model was computed with likelihood ratio tests (LRTs) using the 'Anova' function in the 'car' package (Fox et al. 2013).

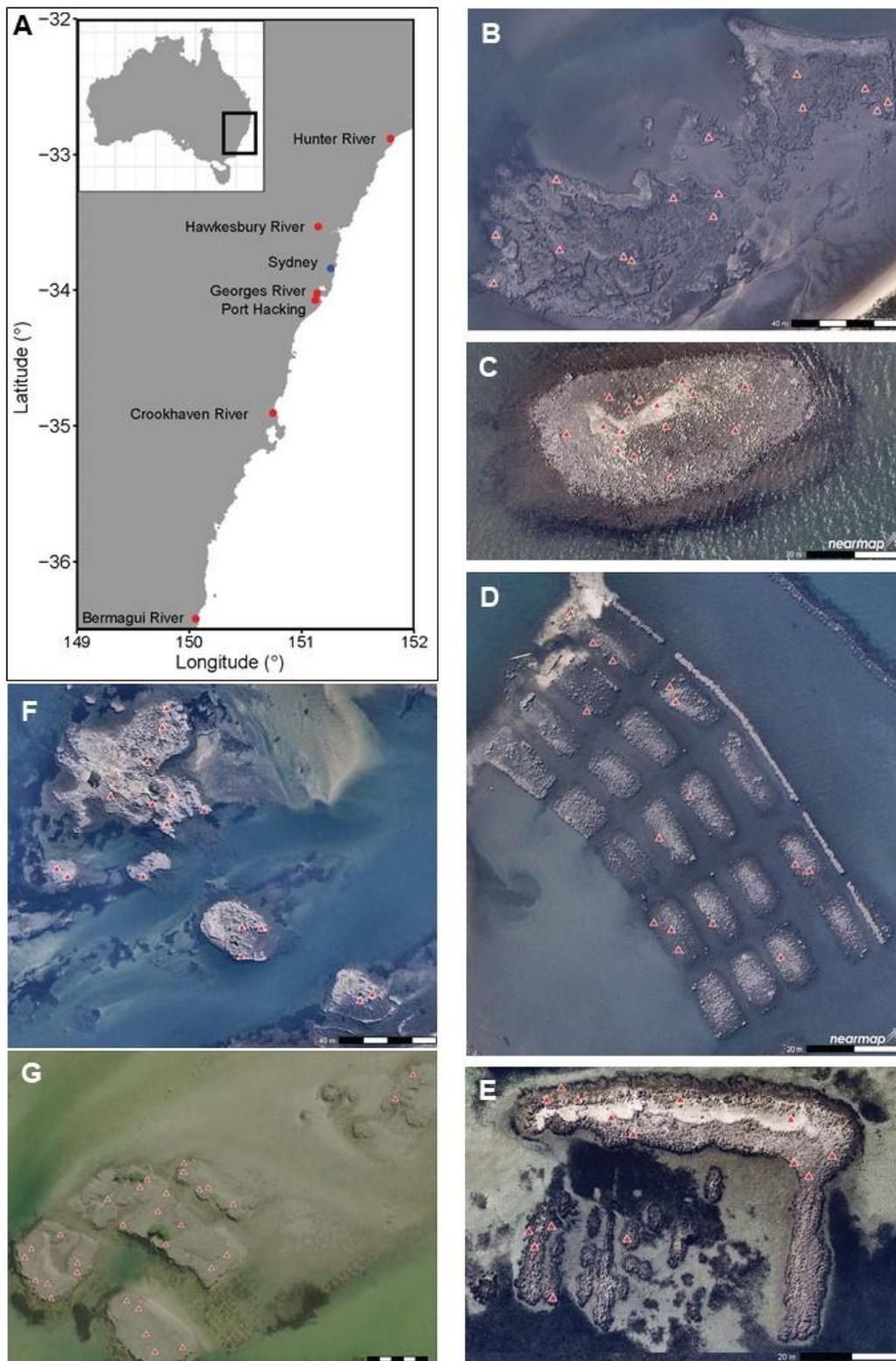


Figure 5.1. A. Location of sampled estuaries (red dots) along the coastline of New South Wales (inset), Australia. Randomised location of tiles and traps (red triangles) on North-facing aerial images of *S. glomerata* reefs in B. Hunter River, C. Hawkesbury River, D. Georges River, E. Port Hacking, F. Crookhaven River and G. Bermagui River. Aerial images B-F and G were obtained from NearMap Ltd (<https://www.nearmap.com/au/en>) and NSW Government Spatial Services (<https://maps.six.nsw.gov.au/>) respectively.



Figure 5.2. A. An example of a paired sediment trap and recruitment tile pictured in on a *S. glomerata* reef complex in Crookhaven River. Top-facing photos of a B. sediment trap and C. recruitment tile during their retrieval periods. Photos were taken by Rick Leong and were not taken to scale.

Table 5.1. The list of sampled estuaries, their GPS locations and total area of reef complexes¹ (obtained from NearMap Ltd) in addition to the setup and retrieval dates, and the number of retrieved sediment traps and recruitment tiles. Note: # Hawkesbury River was affected by major regional floods (NSW Manly Hydraulics Laboratory 2021), ^ Retrieval of tiles from Bermagui River was delayed due to COVID-19 movement restrictions in 2021.

Estuary	GPS location of oyster reefs	Total area of reef complexes (m ²) ¹	Setup date of tiles & sediment traps	Recruitment tiles		Sediment traps	
				Retrieval date	Number of tiles retrieved	Retrieval date	Number of traps retrieved
Hunter River	32°52'58.2"S 151°47'20.9"E	6818.05	12 th December 2020	24 th June 2021	14	9 th January 2021	14
Hawkesbury River	33°31'52.9"S 151°08'45.7"E	1447.15	23 rd December 2020	3 rd July 2021 #	14	21 st January 2021	14
Georges River	34°01'23.2"S 151°08'07.3"E	2679.77	10 th December 2020	25 th June 2021	10	7 th January 2021	10
Port Hacking	34°04'24.2"S 151°07'13.8"E	1870.63	9 th December 2020	21 st June 2021	13	12 th January 2021	13
Crookhaven River	34°54'20.3"S 150°44'42.4"E	3338.24	11 th December 2020	23 rd June 2021	12	8 th January 2021	3
Bermagui River	36°25'17.5"S 150°03'23.0"E	1194.72	14 th December 2020	17 th September 2021 [^]	15	14 th January 2021	15

Table 5.2. Physical and abiotic characteristics of sampled estuaries. Average turbidity, water temperature, pH and salinity of sampled estuaries were obtained from ¹NSW Office of Environment and Heritage (2016) between 2007 to 2015 while average salinity values in Crookhaven River were obtained within 200m radius of oyster reef complexes from ²NSW Manly Hydraulics Laboratory (2012) surveys between 1995 to 1998. Estuary classification and relative positions of oyster reefs were obtained from ³Ryan et al. (2003).

Estuary type	Estuary	Estuary classification & position	Average turbidity \pm SE (NTU) ¹	Average water temperature \pm SE ($^{\circ}$ C) ¹	Average pH \pm SE ¹	Average salinity \pm SE (psu)
High-sediment	Hunter River	Wave-dominated delta – Middle	19.13 \pm 0.16	24.7 \pm 2.5	7.91 \pm 0.20	20.6 \pm 12.0 ¹
	Hawkesbury River	Wave-dominated delta – Middle	11.82 \pm 2.33	25.8 \pm 2.0	7.66 \pm 0.27	18.9 \pm 4.6 ¹
	Georges River	Embayment – Middle	6.59 \pm 0.64	25.5 \pm 1.7	7.58 \pm 0.26	17.7 \pm 6.4 ¹
Low-sediment	Port Hacking	Wave-dominated estuary – Middle	2.38 \pm 0.58	25.7 \pm 2.2	7.81 \pm 0.24	27.7 \pm 6.0 ¹
	Crookhaven River	Wave-dominated delta – Seaward	2.28 \pm 0.19	24.1 \pm 3.0	7.69 \pm 0.30	34.7 \pm 0.3 ²
	Bermagui River	Wave-dominated delta – Seaward	2.27 \pm 0.16	22.8 \pm 2.0	7.76 \pm 0.12	30.4 \pm 4.4 ¹

5.4 Results

Low-sediment estuaries had almost 18x higher total oyster recruits (mean $72 \pm \text{SE } 9$ recruits) compared to high-sediment estuaries (mean $4 \pm \text{SE } 1$ recruits, LRT $X^2= 9.39$, $df=1$, $p=0.003$; Figure 5.3C). Percentages of live recruits ranged from 64.9 % per tile at Hunter River to 100 % per tile in the Hawkesbury River, but they did not differ between estuary types (LRT $X^2= 0.04$, $df=1$, $p=0.857$; Figure 5.3D).

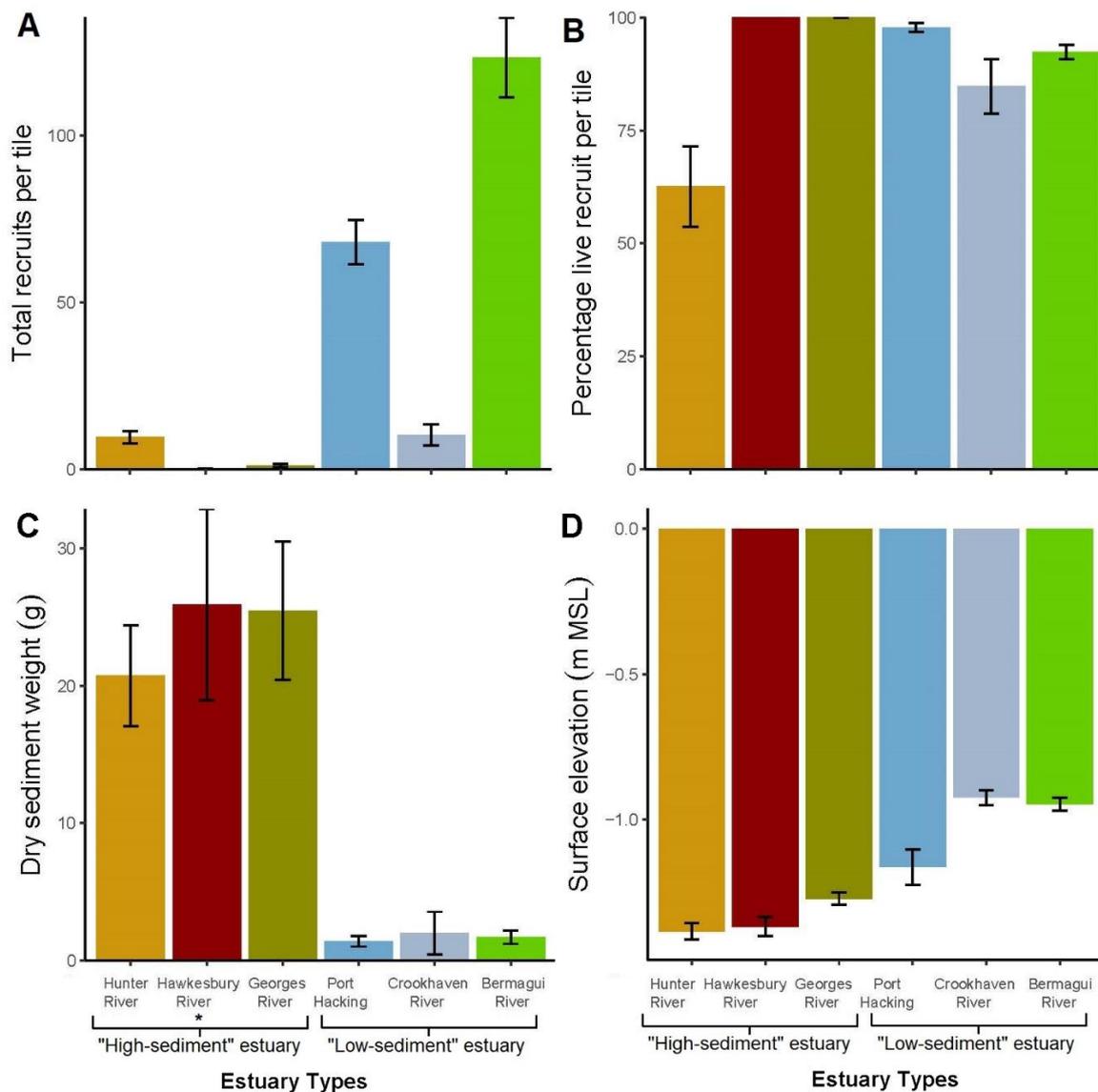


Figure 5.3. A. Mean (\pm SE) total recruitment on top surface of tiles, B. percentage of live recruits on top surface of tiles, C. Measured dry sediment weight and D. surface elevation in sampled estuaries at "high-sediment" estuary (i.e., Hunter River, Georges River and Hawkesbury River) and "low-sediment" estuary. (i.e., Port Hacking, Crookhaven River and Bermagui River). "*" denote statistical significance of 'estuary type' at $\alpha=0.05$ based on Data Analysis (section 5.3.4).

5.5 Discussion

I found that total recruitment was related to the different levels of sedimentation on a regional scale, but surprisingly the percentage of live oysters did not change with the sedimentation levels. While no study had previously investigated how regional-scale sedimentation levels is associated to oyster recruitment, my results corroborate with other oyster studies that illustrate the regional differences of an abiotic factors may associated with recruitment patterns on a regional scale (Byers et al. 2015; Kimbro et al. 2014). For example, across the estuaries along the South Atlantic Bight (SAB), the increase of inundation depth over *C. virginica* reefs was associated with increased recruit abundances (Byers et al. 2015). In addition, regional sedimentation rates may indirectly affect oyster recruitment via altering biotic processes (e.g., reducing predation risk) (Kimbro et al. 2014). For example, reduced foraging movement of predators may have facilitated sediment accumulation on *C. virginica* reefs and therefore indirectly increased survivorship of its recruits, however this observation was only limited to the southern estuary region of SAB (Kimbro et al. 2014). However, the post-settlement survivorship was the same regardless of low or high sedimentation, which suggests that biotic interactions may not influence sediment-post settlement dynamics on oyster reefs in my study, at least for the small oysters settled on my tiles. Beyond oyster reefs, regional recruitment of other foundation species, such as corals were strongly associated to regional sedimentation rates. For instance, coral recruitment was negatively affected by increases in sedimentation rate amongst coral reefs in Palau (Wakwella et al. 2020).

My findings indicate that broadscale recruitment patterns are related to sedimentation and they are not explained by post-settlement mortality which was the same among estuaries. This supports other studies demonstrating that high-sedimentation levels can prevent oyster larvae settlement (Taylor & Bushek 2008) but post-settled recruits can survive various levels of sedimentation (Widdows et al. 1989; Soniat et al. 2004; Hinchey et al. 2006; Baillie & Grabowski 2019). However, long-term exposure to high levels of sedimentation could negatively affect oyster growth and/or survivorship (Rothschild et al. 1994).

Aside from sedimentation, regional variation of other abiotic factors, particularly water pH, salinity, turbidity and temperature can affect oyster recruitment on the same scale either individually or concurrently (Brumbaugh & Coen 2009; Reeves et al. 2020; Esquivel-Muelbert et al. 2022).. However, pH and temperature measures in these estuaries did not change with the sedimentation rates and therefore do not explain the patterns of recruitment I observed (see Table 5.1 and Figure 5.1). On the other hand, I found that estuaries with high sedimentation, also had low salinity and lower recruitment and vice versa (see Table 5.2). Thus, sedimentation may be a proxy for a range of abiotic variables (e.g., turbidity; Davies-Colley & Smith 2001) which could also contribute to recruitment patterns. For example, estuaries with high incidence of runoff have higher turbidity (or higher sedimentation rates), and lower salinity can positively influence oyster recruitment (Soniati et al. 2012; Rodriguez et al. 2014; Reustle & Smee 2020; Grabowski et al. 2020). While hydrodynamic settings may influence sedimentation rates on oyster reefs (Reidenbach et al. 2013), there is no existing literature, to my knowledge that has studied regional-scale hydrodynamic influences on sedimentation rates and recruitment. Therefore, understanding the relationship between regional scale-sedimentation rates and hydrodynamic influences in future studies can further elucidate how sedimentation may impact oyster recruitment on a regional scale.

In summary, my results reiterate that varying levels of an abiotic factor at a regional scale can affect recruitment of oysters to populations at regional scales. Future studies could aim to isolate the role of sedimentation and other associated abiotic factors as described above through experimental studies which add or remove sediment (e.g., using silt curtains) to settlement plates. Therefore, future large-scale restoration efforts should consider the baseline variation of abiotic factors, particularly sedimentation, on a regional scale, in their site suitability models.

Chapter 6

General Discussion

Foundation species form spatially dominant but patchy habitats that are driven by processes occurring at multiple spatial scales (i.e., local to regional scales). While some studies have quantified variation of these processes at various spatial scales (e.g., see reviews by Tschardt et al. 2012; Tjørve et al. 2021; Carroll et al. 2019), most are limited to studies at single-spatial scales and/or single measures of population characteristics (e.g., body size), population processes (e.g., recruitment) and ecosystem function (e.g., biodiversity provision). Hence, there is a need for studies aiming to disentangle the processes driving variation in population characteristics, population processes and ecosystem functions across multi-spatial scales to identify the processes relevant for population persistence of foundation species. Understanding the association of these processes at multiple spatial scales is particularly important for restoration efforts of threatened foundation species, informing cost-effective procedures that target relevant processes for securing long-term restoration success.

In my thesis, I assessed how the spatial variation of threatened *Saccostrea glomerata* reefs affect oyster population characteristics (i.e., density and body size; Chapter 2), population processes (e.g., recruitment; Chapter 4) and ecosystem functioning (e.g., biodiversity provision; Chapter 3) at multiple spatial scales (~1 cm to ~2000 km in range). In Chapters 2, 3 and 4, I found that the largest variation in population characteristics (e.g., oyster density and density) of oysters, the biodiversity supported by oyster reefs, and recruitment to oyster reefs occurred at the regional scale. At smaller spatial scales (e.g., within-patches and landscape scales), reef spatial attributes explained some of variation in oyster characteristics, biodiversity, and recruitment, but their relationships were often in different directions (positive, negative or neutral) for each estuary. These results suggest that processes occurring at regional scales are the most important drivers of oyster demographic processes and associated communities, and likely set the context for the influences of spatial tributaries at smaller scales on biodiversity on oysters and oyster recruitment. Indeed, results indicated

differences in sedimentation between estuaries were associated with variation in total recruitment amongst the estuaries (Chapter 4). Hence in Chapter 5, I experimentally determined how oyster recruitment varied with sedimentation rates on a regional scale. I was able to quantitatively demonstrate that oyster recruitment was associated to sedimentation rates in estuaries, with estuaries with low sedimentation-levels associated to higher rates of recruitment. Overall, the results of my thesis imply that abiotic processes at regional scales are strong drivers of oyster demographic processes and their associated communities.

6.1 Untangling ecological patterns across spatial scales

I found that population characteristics, population processes and the biodiversity provisioned by *S. glomerata* reefs consistently varied on a regional scale (Chapters 2 – 4). These results corroborated existing scientific literature that population characteristics and processes of foundation species and the biodiversity they support can vary on a regional scale (refer to Table 6.1 for comparison of thesis results and literature review). Coupled with the negative correlation found between recruitment and regional-scale sedimentation rates in Chapter 5, my results contribute to mounting evidence that regional-scale processes can influence oyster populations and biodiversity in oyster reefs. My results show that sedimentation rates in estuaries should be an important variable to consider when estimating historical distributions of oyster reefs (e.g., Gillies et al. 2018) and for identifying high-quality habitats for oyster conservation and restoration in current management strategies in Australia. Moreover, the global increases in sedimentation rates observed in coastal areas during the Anthropocene (Zhang et al. 2001) may threaten the long-term resilience of remnant and restored oyster reefs on regional scales. My results also support previous studies in the southeast coastline of the United States showing that regional differences in sedimentation rates interact with trophic cascades, affecting recruitment, density, and biomass of *Crassostea virginica* oyster reefs (Kimbrow et al. 2014; Byers et al. 2015). Therefore, evidence is building around the importance of regional-scale processes on oyster reef resilience.

I also found that oyster populations and the biodiversity they host were also associated to reef attributes at smaller spatial scales (within-patches and landscape-scales). However, the majority of these relationships showed different trends across

estuaries (i.e., they were positive, negative and/or neutral, Table 6.1). These results suggest that the processes driving population characteristics, processes, and ecosystem functions of *S. glomerata* are not limited to regional scales, but also occur across smaller scales. My results concur with studies in other shellfish habitats (e.g., Luckenbach et al. 1999; Hanke et al. 2017b; Grabowski et al. 2020) and other marine foundation species such as saltmarsh (e.g., Angelini et al. 2011), macroalgal beds (e.g., Lloyd et al. 2020) and kelp forests (e.g., Wernberg et al. 2003) that showed that drivers of populations of foundation species and the biodiversity they host occur at multiple spatial scales, and can simultaneously be influenced by large- and local-scale processes (Peters et al. 2007; Gonzalez et al. 2020).

For instance, a macrofaunal defaunation experiment study conducted at multiple spatial scales where macrofaunal community recovery rates were best explained by regional connectivity and local habitat features (e.g., increase in habitat rugosity) (Thrush et al. 2013). This result suggests that large-scale processes, such as regional level-sedimentation rates, set the context for processes affecting population processes at smaller scales. My study hence supports Peters et al. (2007)'s cross-scale interaction framework, where changes in "broad-scale" processes (e.g., regional sedimentation in this thesis) can overpower both "intermediate-scale" processes (e.g., landscape-connectivity) and "fine-scale pattern-process relationships" (e.g., elevation and surface rugosity). My study implies large-scale abiotic processes can structure population characteristics but also the importance of understanding the large-scale process changes can affect local processes at smaller spatial scales.

Table 6.1. Comparison of spatial-ecological relationships from literature review (Table 1.1) and from the obtained relationships in this thesis. '+', '-', or 'Mixed' represent positive, negative, and mixed relationships respectively between a spatial scale and measured estimate respectively. 'Varies' indicates variation in community assemblages. Acronyms in this table: NS: Non-significant, CR: Crookhaven River, HR: Hunter River and PH: Port Hacking.

Spatial scale	Measured population and community estimates	Literature reviewed spatial-ecological relationships	Spatial-ecological relationships obtained in this thesis
Regional scale	<i>Population Density</i>	Varied amongst regions	Varied amongst estuaries.
	<i>Population Body Size</i>	Varied amongst regions	Varied amongst estuaries.
	<i>Biodiversity</i>	<i>Species richness</i> : Varied amongst regions	Varies amongst estuaries
		<i>Total abundance</i> : Varied amongst regions	Varied amongst estuaries.
		<i>Community assemblage</i> : Varied amongst regions	Varied amongst estuaries.
	<i>Recruitment</i>	<i>Total recruitment</i> : Varied amongst regions	Varied amongst estuaries (Chapter 5).
<i>Proportion of live recruits</i> : Varied amongst regions		Indifferent amongst estuaries (Chapter 5).	
Landscape-scale (Connectivity measure)	<i>Population Density</i>	Mixed	-: Only one estuary (CR)
	<i>Population Body Size</i>	Mixed	+: Only one estuary (PH)
	<i>Biodiversity</i>	<i>Species richness</i> : +	-: Two estuaries (CR and PH)
		<i>Total abundance</i> : +	-: Only one estuary (CR)
		<i>Community assemblage</i> : Varies	NS
	<i>Recruitment</i>	<i>Total recruitment</i> : +	Mixed. -: HR & +: PH (Chapter 4)
<i>Proportion of live recruits</i> : +		Mixed. +HR & CR, -: PH (Chapter 4)	
	<i>Total live cover area</i> : +	+: All estuaries (Chapter 4)	
Patch-scale <i>Patch-area</i>	<i>Population Density</i>	+	-: Only one estuary (HR)
	<i>Population Body Size</i>	+	-: Only one estuary (PH)

		<i>Species richness</i> : Mixed	+: only one estuary (PH)
	<i>Biodiversity</i>	<i>Total abundance</i> : Mixed	Mixed. -: CR & +:PH
		<i>Community assemblage</i> : Mixed	NS
	<i>Recruitment</i>	<i>Total recruitment</i> : +	+: all estuaries (Chapter 4)
		<i>Proportion of live recruits</i> : +	-: all estuaries (Chapter 4)
		<i>Total live cover area</i> : +	-: all estuaries (Chapter 4)
	<i>Population Density</i>	Mixed	-: Only one estuary (HR)
	<i>Population Body Size</i>	Mixed	Mixed. +: PH & -: CR
Patch-scale Shape (Fractal- dimensionality)	<i>Biodiversity</i>	<i>Species richness</i> : Mixed	-: Two estuaries (CR and PH)
		<i>Total abundance</i> : Mixed	NS
		<i>Community assemblage</i> : Mixed	NS
	<i>Recruitment</i>	<i>Total recruitment</i> : +	NS (Chapter 4)
		<i>Proportion of live recruits</i> : +	NS (Chapter 4)
		<i>Total live cover area</i> : +	-: One estuary (HR) (Chapter 4)
	<i>Population Density</i>	Mixed	NS
	<i>Population Body Size</i>	Mixed	-: Two estuaries (CR and HR)
Within- patch scale Distance to nearest patch edge	<i>Biodiversity</i>	<i>Species richness</i> : Mixed	-: only one estuary (HR)
		<i>Total abundance</i> : Mixed	NS
		<i>Community assemblage</i> : Mixed	NS
	<i>Recruitment</i>	<i>Total recruitment</i> : -	NS (Chapter 4)
		<i>Proportion of live recruits</i> : -	-: all estuaries. (Chapter 4)
		<i>Total live cover area</i> : -	NS (Chapter 4)
	<i>Population Density</i>	-	Mixed. -:CR and HR & +:PH
	<i>Population Body Size</i>	-	NS
Within- patch scale Surface elevation	<i>Biodiversity</i>	<i>Species richness</i> : Mixed	Mixed. -:CR and PH & +:HR
		<i>Total abundance</i> : Mixed	+: Two estuaries (HR and PH)
		<i>Community assemblage</i> : Mixed	Significant in two estuaries (CR and PH):
	<i>Recruitment</i>	<i>Total recruitment</i> : -	-: All estuaries (Chapter 4)
		<i>Proportion of live recruits</i> : -	NS (Chapter 4)
		<i>Total live cover area</i> : -	-: Two estuaries (HR & PH) (Chapter 4)

6.2 Implications for oyster reef restoration

As efforts are mounting to restore degraded habitats, understanding baseline ecological processes (e.g., recruitment) of a target species is crucial to develop adequate restoration strategies to restore ecosystem function and services of the species (Lindenmayer 2020). For foundation species such as oyster reefs that appear in multiple spatial scales, the variation of its population characteristics and ecosystem functioning across multiple spatial scales can inform important spatial scales for restoration strategies that aim to maximise ecosystem functions and services in targeted habitats (Callicott 2002; Puckett & Eggleston 2012; Bayraktarov et al. 2016). The outcomes of my thesis clearly show variation in population characteristics, population processes and ecosystem amongst multiple spatial scales *S. glomerata* exist in and thus have important implications for the restoration efforts planned for this species.

6.2.1 Maximising recruitment for oyster restoration

Oyster recruitment is one of the key criteria monitored by restoration practitioners to evaluate long-term success of oyster reef restoration projects (Luckenbach et al. 1999; Baggett et al. 2015; Smith et al. 2022). This is due to a need to support oyster recruitment to ensure that restored oyster reefs are self-sustainable over long periods of time. To achieve this, based upon the correlation between regional scale-sedimentation rates and oyster recruitment on reefs, *S. glomerata* reef restoration efforts should select target sites based on baseline surveys of sedimentation rates. Since lower sedimentation was associated to higher recruitment, restoration efforts should be prioritised in these areas to increase restoration success. Amongst the sampled estuaries in this thesis, low-sedimentation estuaries such as Port Hacking, Bermagui River and Crookhaven River are likely to be more favourable for recruitment in future restoration projects in New South Wales in comparison to highly-sedimented estuaries such as Hunter River, Hawkesbury River and Georges River. However, it is important to note that sedimentation rates can differ across positions along the estuary (Kench 1999; Dyer 1995), and even in high-sedimentation estuaries, there may be low depositional areas that may better support oyster reef restoration. Nevertheless, restoration efforts in high-sedimented estuaries may not be futile due to the high percentages in

survivorship of recruits in all estuaries. Moreover, excessive accumulation of sedimentation on targeted restoration sites may be reduced with establishing high-relief reefs with a threshold height (Colden et al. 2017; Lenihan 1999; Jordan-Cooley et al. 2011).

Within reef complexes, oyster recruitment was observed to relate to spatial attributes within-patch (e.g., surface elevation), whole-patch (e.g., patch-area) and at landscape scales (e.g., isolation). However, the direction of the relationships between small-scale spatial attributes and population and community characteristics are estuary-dependent. Therefore, restoration initiatives using “one-size-fits-all” approaches whereby set recommended guidelines are applied throughout the distribution area of the target species are not appropriate. Instead, pilot studies are needed prior to restoration to assess how important spatial attributes relate to recruitment at each site.

6.2.2 Maximising biodiversity for oyster restoration

One of the main goals for oyster reef restoration is to increase community biodiversity on oyster reefs and the overarching coastal and estuarine systems (Luckenbach et al. 1999; Coen et al. 2007; Howie & Bishop 2021). In order to fulfill this restoration goal, pilot studies are recommended on specific locations and spatial scales to maximise biodiversity on epifaunal communities in the remnant reefs. From Chapter 3, I found that epifaunal assemblages and biodiversity varied on a regional scale (i.e., amongst estuaries) and also with within-patch attributes, particularly surface elevation and mean oyster length-width ratio (a proxy for interstitial volume in oyster structure) albeit at different trends in each estuary. In estuaries where restoration is being proposed, pilot studies investigating these key variables may be necessary in order to maximise biodiversity benefits of restoration.

6.2.3 Other limiting factors of oyster reef restoration with spatial scales

Beyond the spatial configuration and scales of remnant *S. glomerata* reefs, temporal patterns may influence the variation of oyster population characteristics and the abiotic factors associated with the observed variations (Grabowski et al. 2020; Byers & Grabowski 2014). While I measured recruitment success following an entire cycle of

annual recruitment in Chapter 4, there could be temporal variation between recruitment cycles and associated changes in abiotic factors (e.g., sedimentation rate) that could influence the spatial-recruitment relationships observed (Michener & Kenny 1991; Lenihan 1999). Therefore, future studies can incorporate temporal assessments on the effects of sedimentation and other population processes identified in this thesis that reduce knowledge gaps for oyster reef restoration efforts (Howie & Bishop 2021).

The processes driving oyster populations and the biodiversity they host could interact with anthropogenic impacts including climate change and sea level rise (Howie & Bishop 2021). These impacts will strongly affect regional-scale abiotic processes via ocean acidification and temperature changes (Breitburg et al. 2015; Ekstrom et al. 2015; Lemasson et al. 2017). Previous studies have shown that these processes can negatively impact early life-stages of *S. glomerata* in terms of mortality and shell length via elevated carbon dioxide and temperature levels (Parker et al. 2009, 2017; Pereira et al. 2020). Hence, ocean acidification, climate change and sea-level rise may affect within-patch attributes of reefs, such as elevation, rugosity and interstitial space. While these effects may ripple up the scales and affect whole-patch attributes, no studies have assessed this. Although Rodriguez et al. (2014) have shown that oyster reef vertical growth can outpace sea level rise, a 29-year aerial survey of *C. virginica* found that 66% of the total reef area was lost in the Gulf of Mexico with their habitats 'migrating inland' over the survey period (Seavey et al. 2011). Therefore, future restoration efforts may need to consider the effects of ocean acidification, climate change and sea-level rise on towards changes in habitat configuration (e.g., increases in relief height, increases in edge effects) of oyster reefs and their associated changes in biophysical gradients (e.g., increases in salinity, inundation frequency and wave exposure) across multiple spatial scales occupied by oyster reefs to ensure long-term restoration success.

6.3. Conclusions

In this thesis, I was able to determine that oyster populations and the biodiversity they host were mainly influenced by processes occurring at regional scales, namely sedimentation, was significantly associated to regional population recruitment. Moreover, regional abiotic processes set the context for smaller scale influences on oyster characteristics, oyster processes and ecosystem function. My thesis highlights the importance of comparing the role of processes at multiple scales, a rarely considered topic of study in foundation species. From a restoration perspective, prioritising the most important processes at multiple spatial scales can aid efforts that maximise long-term oyster reef sustainability, and to enhance restoration success and the services they provide.

Appendix A:

**Leong, R.C., Bugnot, A.B., Marzinelli, E.M.,
Figueira, W.F., Erickson, K.R., Poore,
A.G.B. and Gribben, P.E. (2022),
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RESEARCH ARTICLE

Variation in the density and body size of a threatened foundation species across multiple spatial scales

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Population characteristics (e.g. density and body sizes) of foundation species can affect their own persistence and provisioning of ecosystem functions. Understanding the drivers of population characteristics of foundation species at multiple spatial scales is therefore critical for maximizing ecosystem functions of restored habitats. We analyzed variation in population characteristics (densities, 95th percentile, and median lengths of live oysters) of the Sydney rock oyster, *Saccostrea glomerata*, on remnant oyster reefs at regional scales (among three estuaries) along an approximately 250 km of coastline in New South Wales, Australia. We then analyzed how population characteristics were further related to spatial attributes at smaller spatial scales including within-patches (rugosity, distance to patch-edge, and elevation), whole-patches (size and shape), and among-patch (connectivity) within each estuary. The densities and body sizes of *S. glomerata* were related to spatial attributes occurring within-patch (e.g. elevation), whole-patch (e.g. shape), and landscape (i.e. connectivity) scales, but these relationships varied among estuaries. The greatest variation in oyster density and size occurred at regional scales, suggesting that processes acting at larger spatial scales (e.g. water quality and/or climate) set the context for smaller scale influences on oyster characteristics. Our results highlight the potential importance of incorporating site-specific, spatial attributes in the design of restored oyster reefs to maximize ecosystem services and functions provided by restoration efforts.

Key words: connectivity, foundation species, landscape ecology, oyster reefs, *Saccostrea glomerata*, seascape, spatial scales, structural complexity, Sydney rock oyster

Implications for Practice

- Understanding spatial variations for the population characteristics of target foundation species will maximize the ecosystem benefits provided by the restored habitats.
- The marine foundation species, the Sydney rock oyster (*Saccostrea glomerata*), varied in population characteristics (i.e. density and body size) within habitat-patches and with patch connectivity across landscapes but the largest variation occurred at regional scales (among estuaries).
- Reef restoration should avoid “one-size-fits-all” strategies and consider local ecological knowledge (e.g. size, shape, and connectivity) of the remnant foundation species or utilize pilot studies at the proposed restoration sites.

Introduction

Marine foundation species (sensu Dayton 1972) such as mangroves, seagrasses, seaweeds, and shellfish provide critical ecosystem functions and services, including habitat and food provision for fish and invertebrates, nutrient cycling, water quality improvement, and coastal protection (Ellison et al. 2005; Grabowski & Peterson 2007; Angelini et al. 2015; Bulleri et al. 2018;

Gribben et al. 2019; Lloyd et al. 2020). Despite their importance to ecosystems, foundation species have experienced staggering losses globally. For example, oyster reefs have been globally reduced by 85% (Beck et al. 2011), mangrove forests by 35% over 50 years (Polidoro et al. 2010), and seagrass meadows by up to 29% from 1880 to 1990 (Waycott et al. 2009). Because of the critical services they provide, they are a focus of global

Author contributions: all authors conceived the ideas and designed methodology; RCL, WFF, KRE, ABB collected the data; RCL, WFF, ABB, EMM analyzed the data; RCL, ABB, PEG led the writing of the manuscript; all authors contributed critically to the drafts and gave their final approval for publication.

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Variation of oyster characteristics on reefs

restoration efforts (Lindenmayer et al. 2008; Bayraktarov et al. 2016; Swan et al. 2016).

The population characteristics (e.g. density and body size distribution) of foundation species have strong consequences for their own persistence and the ecosystem functions and services they provide. For example, the density and size of marine foundation species can influence their own growth, recruitment, and survivorship (Gribben et al. 2020), the biodiversity they support (Stelling-Wood et al. 2020), hydrodynamics and wave attenuation (Salvador de Paiva

et al. 2018), and water filtration (Green et al. 2013). From a restoration perspective, population characteristics of a target species may therefore inform the persistence and magnitude of the ecological services in areas of interest, and thus may be a fundamental yet understudied component of many restoration strategies (Baggett et al. 2015; Ladd et al. 2018).

Population characteristics of foundation species can vary across multiple spatial scales (Godron & Forman 1981; Fahrig 2003). At small spatial scales, these characteristics can vary within habitat patches, although patterns are equivocal. For

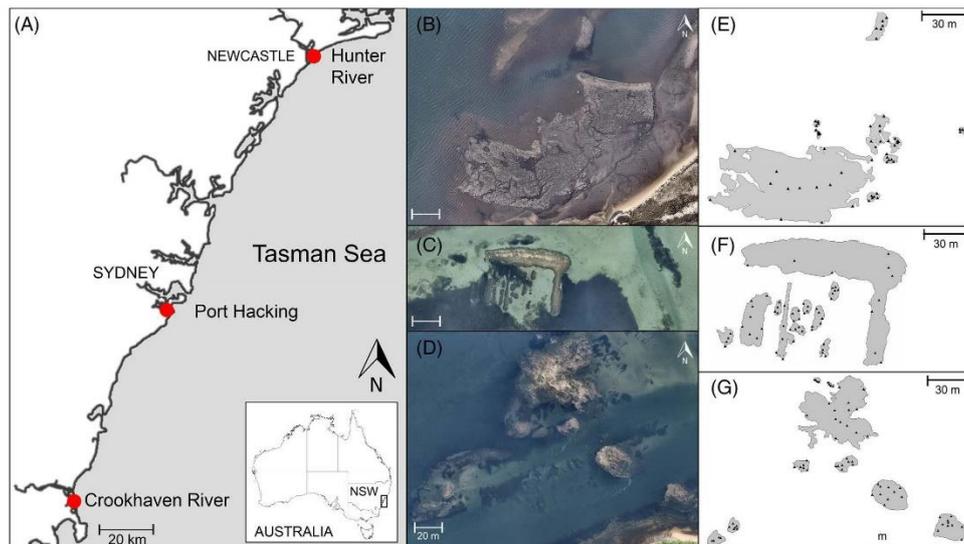


Figure 1. Locations of sampled *Saccostrea glomerata* oyster reefs (red dots) in estuaries in New South Wales (NSW), Australia (inset; A). Satellite imagery of the reefs (NearMap Ltd.) during low tide and the corresponding sample locations (see triangles) on reef contours of the selected reefs in Hunter River (B & E), Port Hacking (C & F), and Crookhaven River (D & G), respectively.

Table 1. Characteristics of estuaries where the sampled oyster reefs are located. Observed and/or calculated characteristics of each estuary were obtained from: ^aOzCoasts (2015), ^bNSW Office of Environment and Heritage (2016) for periods between 2007 and 2015, and ^cNearMap Ltd. unless specified.

Estuary Characteristics	Estuary		
	Hunter River	Port Hacking	Crookhaven River
Estuary-type classification ^a	Wave-dominated estuary	Tide-dominated estuary	Wave-dominated delta
Average annual summer temperature \pm SE ($^{\circ}$ C) ^b	24.7 \pm 0.3	25.7 \pm 0.3	24.1 \pm 0.3
Average annual turbidity \pm SE (NTU) ^b	19.1 \pm 7.2	2.4 \pm 0.6	2.3 \pm 0.2
Disturbance class ^c	High	Low	Medium
Number of reefs ^c	25	14	10
Base material of remnant reefs	Mud banks (McLeod et al. 2019)	Ballast heap (Alhani & Cotis 2013)	Sand and rock boulders (R.C.L., 2018, personal observation)
Approximate distance to estuary mouth (km) ^c	6.5	4.3	2.2
Mean patch area (m ²) \pm SE ^c	237 \pm 155	112 \pm 78	355 \pm 200
Mean distance between reefs (m) \pm SE ^c	32.2 \pm 1.4	12.7 \pm 1.0	80.8 \pm 7.8

example, the population density and mean body size of foundation species can be smaller at patch edges in comparison to patch centers (Hanke et al. 2017), but the opposite pattern also occurs (Bell et al. 2001; Bostrom et al. 2011; Bertolini et al. 2020). Such variation may be explained by within-patch attributes (i.e. distance from patch-edge) interacting with whole-patch attributes such as patch size and shape (edge-to-area ratios), as larger patches are often associated with higher densities of foundation species and may be better at buffering abiotic and biotic stress than smaller patches (Angelini et al. 2011; Livernois et al. 2017; Crotty et al. 2018). Thus, understanding how multiple spatial scales interact to influence the population characteristics of foundation species, and potentially their function, is critical to inform the design of restored habitat patches and maximize ecosystem functions provided and restoration outcomes.

At larger scales, habitat patches can interact with each other across the landscape by altering ecological flows of resources and progeny (Brooks 2003; Ewers & Didham 2006; Zambrano et al. 2019) and ecological interactions (e.g. predation rates; Martin et al. 2018), all of which may influence the population characteristics of foundation species. Indeed, patch configuration and their connectivity can affect population characteristics in both terrestrial (e.g. Fahrig 2017; Thompson et al. 2017) and aquatic ecosystems (Angelini et al. 2011; Crotty et al. 2018). Moreover, the density and traits of foundation species can also be determined by background environmental variation (e.g. temperature) occurring at regional scales (e.g. grassland—Le Roux & McGeoch 2010; macroalgal beds—Leonard 2000). Understanding the roles of landscape and regional scales on controlling population characteristics of foundation species will help identify the configuration of restored patches and site selection that maximizes their ecological functions and resilience, improving on existing restoration strategies (Angelini et al. 2011; Gilby et al. 2018).

In Australian estuaries, oysters once formed extensive reef complexes up to 10 ha in areas from the intertidal to depths of approximately 8 m (Ogbum et al. 2007). However, more than 90% of these complexes, including those of the iconic Sydney rock oyster, *Saccostrea glomerata* (Gould 1850), have been lost through overharvesting for food and lime, disease, and pollution (Ogbum et al. 2007; Gillies et al. 2018). *S. glomerata* reefs are now considered functionally extinct (Beck et al. 2011) and they are a key focus for restoration (Gillies et al. 2018). To date, global oyster restoration efforts consist mostly of substrate provision for recruitment (Westby et al. 2019). Oyster densities and size can affect their own recruitment (Knights & Walters 2010), growth (Honkoop & Bayne 2002), survival (Holliday et al. 1991; Honkoop & Bayne 2002), and filter-feeding capacity (Ozbay 2006), as well as the biodiversity they host (Wilkie et al. 2012). However, few restoration projects have considered how spatial context may influence the persistence of the restored oyster populations and the ecological functions they provide (McAfee et al. 2020). This is due, in part, to a lack of understanding about how population characteristics vary with patch attributes (e.g. edge-vs.-center, size, shape, complexity) and configuration at multiple spatial scales.

In this study, we used the natural variation of patch-size, patch-shape, and connectivity in remnant oyster reefs in three estuaries in southeast Australia to determine how spatial variation from within patches to regional scales influence the population characteristics of *S. glomerata*. At each estuary,

Table 2. List of metrics used to quantify within-, whole-, and among-patch (patch-connectivity) attributes. Formulae of metrics can be found in Table S3.

Attributes	Description
Among-patch	
Nearest-neighbor distance	The shortest Euclidean and edge-to-edge distance between a focal reef and its nearest neighboring reef (McGarigal et al. 2012).
Mean nearest-neighbor distance	Average of the nearest Euclidean and edge-to-edge distances from a focal reef to all other reefs in the same landscape (McGarigal et al. 2012).
Proximity index	Index which measures the distance of a focal reef to other reefs in relation to area of the focal patch. Index for a patch is calculated by summing ratios of focal patch-area to nearest neighbor distances from focal patch to other patches (Gustafson & Parker 1992).
Isolation index	Index is a weighted sum of products between nearest neighbor distance from focal patch to other patches, and the ratios of focal patch area to the total patch area (Moilanen & Nieminen 2002).
Whole-patch	
Two-dimensional fractal dimension index	Standardized and scale-independent measure of perimeter of a patch relative to a square perimeter and patch-area (McGarigal et al. 2012).
Circularity index	Ratio between the patch-area and the smallest circumscribing circle of the patch (McGarigal et al. 2012).
Shape index	Ratio of actual patch-perimeter to hypothetical patch-perimeter as a square with the same area, characterizing total edges of patch (McGarigal et al. 2012).
Perimeter	Perimeter of each patch calculated from satellite image, reef contours.
Perimeter–area ratio	Ratio of patch-perimeter to patch-area for each patch.
Area	Area of each patch calculated from satellite image, reef contours.
Within-patch	
Distance to edge	Shortest distance of each sampled core to the nearest reef edge.
Surface elevation	Height of each sampled core above mean sea level.
Surface rugosity	Surface roughness on each sampled core and 20-cm radius surrounding each core derived from photogrammetry and digital elevation models sensu Figueira et al. (2015).

Variation of oyster characteristics on reefs

Table 3. Selected spatial attributes that relate to oyster density, 95th percentile length, and median length from “best” models obtained for Crookhaven River (CR), Hunter River (HR), and Port Hacking (PH) reefs. “+” and “-” represent positive and negative estimates, respectively, for selected attributes. White and black cells represent attributes that were not selected and not included (due to collinearity) in best models, respectively. Refer to Tables S8–S11 for detailed model outputs.

Spatial Scales and Patch Attributes		Population Characteristic and Estuaries								
		Abundance			95th Percentile Length			Median Length		
		CR	HR	PH	CR	HR	PH	CR	HR	PH
Within-patch	Surface elevation	-	-	+	-	-				
	Distance to edge									
Whole-patch	Surface rugosity									
	Area									
	Fractal dimension									
Among-patch	Circularity index				+		+	+		-
	Isolation index									
	Proximity index									

we sampled oyster densities, median, and 95th percentile body size on remnant oyster reefs at local (within- and whole-patch) and landscape (among-patch) scales and regional (among estuaries) scales. We tested the hypotheses that oyster densities and size would be correlated to (1) distance from the patch-edge within patches, (2) area and perimeter-to-area ratios as whole-patches, and (3) proximity of patches. Additionally, we hypothesized that (4) oyster sizes and densities would vary among estuaries due to differences in background environmental conditions operating at regional scales.

Methods

Sampled Estuaries Across the Regional Scale

Remnant *Saccostrea glomerata* reef complexes were sampled in three estuaries across approximately 250 km of the coastline in New South Wales (NSW) Australia; Hunter River (32°52'56.5788"S, 151°47'20.9508"E), Port Hacking (34°4'22.0404"S, 151°7'14.5956"E), and Crookhaven River (34°54'21.04"S, 150°44'48.62"E) (Fig. 1). Reef complexes in Hunter River, Port Hacking, and Crookhaven River were characterized by *S. glomerata* aggregation on mud banks, ballast heaps, and rocky boulders, respectively (Table 1). Each estuary contained different levels of anthropogenic disturbances, annual temperatures, and turbidity measurements (NSW Office of Environment and Heritage 2016; Table 1). Crookhaven River reefs possessed the largest mean patch area and spatial range of all estuaries, followed by Hunter River and Port Hacking (Table 1). Hunter River contained almost twice the number of reefs compared to Crookhaven River and Port Hacking (Table 1). In each estuary, 9–11 reefs ranging in area from 5 to 4,000 m² and consisting of different shapes (e.g. ovoid, elongate, irregular) were randomly selected for mapping and sampling (Table S1). Reef contours were mapped using satellite images from NearMap Ltd.

(<http://maps.au.nearmap.com/>). Small reefs (<5 m²) were not mapped or sampled to avoid damage to them.

Quantifying Oyster Characteristics

On each reef, we sampled oysters by taking 10 × 10 × 10-cm cores with a hammer and chisel during mean low tide (Bureau of Meteorology 2018). All cores were sampled in Austral spring (late October–early November 2018) outside of the recruitment period of *S. glomerata* (Diggle 2017) to focus on the oyster characteristics of postrecruitment individuals as these are likely providing the ecological functions on reefs. The number of cores sampled on each reef differed according to reef area (Table S2), with a minimum of four cores sampled on the smallest reefs (5–25 m²) and a maximum of 14 cores on the largest reefs (≥2,000 m²). Sampling locations were randomly selected within reef contours using function “spsample” from package “sp” (Pebesma & Bivand 2005) in R (v4.0.3, 2020; Fig. 1E–G) and were mapped with a real-time kinematic and differential global positioning system (RTK-DGPS; Leica GNSS 14, Leica Geosystems, Switzerland, vertical accuracy ±8 mm; horizontal ±13 mm).

Cores were fixed in 10% formalin mixed in seawater. Total volume of oysters in each core (hereafter biovolume) was estimated by displaced volume in water. The majority of live oysters were identified as *S. glomerata* (93.2% in Crookhaven River, 99.9% in Hunter River, and 92.1% in Port Hacking) following dissection methods in Wilkie et al. (2012), with the remaining identified as the invasive Pacific oyster (*Magallana gigas* Thunberg 1793, formerly *Crassostrea gigas*). Although competition between both species altered the density and body size of *S. glomerata* at low- and mid-intertidal heights on aquaculture farms (Krassoi et al. 2008), we assumed limited effects of competition, at the time of sampling, owing to small proportions (i.e. <8% at any sampled estuary) of *M. gigas* currently present on intact *S. glomerata* reefs.

We measured the shell length of all live oysters with Vernier calipers (±0.1 cm) along the anterior–posterior axis as this is

correlated to body size for live oysters (Gribben et al. 2020). Postmeasurement, we calculated the median (50th) and 95th length percentiles per core as proxies of “average” and “largest” oyster sizes in each core, respectively. We also counted all live oysters per core where individuals were categorized as either “juvenile” (defined as settled spat <1 cm in length and flesh attached) or “adults” (oysters ≥ 1 cm in length). Both adult and juvenile counts were highly correlated to each other (Pearson correlation coefficient, $r = +0.78$, $p < 0.001$); hence, they were combined as total densities per core for the statistical analyses.

Quantifying Within-Patch, Among-Patch, and Whole-Patch Attributes

We defined “patch attributes” as the spatial characteristics of reefs for all spatial measurements. We quantified within-patch attributes at each sampled core on each reef. These included surface elevations of the sampled cores, distance to the nearest patch-edge, and the surface complexity around the samples. Elevation relative to sea level at each coring point was measured with the RTK-DGPS unit as height above mean sea level. The distance of each core to the nearest reef edge was calculated in ArcGIS (v10.3; ESRI 2016) using the NEARDIST function with cores’ xy coordinates and reef-contour maps.

To quantify surface complexity of reefs on each core, oyster reefs were mapped during low tide via photogrammetry prior to coring (see [Figueira et al. 2015](#) for methods). We used this method as it is more accurate (i.e. lower error and variance) than traditional methods, such as the chain method ([Friedman et al. 2012](#)). All reefs in Port Hacking and Crookhaven River were mapped but not all were mapped in Hunter River due to time constraints. Digital elevation models (DEMs) produced from mapped reefs were created in Agisoft Metashape PhotoScan (v1.1.6, 2015), trimmed to reef edges, and imported to ArcGIS (v10.3; ESRI 2016). Resulting three-dimensional models had an average mesh resolution (distance between vertices) of 8.2 mm and average model error of 4.7 mm, while DEMs had an average cell size of 2.5 mm. DEMs were imported into ArcGIS and sample points (based on xy coordinates) were buffered with a 20-cm radius circle. Surface rugosity independent of surface slope (hereafter “rugosity”) was calculated for each of these buffered areas (corresponding to the location of each sample core) with the arch-ratio rugosity index function ([Du Preez 2015](#)) in the Benthic Terrain Modeler plugin (v3.0; [Walbridge et al. 2018](#)) in ArcGIS (see [Supplement S1](#) and [Figs. S1-S2](#) for detailed method description). Five whole-patch attributes ([Table 2](#)) were calculated based on shape, area, and perimeter ([McGarigal et al. 2012](#)) using the function “calculate_lsm” in “landscape metrics” package in R ([Hesselbarth et al. 2019](#)).

We defined the “oyster reef landscape” as the mosaic of oyster reefs within an unstructured matrix (i.e. sandy and/or muddy bottom; [Turner 1989](#)). To quantify the connectivity within an oyster reef landscape, we used four metrics of habitat “isolation” ([McGarigal et al. 2012](#); see [Table 2](#)) based on reef areas and inter-reef distances ([Cushman & McGarigal 2002](#)). The metrics were obtained in R using the reef-contour maps. The nearest neighbor distance was calculated using the function in “gdistance” package

([van Etten 2017](#)). The proximity index was calculated using the function “ProxIndex” in package “spatialEco” ([Evans 2015](#)). The mean nearest neighbor distance and the isolation index were manually calculated (see [Table S3](#) for formula for each metric).

Data Analysis

Oyster Characteristics Across the Regional Scale. Because patch attributes related to population characteristics differently within each estuary ([Table 3](#); [Figs. 3–5](#)), we first tested for regional differences in oyster population characteristics (abundance, median length, and 95th percentile length) via the comparisons among estuaries. We tested relationships between

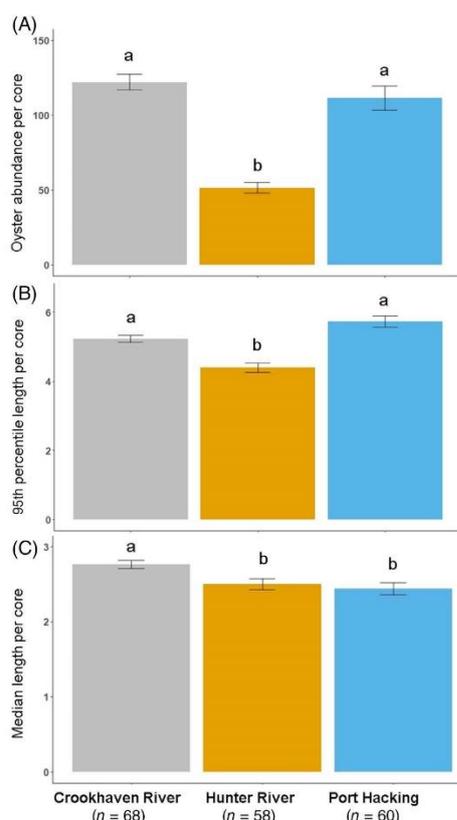


Figure 2. Mean (\pm SE) oyster abundance (A), 95th percentile length (B), and median length (C) of oysters sampled in Crookhaven River, Hunter River, and Port Hacking. Number of sampling cores per estuary is denoted as n . Different lowercase letters represent significantly different results ($p < 0.05$) from Tukey post hoc tests.

Variation of oyster characteristics on reefs

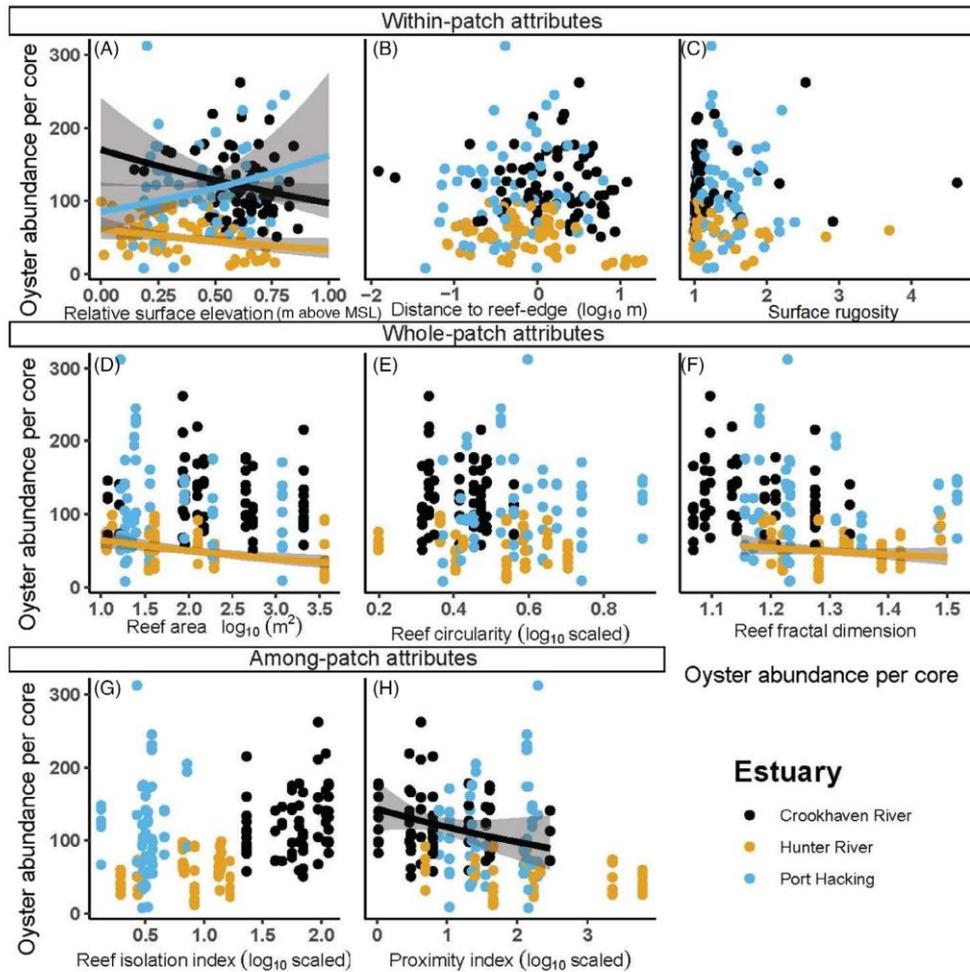


Figure 3. Relationships between oyster abundance and spatial attributes (A, elevation; B, distance to reef-edge; C, surface rugosity; D, area; E, circularity index; F, fractal dimension index; G, isolation index; H, proximity index) at sampled estuaries. Regression lines and 95% CI (shaded area) were plotted for selected spatial attributes from model selection (see “Data Analysis” section and Table 3). MSL, mean sea level.

population characteristics and patch attributes within each estuary separately (see next subsection).

We used a generalized linear mixed model (GLMM) assuming a negative binomial distribution for oyster density and linear mixed models (LMMs) for median and 95th percentile oyster lengths as response variables, with estuaries as a fixed factor. Biovolume per core (i.e. the volume of sampled structure including live oysters and dead oyster shell) was included as a

continuous covariate in each model to account for potential differences in shell matrix in each core. Reef (hereafter “reef_id”; i.e. unique reef complexes) was included as a random factor to account for potential nonindependence between samples cores from within the same patch. The GLMM was performed using “glmmTMB” package (Magnusson et al. 2020) and LMMs with the lme4 package (Bates et al. 2015). Statistical significance of estuary for each model was computed with likelihood ratio tests

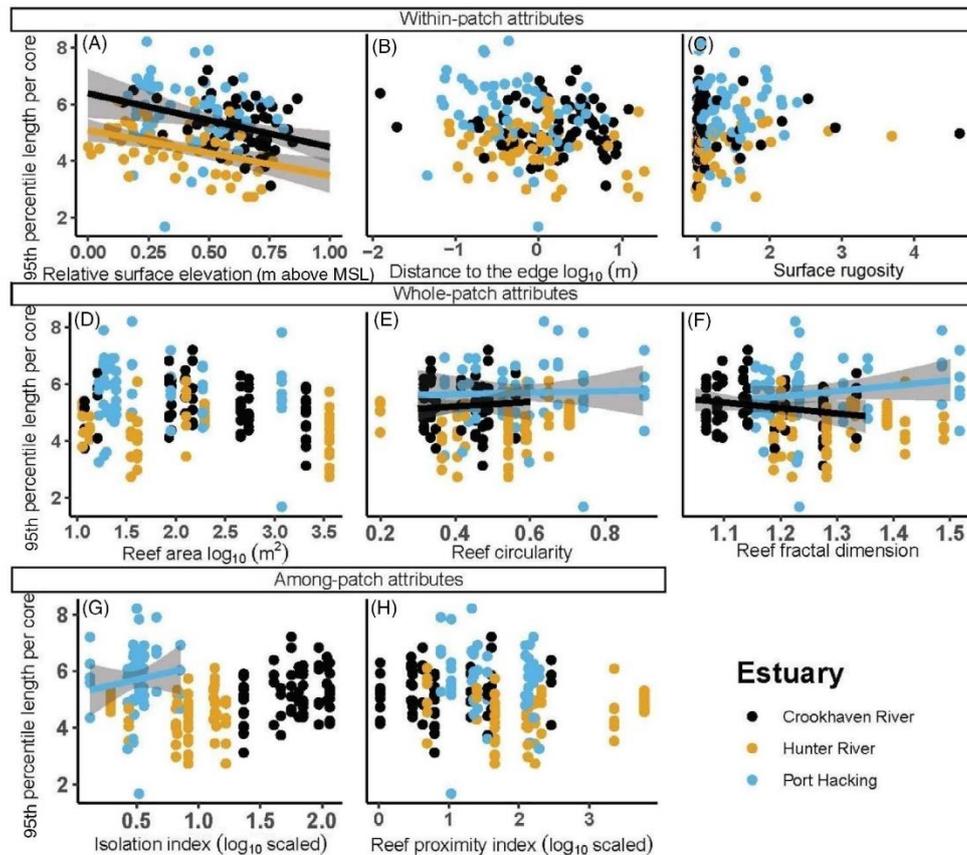


Figure 4. Relationships between largest oyster sizes and spatial attributes (A, elevation; B, distance to reef-edge; C, surface rugosity; D, area; E, circularity index; F, fractal dimension index; G, isolation index; H, proximity index) at sampled estuaries. Regression lines and 95% CI (shaded area) were plotted for selected spatial attributes from model selection (see “Data Analysis” section and Table 3). MSL, mean sea level.

(LRTs) using the “Anova” function in the “car” package (Fox et al. 2013). Post hoc tests with Tukey were performed using function “lsmeans” (Lenth 2016) in lieu of statistical significance of estuaries (see Table S6).

Oyster Characteristics Across Within-, Whole-, and Among-Patch Attributes. We tested relationships between each oyster characteristic (abundance, median length, and 95th percentile length) and patch attributes (within-, whole-, and among-patches) of the remnant reefs through model fitting and selection.

For each estuary, we first tested for collinearity of patch attributes prior to model fitting (Zuur et al. 2009); where two or more variables were correlated (Pearson’s correlation coefficient,

$r \geq 0.7$), we left one of those variables in the model and excluded the remainder (see Supplement S2 for procedure to assess co-linearity between spatial attributes and Fig. S3 for correlation matrices between attributes per estuary). We then fitted each oyster characteristic as a response variable using GLMMs and LMMs where biovolume and “reef_id” were also included in each model as a continuous covariate and random factor, respectively. A total of nine models were fitted; one for each oyster characteristic (density, median length, and 95th percentile length) repeated in each of the three estuaries (see Table S7 for equation of each model fit). For each Hunter River model, rugosity was excluded as a covariate due to substantial absence of data points (refer to “Quantifying within-patch attributes” subsection) to prevent loss of precision of model estimates (Bartlett et al. 2014).

Variation of oyster characteristics on reefs

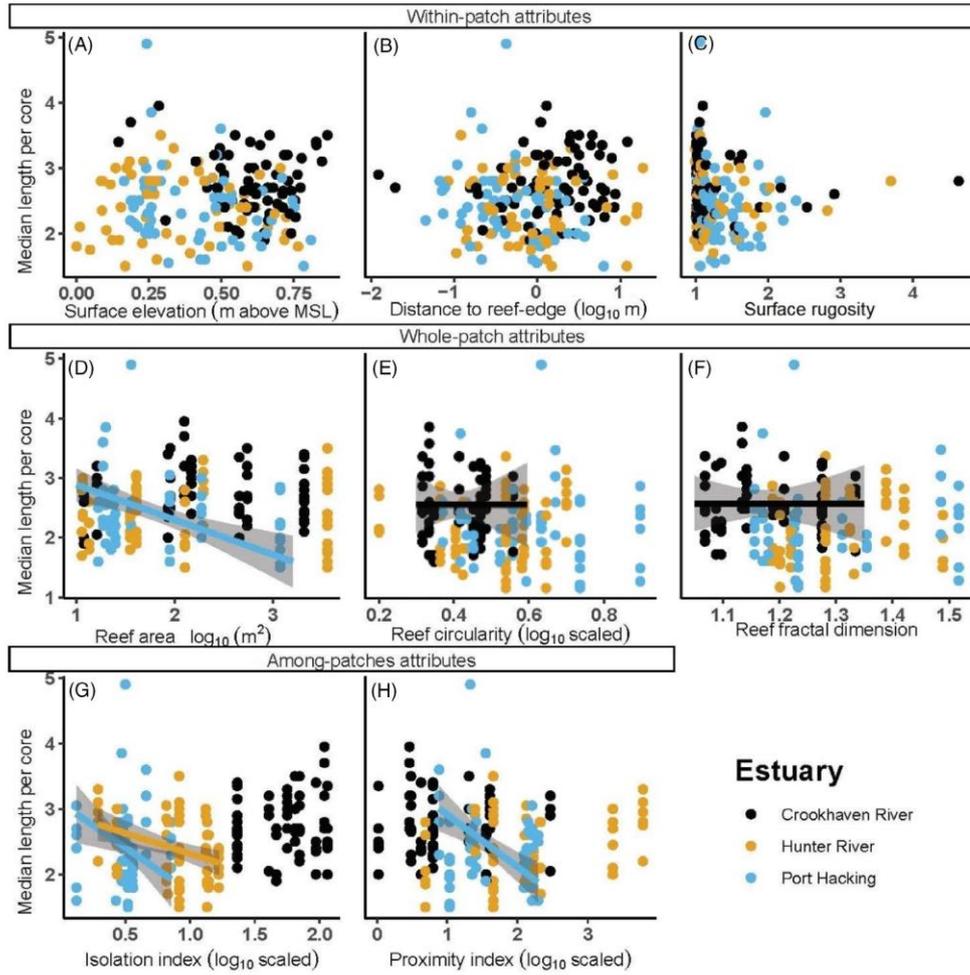


Figure 5. Relationships between median oyster lengths and spatial attributes (A, elevation; B, distance to reef-edge; C, surface rugosity; D, area; E, circularity index; F, fractal dimension index; G, isolation index; H, proximity index) at sampled estuaries. Regression lines and 95% CI (shaded area) were plotted for selected spatial attributes from model selection (see “Data Analysis” section and Table 3). MSL, mean sea level.

For each model, we conducted stepwise model regression with all possible combinations of patch attributes as predictors, using the “dredge” function in “MuMIn” package (Bartoń 2009). The most parsimonious/“best” model in each set was chosen based upon the model combination with the lowest small-sample corrected Akaike information criterion (Burnham & Anderson 2002). Selected models and their corresponding patch attributes were validated using histograms of the residuals and plots of the

residuals versus the fitted values (Zuur et al. 2009). See Tables S8–S11 for model selection outputs.

Results

Oyster Characteristics Across the Regional Scale

The abundance of oysters per core differed on a regional scale (LRT $\chi^2 = 41.7$, $df = 2$, $p < 0.001$; Table S4), with lower abun-

dances in Hunter River compared to Crookhaven River and Port Hacking (post hoc Tukey, Crookhaven River = Port Hacking > Hunter River; Fig. 2A, Table S5). Largest oysters (i.e. 95th quantile lengths per core) also differed across all estuaries (LRT $\chi^2 = 35.5$, $df = 2$, $p < 0.001$; Table S4), with shorter lengths in Hunter River compared to Crookhaven River and Port Hacking (post hoc Tukey, Crookhaven River = Port Hacking > Hunter River; Fig. 2B, Table S5).

Median oyster lengths also differed across estuaries (LRT $\chi^2 = 7.2$, $df = 2$, $p = 0.027$; Table S4); Crookhaven River had greater lengths than Port Hacking and Hunter River (post hoc Tukey, Crookhaven River > Port Hacking = Hunter River; Fig. 2C, Table S5).

Oyster Characteristics Across Within-, Whole-, and Among-Patch Attributes

Among all estuaries, oyster abundances were best explained by within-patch and whole-patch attributes, with different combinations found across estuaries (Table 3; Fig. 3). Surface elevation was the only attribute that was strongly related to oyster abundances at all estuaries (Table 3; Fig. 3A). However, the elevational trends were not the same across the estuaries; oyster abundance significantly decreased at higher reef elevations at Crookhaven River and Hunter River but increased at Port Hacking (Fig. 3A). Oyster abundance was highest for the least fractal and smaller reefs at Hunter River (Fig. 3B & 3C). Higher reef proximities were only associated with lower abundances in Crookhaven River.

The size of the “largest” oysters per core (as measured by the 95th percentile oyster lengths) was also best explained by within-patch and whole-patch attributes, with different combinations found across each estuary (Table 3; Fig. 4). Higher surface elevation of reefs was associated with smaller oysters in Crookhaven River and Hunter River (Fig. 4A). Circle and fractal dimensionality indices of reefs were associated with large oysters in Crookhaven River and Port Hacking; the former showing positive correlation with size of large oysters and the latter showing opposing relationships in both estuaries (Fig. 4E & 4F).

By contrast, median oyster lengths were associated with whole-patch and patch-connectivity attributes at two of three estuaries (Table 3; Fig. 5). None of the within-patch attributes included explained median oyster lengths. Like 95th percentile lengths, oyster median lengths were associated with decreased fractal dimensionality of reefs and increased reef circle index in Crookhaven River (Fig. 5E). At Port Hacking, median lengths were best explained by isolation index, proximity index, and reef area (Fig. 5D, 5G, & 5H) where they were negatively associated with isolation index.

Discussion

The population characteristics (e.g. densities and body size) of foundation species can mediate the functions they provide (e.g. habitat provisioning, water filtration). Thus, understanding the spatial processes that govern these may help inform the spatial design of restored oyster reefs and enhance the ecosystem

services and functions they provide. Here, we determined how the density and body size of the reef-forming Sydney rock oyster, *Saccostrea glomerata*, varied at multiple spatial scales. Our study revealed that the density and body size of *S. glomerata* were related to reef attributes at within-patch, whole-patch, and landscape scales. However, the greatest variation in both oyster density and size was observed at regional scales, suggesting that processes operating at this scale set the context for smaller scale habitat influences on oyster population characteristics.

Our results support previous studies showing that oyster characteristics can differ among estuaries (Powers et al. 2009; McAfee et al. 2016; Kimbro et al. 2020). The larger oyster sizes and densities observed in Crookhaven River and Port Hacking could be linked to better water quality and greater wave action at these sites, which can increase recruitment, food supply, and filtration rates, driving greater survival and growth (Dove & Sammut 2007; Diggles 2013; Theuerkauf et al. 2017; Vozzo et al. 2020). Hence, the potentially poorer water quality at the Hunter River, as evidenced by the greater turbidity that occurs in the river, might explain the lower densities and body sizes found at this estuary. Differences in temperature among estuaries—such as may occur with latitudinal gradients—do not explain patterns in density and shell length as there is little difference in temperature among estuaries and our warmest site is in the middle so oyster lengths are not related to any latitudinal gradient in temperature that may exist over the 250 km of coastline our estuaries span. Differences in biotic interactions could also explain patterns in body size and density among estuaries. Indeed, oyster predation in Australia is driven by fish (Anderson & Connell 1999). At the same time as this study, Erickson (2019) studied fish assemblages in Port Hacking and Crookhaven River. This study found greater fish predation at Port Hacking than Crookhaven River, which is one of the sites with high density and size of oysters. Moreover, at Hunter River, we would expect predation to be low due to high turbidity at this site as has been observed in other systems (Lunt & Smee 2014; Reustle & Smee 2020). Hence, it is unlikely that differences in rates of predation explain differences in oyster length and density among estuaries. Studies explicitly assessing how variation in water quality among estuaries influences oyster population characteristics at regional are needed to further explore these relationships.

Our models showed that factors acting at scales within estuaries also play an important role in determining oyster density and body size. Within-patch characteristics explained oyster abundances and length of the largest oysters at all estuaries, but the specific characteristics and trends varied between estuaries. For example, at Port Hacking, while densities increased with elevation, as reported in previous studies (Lenihan 1999; Schulte et al. 2009; Colden et al. 2017), the opposite trends were observed in Crookhaven River and Hunter River. Interestingly, these reefs were at higher elevation relative to sea level than Hunter River; hence, they might be at the upper limit of their optimal tidal elevation and likely affected by a reduced hydroperiod resulting in lower densities and smaller sizes at their highest points (Bartol et al. 1999; Bishop & Peterson 2006; Byers et al. 2015). Regardless, our

results support the current understanding that tidal elevation is an important environmental factor to consider when restoring oyster reefs (Walles et al. 2016).

In terms of whole-patch attributes, our results showed that patch shape explained variation in oyster size in two out of three estuaries. Specifically, increases in circle index (i.e. narrower and elongated patches) were linked to larger oysters in Crookhaven River and Port Hacking. Meanwhile, fractal dimensionality (i.e. the geometric complexity the edge of the patch) was positively associated with large oyster sizes at Port Hacking, but negatively at Crookhaven River. These results, although variable across estuaries, suggest that patch-shape influences oyster sizes particularly at exposed sites. Reef shape at these sites might be interacting with the local hydrodynamics, with elongate and complex reef shapes providing better protection for oysters. These results indicate that oyster restoration initiatives at exposed sites might benefit from incorporating more elongate and complex shapes, while this might not be necessary for protected sites.

Patch size and edge of foundation species have well described effects on population characteristics (Godron & Forman 1981; Kennedy & Bruno 2000; Hanke et al. 2017). Moreover, surface rugosity can both influence and be influenced by the population characteristics of foundation species, as it can control larval settlement, recruitment, and postrecruitment growth by altering water flow, food supply, and predation (Scharf et al. 2006; Whitman & Reidenbach 2012; Colden et al. 2017). Somewhat surprisingly, this study found little or no relationships between population characteristics and these spatial attributes, highlighting that the spatial attributes affecting densities and size are highly variable between estuaries. Restoration projects should therefore be informed by knowledge of the ecological processes relevant to the areas targeted for restoration.

Patch-connectivity indices were related to oyster densities at Crookhaven River and oyster sizes at Port Hacking, while no effect on population characteristics was found at Hunter River. At Port Hacking, isolated patches had smaller median length of oysters, but tended to have the largest oysters. Meanwhile, at Crookhaven River, oyster abundance was greater in more isolated reefs. There is a range of factors that could be explaining these patterns. For example, these differences could be driven by the different predation pressures between isolated patches, as observed by previous studies (Harwell et al. 2011; Duncan et al. 2019). In fact, lower abundances of fish were observed in more isolated patches at Crookhaven River (Erickson 2019). Moreover, differences between patches in processes such as the timing of recruitment and growth rates can also influence oyster larval and thus reef connectivity (Theuerkauf et al. 2017). Future studies are needed to disentangle these possible explanations.

Restoration strategies for oyster reefs and, by extension, the functions they perform currently rely on build-it-and-they-will-come approaches, typically putting out substrate to encourage recruitment by increasing the availability of surfaces for settlement. These efforts usually consider the material used (e.g. oyster shells, rock, concrete; Westby et al. 2019), but they seldom consider the spatial arrangement of this material (McAfee et al. 2020; Reeves et al. 2020). Restoration programs that leverage the relationships between reef configuration and

oyster characteristics may significantly enhance their outcomes. Importantly, small-scale factors (size, shape, and connectivity) related to the reefs themselves had important implications for body size and density of oysters, so integrating these aspects into reef construction—which could be easily done—should maximize the ecosystem benefits provided. Moreover, although these reef attributes were common among estuaries, often their relationships with oyster density or body size were in opposite directions. In fact, our models suggest that the reef attributes to manipulate will be dependent on the region or environmental setting, as this was the scale at which most variation in oyster body size and density occurred. These results emphasize that a “one-size-fits-all” approach to oyster reef restoration may not be appropriate. Rather, restoration efforts need to be informed by local ecological knowledge of the remnant foundation species or pilot studies at the proposed restoration site. While this adds a level of complexity to restoration efforts, our study suggests that maximizing the benefits to oyster restoration needs to consider processes acting across multiple spatial scales.

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Variation of oyster characteristics on reefs

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Supporting Information

The following information may be found in the online version of this article:

- Figure S1.** Photo depicting how burst-shot photos for photogrammetry were taken by a field assistant (Katie Erickson) for a sampled reef.
- Figure S2.** Top view of a three-dimensional mesh model of Crookhaven River Reef 4 captured from Agisoft Metashape PhotoScan photogrammetry software.
- Figure S3.** Multi-correlation plots of all patch-attributes tested in each estuary.
- Table S1.** List of estuary site, reefs, reef area, reef-shape, corresponding number of cores sampled, and range of edge-proximity within each reef.
- Table S2.** Reef area ranges and corresponding number of samples per reefs, number of reefs per area range within each estuary site, and the total number of samples per site.
- Table S3.** Formulae of patch-connectivity metrics.
- Table S4.** Output of GLMM and LMMs of oyster population characteristics as function of biovolume and estuaries as main effects.
- Table S5.** Pair-wise post hoc least square means tests with Tukey correction across estuaries with Bonferroni corrected *p*-values.
- Table S6.** Pair-wise correlation comparison between response variables to assess co-linearity among oyster population characteristics.
- Table S7.** List of noncollinear spatial attributes.
- Table S8.** Selected patch attributes from each “best” model selection for oyster density.
- Table S9.** Model outputs within $\Delta AICc < 2$ from stepwise regression of oyster density.
- Table S10.** Model outputs within $\Delta AICc < 2$ from stepwise regression of 95th percentile oyster lengths.
- Table S11.** Model outputs within $\Delta AICc < 2$ from stepwise regression of median oyster lengths.
- Supplement S1.** High-resolution mapping and photogrammetry procedure.
- Supplement S2.** Assessing co-linearity between spatial attributes in each estuary.

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Appendix B: Chapter 2 Supplementary Material

Table B.1. List of estuary site, reefs, reef area, reef-shape, corresponding number of cores sampled and range of edge-proximity within each reef. 'NM' = Not available value as reef was not mapped.

Site	Reef Number	Reef Area	Number of samples on reef	Range of edge-proximity (m)	Reef Shape	Type of 3D Model captured	Mean resolution 3D model (mm)	Model error (mm) of reef model	DEM model resolution (mm)
Crookhaven River	1	125.0	6	0.64-3.96	Irregular	Entire reef	10.61	0.41	3.40
Crookhaven River	2	85.3	6	0.68-3.18	Irregular	Entire reef	11.07	1.01	3.42
Crookhaven River	3	16.1	4	0.01-0.96	Ovoid	Entire reef	11.44	1.28	3.28
Crookhaven River	4	11.9	4	0.18-0.96	Ovoid	Entire reef	10.63	0.22	3.31
Crookhaven River	5	2072.9	14	0.38-12.00	Ovoid	Entire reef	12.99	5.90	3.74
Crookhaven River	6	90.2	6	0.16-3.14	Ovoid	Entire reef	13.78	1.06	3.70
Crookhaven River	7	147.7	8	0.36-3.11	Ovoid	Entire reef	12.21	1.48	3.62
Crookhaven River	8	545.9	10	0.38-6.38	Ovoid	Entire reef	11.31	2.63	3.52
Crookhaven River	9	453.5	10	0.02-8.36	Ovoid	Entire reef	9.78	2.07	3.52
Hunter River	1	3579.8	14	0.12-18.49	Ovoid	Reef sections (3 sections)	7.48	18.15	2.36
Hunter River	2	35.1	6	0.19-1.71	Ovoid	Entire reef	NM	NM	NM
Hunter River	3	11.6	4	0.26-0.54	Ovoid	Entire reef	NM	NM	NM

Hunter River	4	13.4	4	0.49-1.03	Ovoid	Entire reef	NM	NM	NM
Hunter River	5	40.7	6	0.14-1.88	Ovoid	Entire reef	NM	NM	NM
Hunter River	6	194.3	6	0.08-2.51	Irregular	Entire reef	NM	NM	NM
Hunter River	7	40.8	6	0.22-1.36	Ovoid	Entire reef	NM	NM	NM
Hunter River	8	11.3	4	0.11-1.08	Ovoid	Entire reef	NM	NM	NM
Hunter River	9	127.0	8	0.15-2.90	Ovoid	Entire reef	NM	NM	NM
Port Hacking	1	1179.9	10	0.16-6.22	Irregular	Entire reef	7.02	5.79	2.20
Port Hacking	2	187.0	8	0.29-3.73	Ovoid	Entire reef	7.16	1.67	2.34
Port Hacking	3	16.7	4	0.25-1.04	Ovoid	Entire reef	11.29	3.72	2.12
Port Hacking	4	89.0	6	0.08-3.73	Ovoid	Entire reef	6.82	3.80	2.16
Port Hacking	5	22.5	4	0.12-0.88	Ovoid	Entire reef	6.98	3.80	2.16
Port Hacking	6	18.8	4	0.05-0.74	Ovoid	Entire reef	6.76	3.45	2.22
Port Hacking	7	19.9	4	0.07-1.50	Ovoid	Entire reef	6.88	3.95	2.23
Port Hacking	8	25.0	6	0.30-1.60	Ovoid	Entire reef	6.87	4.59	2.20
Port Hacking	9	36.1	6	0.13-1.72	Ovoid	Entire reef	6.57	2.21	2.19
Port Hacking	10	18.6	4	0.12-0.55	Ovoid	Entire reef	6.74	4.61	2.27
Port Hacking	11	23.9	4	0.07-1.67	Ovoid	Entire reef	7.76	5.90	2.29

Table B.2. Reef area ranges and corresponding number of samples per reefs, number of reefs per area range within each estuary site and the total number of samples per site.

Reef area range (m ²)	No. of samples per reef	Number of reefs in Crookhaven River	Number of reefs in Hunter River	Number of reefs in Port Hacking
5 - 24	4	2	3	6
25 - 150	6	3	4	3
151 - 500	8	1	1	1
501-1200	10	2	0	1
1201-2000	12	0	0	0
≥2001	14	1	1	0
TOTAL SAMPLE (sample # x number of reefs)		68	58	60

Supplementary B1. High-resolution mapping and photogrammetry procedure

The mapping system consisted of two cameras (GoPro Hero 5,7 or 8s, 12MP linear FOV) mounted 30cm apart on a fixed frame which included an extendable pole and articulating joint such that the cameras could be held away from the mapper but kept parallel to the ground (See Supplementary Figure B1 below). Prior to mapping, between 2 and 8 (depending on the size of the reef) “dumbbell” scale features and 1 “triax” scale feature were placed around the site. The “dumbbell” features consisted of pairs of coded targets (Agisoft, 12bit, inverted colour, 150 mm diameter) separated by 300 mm printed as stickers and affixed to pre-cut aluminium plates. The “triax” feature included three 150mm diameter targets (as above) fixed in a triangular array such that one target was elevated (~300mm) about the others, with the entire feature being levelled on deployment. The exact position of at least one target from each feature (two for the triax) were captured with the dGPS. Mapping consisted of carefully traversing the entire reef in a regular pattern with cameras held approximately 1.5m off the ground and shooting one frame per second. Pacing was kept to ensure 80-90% overlap in neighbouring images and some larger reefs were mapped in sections to simplify logistics. Photos were processed as per Figueira et al. (2015) to create 3D models using photogrammetry software (Agisoft Metashape PhotoScan v1.1.6, 2015).

Each reef model was trimmed to remove bare sediment surrounding reef edge. All mesh models had an average mesh resolution of 8.2 mm and average model error of 4.7 mm (see Supplementary Figure B2 below). Following model trimming, models were exported as digital elevation models (DEMs) and processed in ArcGIS (v10.3, ESRI, 2016) georeferenced to Universal Transverse Mercator (UTM, Zone 56) coordinate system. Coordinates of sampled locations were loaded and overlaid on the DEMs. To estimate average surface rugosity across the sample points and their peripheral area, we created 20 cm-radius circular clipping templates surrounding each point with the ‘Buffer’ function. DEMs were then clipped based on the sampled locations. We obtained surface rugosity values independent of the surface slope by using the ‘arc-chord ratio’ (ACR) rugosity index function (Du Preez 2015) in the Benthic Terrain Modeller (BTM) plugin (v3.0; Walbridge et al., 2018).

Workflow process	Settings
Photo alignment (sparse point cloud)	High accuracy, reference preselection, Key point limit 40 000, Tie point limit 4000, no adaptive camera model fitting.
Optimising alignment	All optimisation properties except for Fit b1, Fit b2, Fit k4, Fit p3, Fit p4.
Dense point cloud	Medium quality, mild filtering.
Mesh (create 3D surface)	High face count, arbitrary surface type, source data dense cloud, interpolation enabled.
Texture (photo mapping)	Generic mapping mode, mosaic blending mode, texture size 8192, texture count 1, enable hole filling and ghosting filter.

Summary of Agisoft Metashape parameters used to build oyster reef model



Figure B.1. Photo depicting how burst-shot photos for photogrammetry were taken by a field assistant (Katie Erickson) for a sampled reef. Photo is taken by RCL in 2019.



Figure B.2. Top-view of a three-dimensional mesh model of Crookhaven River Reef 4 captured from AgiSoft PhotoScan Professional (2015, v1.1.6) Agisoft LLC, Russia. Triax scale feature can be seen in the middle of the reef model while dumbbell scale features are observed in the top and bottom side of the model.

Table B.3. Formulae of patch-connectivity metrics. Formulae adapted from McGarigal et al. (2012) and/or Hesselbarth et al. (2019).

Patch-Attribute	Formula
Nearest-neighbour distance (ENN)	$ENN = h_{ij}$ <p>h_{ij} = distance (m) from patch ij to nearest neighbouring patch of the same type (class), based on patch edge-to-edge distance, computed from cell centre to cell centre. Values were obtained 'gdistance' function and package (van Etten 2017).</p>
Mean nearest-neighbour distance (MNN)	$MNN = \text{mean}(ENN[\text{patch}_{ij}])$ <p>where ENN [patch_{ij}] is the Euclidean nearest-neighbour distance of each patch. Values were obtained from ENNs from 'gdistance' function and package (van Etten 2017).</p>
Proximity index (Prox.Index)	$PROX = \sum_{s=1}^n \frac{a_{ijs}}{b_{ijs}^2}$ <p>a_{ijs} = area (m²) of patch ijs within specified neighborhood (m) of patch ij.</p>

h_{ijs} = distance (m) between patch ijs and patch ijs , based on patch edge-to-edge distance, computed from cell centre to cell centre. (Gustafson & Parker 1992).

The proximity index was calculated using the function 'ProxIndex' in package 'spatialEco' (Evans 2015).

$$IsoIndex_i = \sum_r^R Distance_r * \frac{Area_r}{TotalArea}$$

Isolation index
(Iso.Index)

Summing the relative area-weighted distance from the focal reef (i) to all others reefs (r) in the network of R reefs, where Total Area is the sum of all reef areas in the network. (Moilanen & Nieminen 2002).

Index was calculated manually with Excel using (a) shortest distances between patches 'gdistance' function and package (van Etten 2017) and area from reef contours.

$$FRAC = \frac{2 * \ln * (0.25 * p_{ij})}{\ln a_{ij}}$$

Two-dimensional
Fractal Dimension
Index (FRAC)

Quantifies patch-shape as a metric where p_{ij} is the perimeter in meters and a_{ij} is the area in square meters. Metric is independent of scale as it is based on the standardised patch perimeter and the patch area.

Metrics range between 1 and 2 where FRAC = 1 is equivalent to square patch and FRAC = 2 is an irregular patch.

Calculated with the 'lsm_p_frac' function in 'landscapemetrics' package (Hesselbarth et al. 2019).

$$CIRCLE = 1 - \left(\frac{a_{ij}}{a_{ij}^{circle}} \right)$$

Circle (CIRCLE)

A metric that characterises the compactness of the patch and is comparable among patches and circularity of patches where a_{ij} is the area in square meters and a_{ij}^{circle} the area of the smallest circumscribing circle. a_{ij}^{circle} is calculated based upon the 'diameter' of the patch connecting the opposing corner points of the two cells that are the furthest away from each other.

Metrics range between 0 and 1 where CIRCLE = 0 is circular patch and approaches CIRCLE = 1 for a linear patch.

Calculated with the 'lsm_p_circle' function in 'landscapemetrics' package (Hesselbarth et al. 2019).

$$SHAPE = \frac{p_{ij}}{\min p_{ij}}$$

Shape Index (SHAPE)

Shape Index is a metric that measures the ratio between the perimeter of a patch p_{ij} and the hypothetical minimum perimeter of a patch.

Values range equal or more than 1 where SHAPE = 1 equates to a square patch (compact) and SHAPE >1 relates to higher complexity

of patches.

Calculated with the 'lsm_p_patch' function in 'landscapemetrics' package (Hesselbarth et al. 2019).

Table B.4. Output of GLMM and LMMs of oyster population characteristics as function of biovolume and estuaries as main effects. 'X²', 'p' and 'df' denotes Chi-square distribution value, probability, the degrees of freedom of tests respectively. Significant patch-attributes at $\alpha = 0.05$, denoted by '*'.

Predictor variables	Population characteristics (Response variables)								
	Abundance			95 th percentile length			Median length		
	df	X ²	p	df	X ²	p	df	X ²	p
Biovolume	1	1.37	0.300	1	0.04	0.839	1	0.38	0.662
Estuary	2	41.68	<0.001*	2	35.48	<0.001*	2	7.16	0.027

Table B.5. Pair-wise post-hoc Least Square Means tests with Tukey correction (Lenth 2016) across estuaries with Bonferroni corrected p-values. Statistical significance at $\alpha = 0.05$, denoted by *. CR= Crookhaven River, HR = Hunter River and PH = Port Hacking.

Response variable	Pair-wise comparison	Estimate	df	T-ratio	p
Total oyster	CR - HR	0.808	180	6.290	<0.001*
	CR - PH	0.198	180	1.774	0.182
	HR - PH	-6.109	180	-4.966	<0.001*
95th quantile length	CR - HR	0.847	26	3.596	0.004*
	CR - PH	-0.450	23	-2.113	0.109
	HR - PH	-1.297	28	-5.933	<0.001*
Median length	CR - HR	0.309	27	2.115	0.106
	CR - PH	0.326	25	2.492	0.049*
	HR - PH	0.023	27	0.168	0.986

Table B.6. Pair-wise correlation comparison between response variables to assess co-linearity amongst oyster population characteristics. Correlation coefficient (r^2) and p-value of Pearson's Correlation.

	Total oyster (Abundance)	Median length	Quartile 95 length	Standard Error length
Total oyster (Abundance)		$r^2 = -0.06$, $p = 0.416$	$r^2 = +0.31$, $p < 0.001$	$r^2 = -0.43$, $p < 0.001$
Median length			$r^2 = +0.43$, $p < 0.001$	$r^2 = +0.21$, $p < 0.001$
Quartile 95 length				$r^2 = +0.36$, $p < 0.001$
Standard Error length				

Statistics – Within Estuaries:Supplement B2. Assessing co-linearity between spatial attributes in each estuary

Prior to all model runs and selections, following methods from Zuur et al. (2009), we checked for normality of each continuous patch-attribute/covariate by assessing quantile-quantile plots and then performing data-transformations, where applicable. Some spatial attributes had been transformed prior to main analyses. Relationships between continuous co-variates across all estuaries, and within each estuary, were observed. When paired co-variates showed strong Pearson correlation coefficients ($R^2 \geq 0.7$), only one co-variate was retained for the further analysis (see Supplementary Figure iii). For co-variates presenting strong pair-wise coefficients in groups (i.e., ≥ 3 co-variates), the co-variate with the highest coefficient was retained to best represent the group. The final patch-attributes chosen for models are found in Supplementary Table S7 below. Spatial attributes removed from analysis were '*shape*' and '*Frac*' for Crookhaven, '*shape*' and '*Prox.Index*' for Hunter River and '*shape*' for Port Hacking.

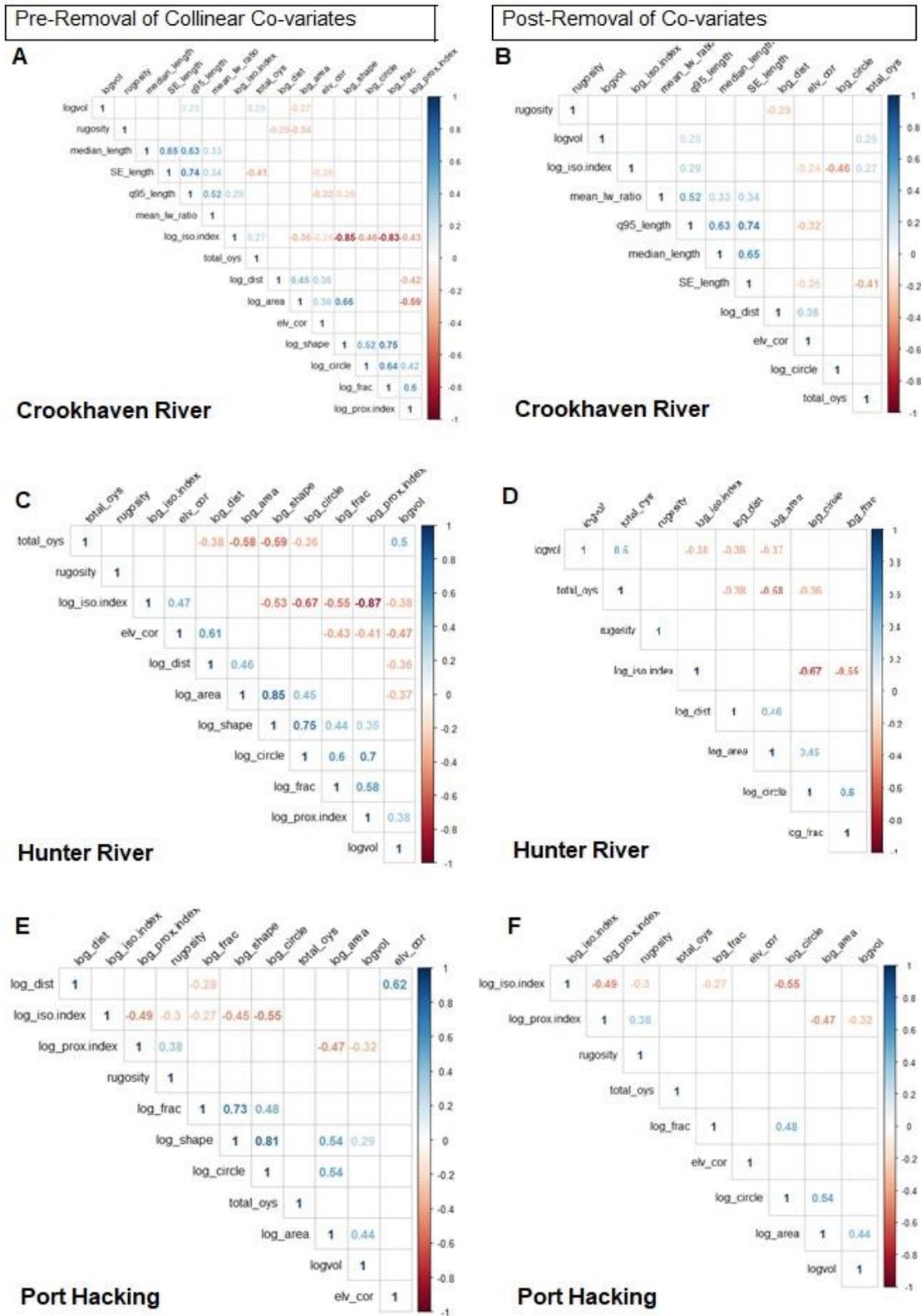


Figure B.3. Multi-correlation plots of all patch-attributes tested in each estuary before (A,C,E) and after removal (B,D,F) of collinear attributes in Crookhaven River (A&B), Hunter River (C&D) and Port Hacking (E&F). Statistically significant ($p < 0.05$) correlation coefficients are visible in grids of the plot. Correlation between oyster characteristics and patch-attributes are ignored.

Table B.7. List of non-collinear spatial attributes that have been modelled against oyster population characteristics and the type of statistical approach for each model obtained with package 'glmmTMB' (Magnusson et al. 2020) in R.

Oyster population characteristics	Model type	Estuary	Non-collinear patch-population characteristics
Abundance	GLMM with negative binomial distribution	Crookhaven River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{Prox.Index} + \text{Edge} + \text{elevation} + \text{rugosity} + (1/\text{reef_id})$
		Hunter River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{frac} + \text{Edge} + \text{elevation} + (1/\text{reef_id})$
		Port Hacking	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{frac} + \text{Iso.Index} + \text{Prox Index} + \text{Edge} + \text{elevation} + \text{rugosity} + (1/\text{reef_id})$
Size (95 th percentile length)	LMM with Gaussian distribution	Crookhaven River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{ProxIndex} + \text{Edge} + \text{elevation} + \text{rugosity} + (1/\text{reef_id})$
		Hunter River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{frac} + \text{Edge} + \text{elevation} + (1/\text{reef_id})$
		Port Hacking	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{frac} + \text{Iso.Index} + \text{Prox Index} + \text{Edge} + \text{elevation} + \text{rugosity} + (1/\text{reef_id})$
Size (Median length)	LMM with Gaussian distribution	Crookhaven River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{ProxIndex} + \text{Edge} + \text{elevation} + \text{rugosity} + (1/\text{reef_id})$
		Hunter River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{frac} + \text{Edge} + \text{elevation} + (1/\text{reef_id})$
		Port Hacking	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{frac} + \text{Iso.Index} + \text{ProxIndex} + \text{Edge} + \text{elevation} + \text{rugosity} + (1/\text{reef_id})$

Table B.8. Selected patch attributes from each 'best' model selection for oyster density, 95th percentile length in each estuary. '+' and '-' represent positive and negative estimates of selected attributes from model summaries. The initial AICc values for each model are in parentheses, below the Δ AICc of the selected model.

Estuary	Selected Attributes for Best Model			Δ AICc for Best Model (Full/Initial model AICc)		
	Abundance	95 th Percentile Length	Median Length	Abundance	95 th Percentile Length	Median Length
Crookhaven River	-Proximity index -Elevation +Biovolume	-Fractal dimension +Circle -Elevation +Biovolume	-Fractal dimension +Circle	-8.2 (692.7)	-10.7 (174.0)	-15.5 (109.5)
Hunter River	-Area -Elevation -Fractal dimension +Biovolume	-Elevation +Biovolume	-Isolation index	-12.5 (347.6)	-14.6 (102.4)	-20.7 (77.7)
Port Hacking	+Elevation -Biovolume	+Isolation index + Circle +Fractal dimension -Biovolume	-Isolation index -Proximity index -Area	-12.9 (608.3)	-7.0 (179.4)	-11.1 (112.2)

Table B.9. Model outputs within $\Delta AICc < 2$ from step-wise regression of oyster density (abundance per core) against non-collinear patch-attributes (columns in blue). For each estuary, each row represents a selected model from the best model, with the lowest AICc (italicised and top row) followed by the subsequent models within $\Delta AICc < 2$. Selected patch attributes in each model are noted with a coefficient estimate with '-' denoting a negative estimate of oyster density. Non-selected attributes are denoted as 'NA' per model. Grey columns denote significant co-linear attributes and rugosity (insufficient data points; only for Hunter River) that were omitted from the step-wise regressions (as per Table B7). Weight represents proportional weight of a model in relation to all the model combinations during step-wise regression.

Area	Circle	Edge	Elevation	Frac	Iso.Index	Prox. Index	Rugosity	Biovolume	df	logLik	AICc	$\Delta AICc$	Weight
Crookhaven River													
NA	NA	NA	-0.66068	NA		-0.12178	NA	0.001497	6	-336.703	686.8058	0	0.069602
NA	NA	NA	-0.64013	NA		-0.13655	0.094138	0.001498	7	-336.332	688.562	1.756216	0.028924
NA	NA	NA	-0.56891	NA		NA	NA	0.001394	5	-338.797	688.5769	1.771119	0.028709
NA	NA	-0.06041	-0.59649	NA		-0.13902	NA	0.001419	7	-336.365	688.6287	1.822899	0.027975
NA	NA	NA	-0.6833	NA		-0.11325	NA	NA	5	-338.869	688.7218	1.916053	0.026702
Hunter River													
-0.28801		NA	-0.72174	-1.07719	NA			NA	6	-251.365	516.3778	0	0.098712
-0.27629		NA	-0.55027	NA	NA			NA	5	-252.66	516.4744	0.096683	0.094054
-0.27014		NA	-0.65741	-1.09122	NA			0.001541	7	-250.197	516.633	0.255298	0.086883
-0.26226		NA	-0.48737	NA	NA			0.001426	6	-251.759	517.1645	0.786702	0.06661
-0.30784		NA	NA	NA	NA			0.001684	5	-253.327	517.8083	1.430583	0.048275
-0.33009		NA	NA	NA	NA			NA	4	-254.551	517.8575	1.479722	0.047104
-0.28185		-0.15385	NA	NA	NA			NA	5	-253.428	518.0103	1.632515	0.043639
Port Hacking													
NA	NA	NA	0.714819	NA	NA	NA	NA	-0.00445	5	-312.828	636.8101	0	0.043005
NA	0.66819	NA	0.714484	NA	NA	NA	NA	-0.00498	6	-311.875	637.3969	0.58678	0.03207
NA	1.282226	NA	0.693173	NA	0.820435	NA	NA	-0.00527	7	-310.692	637.6235	0.813407	0.028634
NA	1.835467	NA	0.642133	NA	1.533752	0.288861	NA	-0.00464	8	-309.569	638.0764	1.266321	0.022832
NA	NA	NA	NA	NA	NA	NA	NA	-0.00401	4	-314.756	638.2667	1.456594	0.02076
NA	2.820124	NA	NA	-1.27227	2.025738	0.44108	NA	-0.0046	8	-309.731	638.4014	1.591301	0.019407
NA	NA	NA	0.78156	NA	NA	NA	-0.20266	-0.00476	6	-312.387	638.4219	1.611757	0.01921
NA	NA	0.209386	NA	NA	NA	NA	NA	-0.00437	5	-313.687	638.5278	1.717672	0.018219

NA	0.752437	0.237585	NA	NA	NA	NA	NA	-0.00502	6	-312.48	638.608	1.797913	0.017503
NA	1.932784	NA	NA	NA	1.671909	0.328758	NA	-0.00422	7	-311.254	638.7488	1.938674	0.016313

Table B.10. Model outputs within $\Delta AICc < 2$ from step-wise regression of 95th percentile oyster lengths against non-collinear patch-attributes (columns in blue). For each estuary, each row represents a selected model from the best model, with the lowest AICc (italicised and top row) followed by the subsequent models within $\Delta AICc < 2$. Selected patch attributes in each model are noted with a coefficient estimate with ‘-’ denoting a negative estimate of oyster lengths. Non-selected attributes are denoted as ‘NA’ per model. Grey columns denote significant co-linear attributes and rugosity (insufficient data points; only for Hunter River) that were omitted from the step-wise regressions (as per Supplementary Figure 3). Weight represents proportional weight of a model in relation to all the model combinations during step-wise regression.

Area	Circle	Edge	Elevation	Frac	Iso.Index	Prox. Index	Rugosity	Biovolume	df	logLik	AICc	$\Delta AICc$	weight
Crookhaven River													
NA	<i>0.812266</i>	NA	-1.88762	-1.94918		NA	NA	NA	6	-75.9852	165.3704	0	0.181252
NA	NA	NA	-1.86617	-1.4851		NA	NA	NA	5	-77.5494	166.0824	0.711996	0.126962
NA	-0.54432	NA	-1.76123	NA		NA	NA	NA	5	-78.1068	167.1972	1.826827	0.07271
Hunter River													
NA		NA	-1.59303	NA	NA			NA	4	-64.8005	138.3558	0	0.287776
NA		NA	-1.5152	0.423477	NA			NA	5	-63.6828	138.5195	0.163684	0.265162
Port Hacking													
NA	<i>0.255223</i>	NA	NA	1.928971	0.977094	NA	NA	NA	6	-85.7034	185.0539	0	0.031017
NA	NA	NA	NA	2.060114	0.862359	NA	NA	NA	5	-86.97	185.0938	0.039912	0.030404
NA	NA	NA	NA	1.707144	NA	NA	NA	NA	4	-88.2519	185.2585	0.204562	0.028002
NA	-0.38672	NA	NA	1.97701	NA	NA	NA	NA	5	-87.1243	185.4025	0.34861	0.026056
NA	0.27807	NA	-0.06618	1.908339	0.984006	NA	NA	NA	7	-84.9496	186.1391	1.085206	0.018028
NA	NA	NA	-0.03286	2.055698	0.86069	NA	NA	NA	6	-86.2484	186.1439	1.090015	0.017985
NA	NA	NA	-0.06425	1.699846	NA	NA	NA	NA	5	-87.5308	186.2155	1.1616	0.017353
NA	-0.38336	NA	-0.01212	1.973292	NA	NA	NA	NA	6	-86.379	186.405	1.351099	0.015784
NA	0.814839	-0.37689	NA	1.199856	1.265171	NA	NA	NA	7	-85.2396	186.7192	1.665264	0.01349
NA	-0.73207	NA	NA	2.415218	0.029505	-0.35701	NA	NA	7	-85.2485	186.737	1.683112	0.01337
NA	1.105815	NA	NA	NA	1.032783	NA	NA	NA	5	-87.8489	186.8516	1.797649	0.012626
NA	0.816127	-0.56194	0.792192	1.08883	1.323887	NA	NA	NA	8	-83.988	186.9148	1.860915	0.012232
NA	NA	-0.31719	NA	1.688489	0.893078	NA	NA	NA	6	-86.6984	187.0438	1.989897	0.011468
NA	-0.75758	NA	NA	2.424056	NA	-0.363	NA	NA	6	-86.7004	187.0478	1.993906	0.011445

Table B.11. Model outputs within $\Delta\text{AICc} < 2$ from step-wise regression of median oyster lengths against non-collinear patch-attributes (columns in blue). For each estuary, each row represents a selected model from the best model, with the lowest AICc (italicised and top row) followed by the subsequent models within $\Delta\text{AICc} < 2$. Selected patch attributes in each model are noted with a coefficient estimate with '-' denoting a negative estimate of oyster lengths. Non-selected attributes are denoted as 'NA' per model. Grey columns denote significant co-linear attributes and rugosity (insufficient data points; only for Hunter River) that were omitted from the step-wise regressions (as per Supplementary Figure 3). Weight represents proportional weight of a model in relation to all the model combinations during step-wise regression.

Area	Circle	Edge	Elevation	Frac	Iso.Index	Prox. Index	Rugosity	Biovolume	df	logLik	AICc	ΔAICc	weight
Crookhaven River													
NA	<i>0.010189</i>	NA	NA	-0.02591		NA	NA	NA	5	-41.4779	93.93935	0	0.100591
NA	NA	NA	NA	NA		NA	NA	NA	3	-43.8002	93.9813	0.041956	0.098503
NA	-0.02075	NA	NA	NA		NA	NA	NA	4	-42.7962	94.23754	0.298194	0.086658
NA	NA	NA	NA	-0.01233		NA	NA	NA	4	-42.8653	94.37581	0.436463	0.080869
NA	NA	NA	-0.38107	NA		NA	NA	NA	4	-43.3863	95.4178	1.478458	0.048030
NA	0.059811	NA	-0.30315	-0.06548		NA	NA	NA	6	-41.1917	95.78341	1.844064	0.040006
NA	0.002278	NA	-0.34266	NA		NA	NA	NA	5	-42.4495	95.88264	1.943299	0.038069
Hunter River													
NA		NA	NA	NA	-0.62754			NA	4	-39.0156	86.78599	0	0.371762
NA		NA	NA	NA	-0.61948			NA	5	-38.3547	87.86333	1.077333	0.216933
Port Hacking													
-0.58429	NA	NA	NA	NA	-1.3615	-0.79501	NA	NA	6	-45.3983	104.4438	0	0.100447
-0.56322	-0.40613	NA	NA	NA	-1.64184	-0.84295	NA	NA	7	-44.6483	105.5365	1.092768	0.058163
-0.60448	NA	NA	NA	-0.25537	-1.4616	-0.81637	NA	NA	7	-44.8557	105.9513	1.507565	0.047269
-0.54189	NA	NA	-0.38997	NA	-1.29044	-0.75974	NA	NA	7	-44.9209	106.0817	1.637988	0.044285

Appendix C: Chapter 3 Supplementary Material

Table C.1. List of epifauna species and the taxa count sampled in each estuary.

Taxa	Major taxa group	Number of individuals			
		Crookhaven River	Hunter River	Port Hacking	Grand Total
<i>Omobranchus anolius</i>	Actinopterygii	0	1	2	3
<i>Trichomya hirsuta</i>	Bivalvia	30	6	103	139
<i>Laseae australis</i>	Bivalvia	3539	3	494	4036
<i>Mytilus</i> sp.	Bivalvia	11	5	1	17
<i>Irus crenatus</i>	Bivalvia	174	21	28	223
<i>Musculus impactus</i>	Bivalvia	25	0	1	26
<i>Plebidonax</i> sp.	Bivalvia	1	0	0	1
Actiniaria	Cnidaria	1878	0	0	1878
Corophiidae	Crustacea	6	835	2	843
Dexaminidae	Crustacea	0	0	2	2
Munnidae	Crustacea	52	0	1	53
Hyalidae	Crustacea	50	51	0	101
<i>Hippolyte</i> sp.	Decapoda	0	0	1	1
Cirripedia	Crustacea	174	5562	15411	21147
<i>Dynoides barnadii</i>	Crustacea	2	4	0	6
<i>Eurylana arcuata</i>	Crustacea	2	0	0	2
<i>Pilumnopeus serratifrons</i>	Decapoda	33	174	97	304
<i>Majidae</i> sp.	Decapoda	0	0	2	2
Chironomidae	Diptera	48	0	13	61
<i>Ophiactis</i> sp.	Echinodermata	0	0	2	2
<i>Parvulastra exigua</i>	Echinodermata	0	0	6	6
<i>Bembicium auratum</i>	Gastropoda	1094	1477	1325	3896

<i>Pseudoliotia micans</i>	Gastropoda	35	8	17	60
<i>Afrolittorina acutispira</i>	Gastropoda	524	6	126	656
<i>Turbonilla portseaensis</i>	Gastropoda	0	0	3	3
Cerithiidae	Gastropoda	11	0	50	61
<i>Bedevea paivae</i>	Gastropoda	0	0	17	17
<i>Tenguella marginalba</i>	Gastropoda	16	0	8	24
<i>Bembicium nanum</i>	Gastropoda	12	0	1	13
<i>Austrocochlea porcata</i>	Gastropoda	76	0	5	81
<i>Nerita melanotragus</i>	Gastropoda	35	0	1	36
<i>Laemodonta typica</i>	Gastropoda	0	0	14	14
<i>Diala megapicalis</i>	Gastropoda	0	0	6	6
<i>Amphithalamus jacksoni</i>	Gastropoda	0	0	1	1
<i>Mitrella semiconvexa</i>	Gastropoda	0	0	2	2
<i>Eurytrochus strangei</i>	Gastropoda	6	0	0	6
<i>Patelloida mimula</i>	Gastropoda	2736	1988	556	5280
<i>Diodora lineata</i>	Gastropoda	0	0	1	1
<i>Montfortula rugosa</i>	Gastropoda	8	0	2	10
<i>Patelloida latistrigata</i>	Gastropoda	12	0	0	12
<i>Melanella acicula</i>	Gastropoda	0	0	1	1
<i>Rissoina angasii</i>	Gastropoda	0	0	2	2
<i>Eutriphora tricolor</i>	Gastropoda	0	0	4	4
Triphoridae	Gastropoda	0	0	3	3
<i>Coriophora fusca</i>	Gastropoda	0	0	13	13
Pyramellidae	Gastropoda	0	0	1	1
<i>Circulus lodderae</i>	Gastropoda	0	0	1	1
<i>Batillaria australis</i>	Gastropoda	0	0	11	11
Trochidae	Gastropoda	0	0	1	1
<i>Finella pupoides</i>	Gastropoda	0	0	1	1

<i>Cingulina</i> sp.	Gastropoda	0	0	6	6
<i>Nassarius</i> sp.	Gastropoda	12	0	14	26
<i>Rissoella micra</i>	Gastropoda	1	0	0	1
<i>Austrocochlea constricta</i>	Gastropoda	22	0	0	22
<i>Merelina cheilostoma</i>	Gastropoda	0	0	4	4
<i>Leuconopsis inermis</i>	Gastropoda	21	0	7	28
<i>Diala sulcifera scobi</i>	Gastropoda	1	0	12	13
<i>Merelina</i> sp.	Gastropoda	1	0	13	14
<i>Nassarius burchardi</i>	Gastropoda	1	0	1	2
<i>Austrolittorina unifasciata</i>	Gastropoda	37	0	16	53
Nemertea	Nemertea	44	25	18	87
<i>Onchidina australis</i>	Onchidiinae	18	0	0	18
<i>Imogine mcgrathi</i>	Platyhelminthes	16	11	4	31
<i>Stylochus</i> sp.	Platyhelminthes	8	0	0	8
<i>Galeolaria caespitosa</i>	Polycheata	725	0	2	727
Orbiniidae	Polycheata	0	0	1	1
Phyllodocidae	Polycheata	7	0	1	8
Lumbrineridae	Polycheata	10	0	0	10
Terebellidae	Polycheata	0	0	8	8
Capitellidae	Polycheata	0	0	60	60
<i>Pseudopotamilla</i> sp.	Polycheata	1	0	1	2
Cirratulidae	Polycheata	10	0	2	12
<i>Ficopomatus enigmaticus</i>	Polycheata	0	1	0	1
Syllidae	Polycheata	118	0	161	279
<i>Harmothoe praeclara</i>	Polycheata	0	0	17	17
<i>Nephtyid australiensis</i>	Polycheata	2	10	3	15
Nereididae	Polycheata	34	78	41	153

<i>Polydora</i> sp.	Polycheata	2746	468	1598	4812
<i>Acanthochitona retrojecta</i>	Polyplacophora	9	0	10	19
<i>Sypharochiton pelliserpentis</i>	Polyplacophora	2	0	0	2
Sipunculid	Sipunculida	71	21	55	147
Asciacea	Tunicata	554	0	39	593
TOTAL NUMBER OF INDIVIDUALS					46249

Table C.2. List of non-collinear spatial attributes that have been modelled against univariate community indices (epifaunal abundance, taxa richness, Shannon Index, taxa evenness) and the type of statistical approach for each model obtained with package 'glmmTMB' (Magnusson et al. 2020) in R.

Oyster population characteristics	Model type	Estuary	Non-collinear patch-population characteristics
Epifauna Abundance	GLMM with negative binomial distribution	Crookhaven River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{Prox.Index} + \text{Edge} + \text{mean_lw_ratio} + \text{elevation} + \text{rugosity} + (1 \text{reef_id})$
		Hunter River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{frac} + \text{mean_lw_ratio} + \text{Edge} + \text{elevation} + (1 \text{reef_id})$
		Port Hacking	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{frac} + \text{Iso.Index} + \text{Prox.Index} + \text{Edge} + \text{mean_lw_ratio} + \text{elevation} + \text{rugosity} + (1 \text{reef_id})$
Taxa Richness	GLMM with negative binomial distribution	Crookhaven River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{Prox.Index} + \text{Edge} + \text{mean_lw_ratio} + \text{elevation} + \text{rugosity} + (1 \text{reef_id})$
		Hunter River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{frac} + \text{mean_lw_ratio} + \text{Edge} + \text{elevation} + (1 \text{reef_id})$
		Port Hacking	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{frac} + \text{Iso.Index} + \text{Prox.Index} + \text{Edge} + \text{mean_lw_ratio} + \text{elevation} + \text{rugosity} + (1 \text{reef_id})$
Shannon Index	LMM with Gaussian distribution	Crookhaven River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{Prox.Index} + \text{Edge} + \text{mean_lw_ratio} + \text{elevation} + \text{rugosity} + (1 \text{reef_id})$
		Hunter River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{frac} + \text{mean_lw_ratio} + \text{Edge} + \text{elevation} + (1 \text{reef_id})$
		Port Hacking	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{frac} + \text{Iso.Index} + \text{Prox.Index} + \text{Edge} + \text{mean_lw_ratio} + \text{elevation} + \text{rugosity} + (1 \text{reef_id})$
Taxa Evenness	LMM with Gaussian distribution	Crookhaven River	$\sim \text{biovolume} + \text{circle} + \text{area} + \text{Iso.Index} + \text{Prox.Index} + \text{Edge} + \text{mean_lw_ratio} + \text{elevation} + \text{rugosity} + (1 \text{reef_id})$

Hunter River	<i>~ biovolume + circle + area + Iso.Index + frac + mean_lw_ratio + Edge + elevation + (1/reef_id)</i>
Port Hacking	<i>~ biovolume + circle + area + frac + Iso.Index + Prox Index + Edge + mean_lw_ratio + elevation + rugosity + (1/reef_id)</i>

Table C.3. Selected attributes from each 'best' model selection for univariate community indices in each estuary. '+' and '-' represent positive, negative estimates of selected attributes from model summaries. '*' represents statistical significance of attribute in best model at $\alpha = 0.05$.

Estuary	Selected Attributes for Best Model				Δ AICc for Best Model (Full/Initial model AICc)			
	Epifauna Abundance	Taxon Richness	Shannon Index	Taxon Evenness	Epifauna Abundance	Taxon Richness	Shannon Index	Taxon Evenness
Crookhaven River	-Area* -Iso.Index* -Prox.Index* +Biovolume*	-Circle -Elevation -Iso.Index -MLWR* +Rugosity +Biovolume	(None)	(None)	-11.3 (777.7)	-1.8 (342.9)	-35.6 (27.2)	-57.7 (-105.8)
Hunter River	+Elevation* +Area* -Frac*	+Elevation* -Edge* -Frac* +MLWR*	+Frac*	+Frac*	-9.5 (480.4)	-7.5 (137.6)	-26.2 (46.3)	-37.9 (0.9)
Port Hacking	+Elevation*	-Elevation* -Rugosity +MLWR +Area* -Frac -Iso.Index +Biovolume *	+Area*	+Elevation* -Biovolume*	-11.3 (542.3)	-0.5 (289.7)	-30.5 (16.2)	-39.9 (-77.9)

Table C.4. Multivariate analysis on assemblage structure with biovolume and estuary as predictor variables. “*” represents statistical significance of attribute in best model at $\alpha = 0.05$.

Attribute	Residual df	Df.diff	X ²	p-value
Biovolume	184	1	368.0438	0.001
Estuary	182	2	2357.2541	0.002*

Table C.5. The 27 taxa that contributed to the differences in assemblage structure amongst the estuaries through univariate p-value adjusted generalised linear model. Highlighted taxa in grey and their means and standard errors per estuary were presented in Figure 3.3.

Taxon	Percentage Contribution to Estuary
<i>Austrocochlea constricta</i>	0.7
<i>Batillaria australis</i>	0.8
<i>Bedevea paivae</i>	0.9
<i>Cerithiidae</i>	1.0
<i>Bembicium auratum</i>	1.1
<i>Irus crenatus</i>	1.2
<i>Capitellidae</i>	1.2
<i>Musculus impactus</i>	1.3
<i>Onchidina australis</i>	1.3
<i>Chironomidae</i>	1.5
<i>Nerita melanotragus</i>	1.5
<i>Harmothoe praeclara</i>	1.6
<i>Munnidae</i>	1.8
<i>Hyalidae</i>	1.9
<i>Trichomya hirsuta</i>	1.9
<i>Austrocochlea porcata</i>	2.2
<i>Afrolittorina acutispira</i>	2.4
<i>Polydora sp</i>	3.4
<i>Galeolaria caespitosa</i>	3.5
<i>Pilumnopus serratifrons</i>	3.5
<i>Ascidacea</i>	3.8
<i>Syllidae</i>	4.3
<i>Patelloida mimula</i>	6.7
<i>Laseae australis</i>	6.9
<i>Corophiidae</i>	8.4
<i>Cirripecta</i>	10.9
<i>Actiniaria</i>	10.9

Table C.6. Selected patch-attributes from step-wise model selection for assemblage structure for each estuary. Change in corrected AIC (ΔAICc) from full to best model selection is reported. The most significant taxa that contributed to the selected of the patch attribute for each estuary were also listed based on correlation tests between taxa abundance and the selected patch attribute. Pearson's correlation tests with significant p-adjusted value (i.e. $p < 0.05$; denoted as *) and marginal significance value (i.e. $0.05 \leq p < 0.10$; denoted as ^) were calculated with their correlation coefficient (r) reported.

Estuary	Selected Patch-attributes from best model	ΔAICc for Best Model (Full/Initial model AICc)	Most prominent taxa per estuary	Pearson's Correlation coefficient (r) and p-adjusted-significance (p) to ordination
Crookhaven River	Surface elevation	-588.11 (8719.01)	<i>Trichoyma hirscuta</i> <i>Lasea australis</i>	$r = -0.45, p = 0.024^*$ $r = +0.36, p = 0.087^{\wedge}$
Hunter River	NIL	-821.08 (4693.66)	NIL	NIL
Port Hacking	Surface elevation	-589.97 (5904.47)	<i>Pseudoliotia micans</i>	$r = -0.23, p = 0.053^{\wedge}$

Table C.7. Model outputs within $\Delta AICc < 2$ from step-wise regression of total epifauna against non-collinear patch-attributes (columns in blue). For each estuary, each row represents a selected model from the best model, with the lowest AICc (italicised and top row) followed by the subsequent models within $\Delta AICc < 2$. Selected patch attributes in each model are noted with a coefficient estimate with ‘-’ denoting a negative estimate of total epifauna. Non-selected attributes are denoted as ‘NA’ per model. Grey columns denote significant co-linear attributes and rugosity (insufficient data points; only for Hunter River) that were omitted from the step-wise regressions (as per Table C.2). Weight represents proportional weight of a model in relation to all the model combinations during step-wise regression.

Area	Circle	Edge	Elevation	Frac	Iso. Index	Prox. Index	Rugosity	Mean_lw_ratio	Biovol	df	logLik	AICc	$\Delta AICc$	Weight
Crookhaven River														
-0.44706	NA	NA	NA		-1.27116	-0.39205	NA	NA	1.451026	7	-375.233	766.3639	0	0.109223
-0.40037	NA	NA	NA		-1.10176	-0.33547	NA	-0.27341	1.442858	8	-374.588	767.6588	1.294944	0.057164
Hunter River														
NA		NA	0.425668	NA	NA			NA	NA	4	-336.273	681.3	0	0.06632
NA		0.177379	0.352463	NA	NA			NA	NA	5	-335.266	681.686	0.385992	0.05468
NA		NA	0.424453	NA	-0.51997			NA	NA	5	-335.494	682.1428	0.842739	0.043516
NA		NA	0.365816	-6.47834	-0.79479			NA	NA	6	-334.336	682.3199	1.019848	0.039828
-0.2722		0.22374	0.320163	-8.95208	-1.04495			NA	NA	8	-331.725	682.3896	1.089583	0.038463
NA		0.176163	0.352781	NA	-0.54348			NA	NA	6	-334.492	682.6313	1.331232	0.034086
NA		NA	0.461311	NA	NA			NA	0.640798	5	-335.857	682.8669	1.566863	0.030298
-0.19762		NA	0.391176	-8.12345	-0.95074			NA	NA	7	-333.357	682.954	1.653998	0.029006
NA		0.172618	0.303304	-6.60192	-0.81898			NA	NA	7	-333.368	682.9766	1.676536	0.028681
NA		NA	0.40439	-3.00678	NA			NA	NA	5	-336.031	683.2149	1.914867	0.025459
Port Hacking														
0.061122		NA	0.217999	NA	NA	NA	-0.22265	NA	1.828858	7	-277.12	570.4797	0	0.087434
0.058522		NA	0.203448	NA	NA	NA	NA	NA	1.89305	6	-278.749	571.1446	0.664861	0.062706
0.064507		NA	0.218583	0.28791	NA	NA	-0.22144	NA	1.820859	8	-276.654	572.2469	1.76718	0.036136
0.052984		0.035825	0.15152	NA	NA	NA	NA	NA	1.891059	7	-278.029	572.2989	1.819227	0.035208
0.056811		0.026385	0.178319	NA	NA	NA	-0.2014	NA	1.833326	8	-276.723	572.3844	1.904689	0.033735

Table C.8. Model outputs within $\Delta AICc < 2$ from step-wise regression of taxa richness against non-collinear patch-attributes (columns in blue). For each estuary, each row represents a selected model from the best model, with the lowest AICc (italicised and top row) followed by the subsequent models within $\Delta AICc < 2$. Selected patch attributes in each model are noted with a coefficient estimate with '-' denoting a negative estimate of taxa richness. Non-selected attributes are denoted as 'NA' per model. Grey columns denote significant co-linear attributes and rugosity (insufficient data points; only for Hunter River) that were omitted from the step-wise regressions (as per Table C.2). Weight represents proportional weight of a model in relation to all the model combinations during step-wise regression.

Area	Circle	Edge	Elevation	Frac	Iso. Index	Prox. Index	Rugosity	Mean_lw_ratio	Biovol	df	logLik	AICc	$\Delta AICc$	Weight
Crookhaven River														
NA	-2.47048	NA	-3.29234		-0.08011	NA	2.71175	-5.37587	8.72692	9	-159.986	341.1292	0	0.060045
-1.26205	0.51353	NA	-3.2719		-2.58934	-	2.36497	-4.80097	7.977773	11	-157.48	341.7592	0.63001	0.04382
NA	-2.34668	NA	-3.27014		NA	NA	2.73091	-5.39706	8.667123	8	-161.655	341.7929	0.663722	0.043088
NA	-2.9543	-0.31095	-2.90082		-0.10743	NA	2.16575	-5.20047	8.498652	10	-159.179	342.2862	1.157037	0.033669
NA	-1.95975	NA	-3.48893		-0.31201	-	3.07276	-5.33137	8.894719	10	-159.243	342.4147	1.285529	0.031574
-0.01349	-2.47282	NA	-3.27895		-0.09138	NA	2.68385	-5.37271	8.707667	10	-159.354	342.6366	1.507421	0.028258
NA	-2.78624	-0.30951	-2.8729		NA	NA	2.19394	-5.22966	8.419613	9	-160.857	342.871	1.741842	0.025133
-1.15362	-0.00471	-0.36523	-2.93174		-2.54497	-	1.97003	-4.61765	7.874698	12	-156.577	342.9308	1.801625	0.024393
NA	-2.47048	NA	-3.29234		-0.08011	NA	2.71175	-5.37587	8.72692	9	-159.986	341.1292	0	0.060045
Hunter River														
NA		-1.11846	0.748847	-10.5353	NA			1.607622	2.523143	8	-95.6111	210.1609	0	0.102945
NA		-0.98447	NA	-18.607	-0.91833			2.222412	1.566516	8	-95.649	210.2367	0.075865	0.099113
NA		-0.967	NA	-14.1008	NA			2.07351	2.176112	7	-97.038	210.3159	0.155054	0.095265
NA		-1.10544	0.626471	-14.1444	-0.61676			1.78376	2.057023	9	-94.6333	211.0166	0.855762	0.067108
NA		-1.07891	0.828982	-10.3928	NA			NA	2.825111	7	-97.5056	211.2511	1.090252	0.059684
NA		-1.06685	NA	-18.9944	-1.07702			2.45073	NA	7	-97.5468	211.3336	1.1727	0.057274
NA		-0.89278	NA	-14.4189	NA			NA	2.528625	6	-99.2447	212.1365	1.975618	0.038336
Port Hacking														
2.576381		NA	-6.33748	-9.50086	-0.17023	NA	-0.06048	0.039226	18.16009	10	-141.426	307.5336	0	0.083124
2.601656		NA	-6.33976	-9.42123	-0.07968	0.05290	-0.11329	0.034543	18.16989	11	-139.914	307.5667	0.033042	0.081762
2.56545		0.071043	-6.43802	-9.30888	-0.17435	NA	-0.00681	0.01288	18.1916	11	-140.145	308.0288	0.495171	0.064894
2.586778		0.06718	-6.43443	-9.254	-0.09984	0.04339	-0.05305	0.010471	18.19793	12	-138.616	308.165	0.631394	0.060621

2.584964		NA	-6.33649	-9.31854	NA	NA	0.00896	-0.02983	18.19919	9	-143.673	309.0967	1.563028	0.038047
2.574458		0.069608	-6.43498	-9.12612	NA	NA	0.06319	-0.05728	18.23099	10	-142.402	309.4849	1.951257	0.031334
2.60109		NA	-6.33405	-9.43375	-0.07052	0.05332	-0.11469	NA	18.1911	10	-142.423	309.5269	1.993319	0.030682

Table C.9. Model outputs within $\Delta AICc < 2$ from step-wise regression of Shannon Index against non-collinear patch-attributes (columns in blue). For each estuary, each row represents a selected model from the best model, with the lowest AICc (italicised and top row) followed by the subsequent models within $\Delta AICc < 2$. Selected patch attributes in each model are noted with a coefficient estimate with '-' denoting a negative estimate of Shannon Index. Non-selected attributes are denoted as 'NA' per model. Grey columns denote significant co-linear attributes and rugosity (insufficient data points; only for Hunter River) that were omitted from the step-wise regressions (as per Table C.2). Weight represents proportional weight of a model in relation to all the model combinations during step-wise regression.

Area	Circle	Edge	Elevation	Frac	Iso. Index	Prox. Index	Rugosity	Mean_lw_ratio	Biovol	df	logLik	AICc	$\Delta AICc$	Weight
Crookhaven River														
<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>		<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	3	7.38769	-8.39444	0	0.198459
NA	NA	NA	-0.2902739		NA	NA	NA	NA	NA	4	7.79642	-6.94768	1.446757	0.096275
NA	NA	NA	NA		NA	NA	NA	NA	0.332281	4	7.73276	-6.82038	1.574061	0.090338
Hunter River														
<i>NA</i>		<i>NA</i>	<i>NA</i>	1.82479	<i>NA</i>			<i>NA</i>	<i>NA</i>	4	-6.65139	22.0575	0	0.304774
NA		NA	NA	1.69769	NA			NA	0.379091	5	-6.4397	24.03324	1.975743	0.113488
Port Hacking														
<i>0.133344</i>		<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	4	12.9575	-17.1603	0	0.200405
0.135155		NA	NA	0.19550	NA	NA	NA	NA	NA	5	13.4493	-15.7448	1.415472	0.098751

Table C.10. Model outputs within $\Delta\text{AICc} < 2$ from step-wise regression of taxon evenness against non-collinear patch-attributes (columns in blue). For each estuary, each row represents a selected model from the best model, with the lowest AICc (italicised and top row) followed by the subsequent models within $\Delta\text{AICc} < 2$. Selected patch attributes in each model are noted with a coefficient estimate with '-' denoting a negative estimate of taxon evenness. Non-selected attributes are denoted as 'NA' per model. Grey columns denote significant co-linear attributes and rugosity (insufficient data points; only for Hunter River) that were omitted from the step-wise regressions (as per Table C.2). Weight represents proportional weight of a model in relation to all the model combinations during step-wise regression.

Area	Circle	Edge	Elevation	Frac	Iso. Index	Prox. Index	Rugosity	Mean_lw_ratio	Biovol	df	logLik	AICc	ΔAICc	Weight
Crookhaven River														
NA	NA	NA	NA		NA	NA	NA	NA	NA	3	84.92139	-163.462	0	0.641403
Hunter River														
NA		NA	NA	1.19892	NA			NA	NA	4	36.77466	-64.7946	0	0.46086
NA		NA	NA	NA	NA			NA	NA	3	34.78085	-63.1172	1.677362	0.199221
Port Hacking														
NA		NA	0.12063	NA	NA	NA	NA	NA	-0.2431	5	70.09066	-129.027	0	0.148841
NA		NA	NA	NA	NA	NA	NA	NA	-0.25449	4	68.67281	-128.591	0.436585	0.119651
NA		0.051538	NA	NA	NA	NA	NA	NA	-0.25241	5	69.84238	-128.531	0.496571	0.116116
NA		NA	0.128661	NA	NA	NA	NA	NA	NA	4	68.33225	-127.91	1.117696	0.085117
NA		NA	NA	NA	NA	NA	NA	NA	NA	3	67.08894	-127.733	1.294046	0.077933

Appendix D: Chapter 4 Supplementary Material

Table D.1. No of tiles per reef and estuary according to reef area.

Estuary	Reef (reef_id)	Reef area (m ²)	Number of settlement tiles setup
Crookhaven River	4	16.12	4
	5	11.92	4
	6	2072.90	24
	7	90.23	9
	8	147.70	18
	9	545.87	24
	10	453.50	24
Port Hacking	1A	648.52	36
	1B	223.07	27
	2	186.98	18
	7	22.48	6
	9	19.86	6
	10	24.89	8
	13	23.85	6
Hunter River	1	3579.76	47
	2	35.15	6
	3	11.58	4
	4	13.41	4
	5	40.68	6
	6	42.36	12
	7	40.78	6
	8	11.33	6
	9	186.00	12

Appendix D1 Correlation between benthic cover groups for recruitment tiles retrieved at the end of the *S. glomerata* recruitment period

Benthic cover for each benthos category (barnacle, dead oyster, live oyster, bare tile, crustose corraline algae (CCA) and turf algae were identified on 50-randomly assigned annotation points on image of the tile using Coral Point Count with Excel extensions (CPCe) by Kohler (2016). The percentage cover for each category was calculated based on proportions the annotated points and converted to percentages.

Table D.2. Multiple pair-wise Pearson's correlation tests (coefficients and p-values reported as r and p respectively) between each benthic cover were calculated and tabulated as below.

	Barnacle	Dead Oyster	Live Oyster	Bare tile	CCA	Turf Algae
Dead Oyster	r= +0.02 p= 0.545					
Live Oyster	r=-0.06 p= 0.032	r= -0.20 p= 0.775				
Bare tile	r= -0.24 p= 0.514	r= -0.11 p= 0.234	r=-0.44 p= 0.346			
CCA	r= -0.05 p= 0.112	r=-0.08 p= 0.118	r=-0.12 p= 0.433	r= -0.77 p= 0.013		
Turf Algae	r= -0.05 p= 0.754	r= -0.05 p= 0.754	r= -0.08 p= 0.754	r= -0.04 p= 0.235	r= 0.00 p= 0.989	

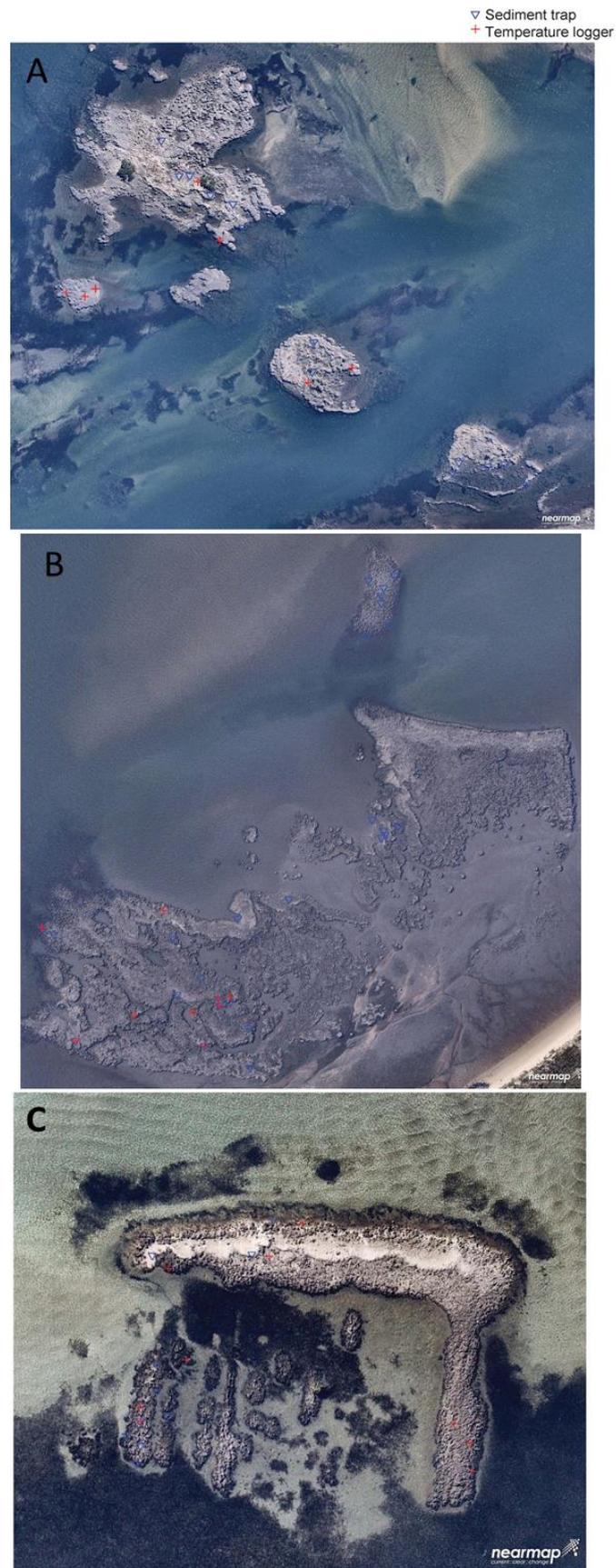


Figure D.1. Locations of sediment traps (Δ) and temperature loggers (+) in (A) Crookhaven River, (B) Hunter River and (C) Port Hacking on aerial maps of *S. glomerata* reefs.

Table D.3. Multiple pair-wise Pearson's correlation tests (coefficients and p-values reported as r and p respectively) between abiotic factors.

	Sedimentation rate	Coefficient of Variation of Temperature	5th percentile temperature	95th percentile temperature
Coefficient of Variation of Temperature	$r = 0.31$ $p = 0.545$			
5th percentile temperature	$r = 0.44$ $p = 0.382$	$r = -0.66$ $p < 0.001$		
95th percentile temperature	$r = 0.51$ $p = 0.298$	$r = 0.53$ $p = 0.006$	$r = 0.22$ $p = 0.291$	

Table D.4. Model outputs within $\Delta\text{AICc} < 2$ from step-wise regression of total recruitment, percentage live recruits and total live cover area against patch attribute-only (grey cells), estuary-only (green cell) and the interaction between estuaries and attributes (blue cells) for each response variable. For each variable, each row represents a selected model from the best model, with the lowest AICc (italicised and top row) followed by the subsequent models within $\Delta\text{AICc} < 2$. Selected patch attributes in each model are noted with a coefficient estimate with '-' denoting a negative estimate of a variable. Non-selected attributes are denoted as 'NA' per model. '+' represents a chosen 'estuary' or 'interaction term with estuary'.

Elevation	Est	Area	Circle	Edge	Frac	Iso. Index	Est: Elevation	Est: Area	Est: Circle	Est: Edge	Est: Frac	Est: Iso.Index	df	logLik	AICc	delta	weight
Total Recruitment																	
<i>-0.79858</i>	+	0.090	NA	NA	NA	3.514	NA	NA	NA	NA	NA	+	10	-979.094	1979.098	0	NA
-0.59541	+	0.118	NA	-	NA	3.529	NA	NA	NA	NA	NA	+	11	-978.123	1979.342	0.243	NA
-0.67987	+	NA	NA	NA	NA	3.495	NA	NA	NA	NA	NA	+	9	-980.476	1979.692	0.594	NA
Percentage Live Recruits																	
<i>2.015998</i>	+	-2.630	-9.283	0.149	NA	11.201	+	+	+	+	NA	+	19	-27974.6	55990.46	0	0.533
Total Live Cover Area																	
<i>NA</i>	+	-0.392	NA	NA	NA	9.898	+	NA	+	NA	+	+	11	-901.735	1828.77	0	NA
-0.50738	+	-1.87	NA	0.185	NA	9.816	NA	+	NA	NA	NA	+	13	-900.686	1828.894	0.123	NA
-0.7883	+	-1.94	NA	NA	NA	9.783	NA	+	NA	NA	NA	+	12	-902.014	1829.327	0.557	NA
<i>NA</i>	+	0.108	NA	0.273	NA	5.735	NA	NA	NA	NA	NA	+	10	-904.356	1829.62	0.849	NA
-0.48385	+	0.118	NA	0.201	NA	5.728	NA	NA	NA	NA	NA	+	11	-903.381	1829.858	1.088	NA
<i>NA</i>	+	NA	NA	0.198	NA	5.807	NA	NA	NA	NA	NA	+	9	-905.605	1829.951	1.180	NA
-0.66357	+	NA	NA	NA	NA	5.726	NA	NA	NA	NA	NA	+	9	-905.64	1830.02	1.249	NA
-0.86674	+	-1.939	-0.930	NA	NA	9.932	NA	+	NA	NA	NA	+	13	-901.337	1830.197	1.426	NA
-0.59281	+	-1.876	-0.768	0.170	NA	9.944	NA	+	NA	NA	NA	+	14	-900.243	1830.25	1.480	NA
-0.42244	+	NA	NA	0.129	NA	5.797	NA	NA	NA	NA	NA	+	10	-904.87	1830.649	1.879	NA
-2.32079	+	-1.543	NA	0.183	NA	9.156	+	+	NA	NA	NA	+	15	-899.316	1830.658	1.887	NA
<i>NA</i>	+	-1.915	-0.459	0.263	NA	9.982	NA	+	NA	NA	NA	+	13	-901.586	1830.696	1.925	NA

Table D.5. Model outputs within $\Delta\text{AICc} < 2$ from step-wise regression of total recruitment, percentage live recruits and total live cover area against temperature variables (i.e., Coefficient of Variation Temperature, 5th percentile temperature and 95th percentile temperature; in grey cells), estuary (in green cell) and interaction term between estuaries and temperature (blue cells) for each response variable. For each recruitment variable, each row represents a selected model from the best model, with the lowest AICc (italicised and top row) followed by the subsequent models within $\Delta\text{AICc} < 2$. Selected patch attributes in each model are noted with a coefficient estimate with '-' denoting a negative estimate of a variable. Non-selected attributes are denoted as 'NA' per model. '+' represents a chosen 'estuary' or 'interaction term with estuary'.

CoV.temp	Estuary	Q5. temp	Q95. temp	Estuary: CoV.temp	Estuary: Q5. temp	Estuary: Q95. temp	df	logLik	AICc	delta	weight
Total Recruitment											
<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	4	-96.1968	206.1436	0	NA
Percentage Live Recruits											
<i>0.879233</i>	<i>NA</i>	<i>2.205116</i>	<i>-0.84623</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	5	-68.0131	149.7763	0	NA
0.869786	+	2.278879	-0.76557	NA	NA	NA	7	-64.3529	150.7058	0.929482	NA
Total Live Cover Area											
<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>	3	-131.884	271.482	0	0.453879
-0.29388	NA	NA	NA	NA	NA	NA	4	-131.097	273.2718	1.789799	0.185477

Table D.6. Model outputs within $\Delta AICc < 2$ from step-wise regression of total recruitment, percentage live recruits and total live cover area against sedimentation rate; in grey cell), estuary (in green cell) and interaction term between estuaries and sedimentation rate (blue cell) for each response variable. For each recruitment variable, each row represents a selected model from the best model, with the lowest AICc (italicised and top row) followed by the subsequent models within $\Delta AICc < 2$. Selected patch attributes in each model are noted with a coefficient estimate with '-' denoting a negative estimate of a variable. Non-selected attributes are denoted as 'NA' per model. '+' represents a chosen 'estuary' or 'interaction term with estuary'.

Estuary	Sedimentation.rate	Estuary: Sedimentation .rate	df	logLik	AICc	delta	weight
Total Recruitment							
<i>+</i>	<i>1.676292</i>	<i>NA</i>	<i>6</i>	<i>-151.072</i>	<i>316.6903</i>	<i>0</i>	<i>0.70954</i>
Percentage Live Recruits							
<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>3</i>	<i>-144.41</i>	<i>297.9628</i>	<i>0</i>	<i>NA</i>
<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>2</i>	<i>-147.127</i>	<i>298.5774</i>	<i>0.614574</i>	<i>NA</i>
<i>+</i>	<i>-0.25997</i>	<i>NA</i>	<i>5</i>	<i>-144.077</i>	<i>299.9187</i>	<i>1.955884</i>	<i>NA</i>
Total Live Cover Area							
<i>NA</i>	<i>2.193996</i>	<i>NA</i>	<i>4</i>	<i>-267.102</i>	<i>543.6848</i>	<i>0</i>	<i>0.628829</i>
<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>3</i>	<i>-269.252</i>	<i>545.3615</i>	<i>1.676744</i>	<i>0.271914</i>

Appendix E: Chapter 5 Supplementary

Material

Table E.1. Output of GLMMs of oyster total recruitment and percentage of live recruits as function of surface elevation and 'estuary.type' as main effects. 'X²', 'p' and 'df' denotes Chi-square distribution value, probability, the degrees of freedom of tests respectively. Significant terms at $\alpha = 0.05$, denoted by '*'.

Term	Total Recruitment			Percentage live recruits		
	Chisq	Df	Pr(>Chisq)	Chisq	Df	Pr(>Chisq)
Intercept	21.149	1	<0.001*	32.4422	1	<0.001*
Elevation	2.326	1	0.127	46.4103	1	<0.001*
Estuary type	9.2944	1	0.003*	1.1792	1	0.278

Table E.2. Mean \pm SE of oyster total recruitment, percentage of live recruits surface elevation and sediment weight across the sampled estuaries and 'estuary.types'.

Estuary	Estuary type	Sediment Weight (g)	Total recruitment	Percentage live recruits (%)	Surface Elevation (m MSL)
Bermagui River	Low-sediment	1.69 \pm 0.47	123 \pm 12	92.4 \pm 1.56	-0.95 \pm 0.02
Crookhaven River		1.99 \pm 1.56	10 \pm 3	84.8 \pm 6.04	-0.92 \pm 0.03
Port Hacking		1.40 \pm 0.38	68 \pm 7	97.8 \pm 1.02	-1.16 \pm 0.06
Hunter River	High-sediment	20.80 \pm 3.67	9 \pm 2	62.6 \pm 8.89	-1.38 \pm 0.03
Hawkesbury River		25.90 \pm 6.97	0 \pm 0	100 \pm NA	-1.37 \pm 0.03
Georges River		25.50 \pm 5.03	1 \pm 0	100 \pm 0	-1.27 \pm 0.02

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