

Ecological Effects of Coastal Armouring on Sedimentary Shorelines

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Summary

As human populations continue to grow in the coastal zone, there is need to protect both natural and man-made infrastructure from coastal erosion and inundation. The construction of seawalls is one common approach to coastal protection, which can have large impacts on the structure and function of ecosystems. Although commonly constructed along sedimentary shorelines, seawall impacts to soft sediment ecosystems remain poorly understood, particularly in the southern hemisphere.

This thesis compares the structure and function of estuarine sedimentary communities between pairs of sites with and without seawalls in estuarine habitats of temperate south-eastern Australia.

Sampling along largely unvegetated shorelines revealed differences in infaunal communities between armoured and unarmoured sites that varied according to environmental setting. Patterns with respect to armouring were strongest at mid-intertidal elevations, with higher abundances at armoured than unarmoured sites at sandy locations, but the reverse pattern was apparent at muddy locations.

Mangrove forests with and without armouring displayed structural differences, with armoured forests narrower in width, with higher pneumatophore densities, and smaller wrack deposits including a greater proportion of terrestrial litter. Wrack on armoured mangrove forests washed away more readily, and decomposed more rapidly when containing terrestrial litter. Densities and richnesses per unit area of epifauna generally displayed idiosyncratic patterns with respect to armouring in mangrove forests, but taxa, such as anemones, that attach to pneumatophores had higher densities at sites with seawalls. Although densities of fauna did not display consistent patterns with respect to armouring, reduced habitat availability was associated with armouring.

Overall the results of this thesis suggest that impacts of seawalls on sedimentary shoreline are highly context dependent and understanding how impacts vary as a function of the local species pool, abiotic conditions, and seawall design will be critical to managing and mitigating impacts.

Declaration of Originality

I declare that this thesis is my own work and has not previously been submitted, in any form, for another degree or diploma at any other university or institution. This thesis contains only original material and any additional help received during the preparation of this work has been indicated in the 'Contributions' section.

Date: 23 Feb 2018

Lincoln P. Critchley

Contributions:

The content within this thesis has been prepared for publication as follows:

Chapter 1: Introduction

I completed the literature review and written content for this chapter with constructive feedback from my supervisor, Melanie Bishop.

Chapter 2: Ecological impacts of seawall: beyond the site scale

Authors: Lincoln P. Critchley, Melanie J. Bishop

This chapter is formatted for submission to *Estuaries and Coasts*.

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Chapter 3: Spatial variation in infaunal communities between sedimentary shorelines with and without seawalls

Authors: Lincoln P. Critchley, Melanie J. Bishop

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My contributions to this research chapter: Concept – 85%, Data Collection – 100%, Data Analysis – 85%, Writing – 70%, Total – 85%

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This chapter was presented at the following conferences:

1. Australian Marine Sciences Association (AMSA) Annual Conference 2015, Geelong, Victoria – oral presentation
2. New Zealand Marine Science Society (NZMSS) - AMSA Joint Conference 2016, Wellington, New Zealand – poster presentation; Winner - Ron Kenney Best Student Poster Award
3. Ecosummit 2016, Montpellier, France – poster presentation; Winner – Outstanding Early Career Researcher Poster Award
4. Estuarine Coastal Sciences Association (ECSA) 56 2016, Bremen, Germany – poster presentation

Chapter 4: Comparison of wrack dynamics and habitat structure between natural and seawall modified mangrove forests

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2. Ecosummit 2016, Montpellier, France – Oral presentation
3. ECSA 56 2016, Bremen, Germany – Oral presentation

Chapter 5: Epifaunal communities in armoured and unarmoured mangrove forests

Authors: Lincoln P. Critchley, Melanie J. Bishop

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My contributions to this research chapter: Concept – 90%, Data Collection – 100%, Data Analysis – 85%, Writing – 70%, Total – 86.3%

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Chapter 6: Discussion

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1. Introduction

Urbanisation and the burgeoning human population

It has been estimated that the human population will grow to over 9.7 billion people by the year 2050 (United Nations 2017). The increased global population will produce an increased demand for resources including space (Crist et al. 2017). As the availability of space diminishes, populations will concentrate through the process of urbanisation (*sensu* Tisdale 1942). Both human population growth, and urbanisation have, historically, been concentrated in coastal environments, where there is a source of fresh water, sheltered harbours to support shipping trade and extractable marine resources such as fisheries that provide a source of protein (Kummu et al. 2016, Seto et al. 2011). Projections indicate that population growth will continue to be focused in the coastal zone (Kummu et al. 2016; Neumann et al. 2015), further stressing this environment by enhancing inputs of pollutants that diminish water quality, by producing further loss and degradation of natural habitats, and by introducing non-native species.

The process of urbanisation replaces natural habitats with built infrastructure, resulting in significant ecological impacts (McDonald 2008, McKinney 2008). The ecological impacts of urbanisation are best known from the terrestrial environment, where urban infrastructure directly drives loss and fragmentation of habitat (DeFries et al. 2010; Jantz et al. 2005), resulting in loss of biodiversity (Thompson et al. 2016), and its associated ecosystem services which include climate regulation, maintenance of clean air and water, provision of resources such as food and fuel, as well as cultural recreational benefits (Eigenbrod et al. 2011; McDonald et al. 2013; Worm et al. 2006). In addition to these direct effects of urbanisation, there is increasing evidence that urbanisation can also produce large indirect effects on ecosystems, through the introduction of light, noise and chemical pollutants (Crain et al. 2008; Halpern et al. 2007), by modifying abiotic conditions and species interactions (Argüeso et al. 2014; Shochat et al. 2006), and by modifying patterns of resource and organismal movement (Bishop et al. 2017). For example, the replacement of pervious with impervious surface can result in impacts that extend into adjacent aquatic environments (Klein 1979), by reducing groundwater recharge rates and peak storm discharge and volume (Ogden et al. 2011; Shuster 2007). Effects of infrastructure are influenced by the surface characteristics of structures (Klok et al. 2012) and the configuration of development (Debbage and Shepherd 2015; Stott et al. 2015). For example, large areas of unshaded impervious surface can lead to the urban heat island effect (Oke 1973).

Increasingly urbanisation is not just a land-based problem. Built infrastructure is spilling over from the land into the water, producing “ocean sprawl” (Firth et al. 2016; Heery et al. 2017). Ocean sprawl includes port and commercial and recreational boating infrastructure, aquaculture facilities, transport infrastructure such as road and rail bridge pylons and tunnels, energy

generating infrastructure, and land reclamation and coastal armouring works (Heery et al. 2017).

As the world increasingly becomes reliant on aquaculture as a source of protein, marine renewables as a source of energy and coastal armouring as a defence against rising sea levels and enhanced storm surge, the amount of ocean sprawl is set to grow (Bugnot et al. in review). As on land, such infrastructure can destroy and fragment natural habitat, introduce pollutants, alter patterns of organism and resource movement and modify physical and biological processes (Chapter 2; Bulleri and Chapman 2010; Bishop et al. 2017). Although it is unclear whether the ecological effects of ocean sprawl will be magnified or muted by the kinetic nature of the coastal zone, it is expected that the ecological repercussions will be wide ranging due to future urbanisation and population growth being concentrated in the coastal zone.

Impacts of urbanisation on estuaries

Estuaries, defined in this thesis as the place where rivers meet the ocean, have long been the focal points for development of human settlements because they provide sheltered harbours, access to inland resources as well as a supply of water (Barragán and Andrés 2015). Estuarine ecosystems underpin many of the services provided by coastal environments such as shoreline stabilisation, water filtration, pollution control, fisheries productivity, and carbon sequestration (Barbier et al. 2011; Barbier 2015; Luisetti et al. 2014; Pinto et al. 2016; Sheaves et al. 2015). Historical reclamation of estuarine wetlands for agriculture and pasture land (Charlier et al. 2005) has directly resulted in loss of estuarine habitat and its ecosystem services. A substantial amount of shoreline continues to be reclaimed to support urban development in the coastal zone (Sengupta et al. 2018). Additionally, as low points in the environment, situated between land and sea, estuaries are particularly susceptible to changes in resource flows. It has long been recognised that land clearing for agriculture and urban development modify estuaries by enhancing freshwater, nutrient, and sediment inputs to receiving waters (Siriwardena et al. 2006), which may have positive or negative effects on productivity.

Increasingly, ocean sprawl also has the potential to produce direct and indirect effects on estuarine ecosystems by displacing and fragmenting natural habitats, by modifying physico-chemical and biological processes as well as resource flows (Bishop et al. 2017; Firth et al. 2016). In particular, continued land reclamation coupled with the risk to coastal infrastructure of sea-level rise and associated flooding of low-lying areas (McGranahan et al. 2007; Neumann et al. 2015) is driving the hardening of estuarine shorelines with protective structures such as seawalls, breakwaters and revetments (hereafter collectively referred to as coastal armouring; Pope 1997). Many urbanised shorelines are now dominated by some form of coastal armouring

with the percentage of shoreline that is armoured in some instances already exceeding 50% and expected to grow further (Dafforn et al. 2015; Dugan et al. 2011; Gittman et al. 2015).

Understanding how coastal armouring modifies physico-chemical and biological processes that shape estuarine ecosystems, and the distribution of the various types of coastal armouring structures, i.e. seawalls, bulkheads, riprap along the shoreline, is critical to the development of management strategies that seek to mitigate and minimise impacts.

Impacts of coastal armouring on estuarine ecosystems

Our existing understanding of how coastal armouring impacts coastal ecosystems is reviewed in detail in Chapter 2, so is only briefly summarised here. Among the mechanisms by which coastal armouring can impact estuarine ecosystems are the destruction (at the site of construction) and fragmentation of habitats, the introduction of novel substrate, the alteration of physico-chemical and biological processes and the alteration of ecological connectivity of organisms and of resources (Chapter 2).

Of the mechanisms by which seawalls impact coastal ecosystems, the introduction of novel habitat has received the most attention in the literature (Chapter 2). As compared to their closest natural analogue – rocky shores – seawalls have a paucity of microhabitats such as crevices and rockpools, and offer a predominantly vertical as opposed to horizontal surface for attachment, providing reduced intertidal area (Chapman 2003; Lam et al. 2009). This coupled with their provision of a bare surface that can readily be colonised by opportunists, such as invasive species, leads to their development of distinct ecological communities as compared to natural rocky shores (Mayer-Pinto et al. 2018).

Habitat loss is another well documented impact of coastal armouring (Fletcher et al. 1997; Dugan and Hubbard 2010) that has consequences for ecosystem functioning (see chapter 2). There has been considerable work documenting effects of seawalls on shoreline profile (Plant and Griggs 1992; Silveira and Psuty 2009; Thankappan et al. 2018). Where shorelines are steepened as consequence of coastal armouring, the availability of intertidal habitats can be reduced (Morley et al. 2012). Additionally, as a consequence of placement, active, and passive losses (Pilkey and Wright 1988; Griggs 2005), seawalls can reduce widths of beaches (Fletcher et al. 1997; Hall and Pilkey 1991; Kraus 1988), mangrove forests (Heatherington and Bishop 2012), and other sedimentary shoreline types (Bozek and Burdick 2005), producing losses of supratidal and high intertidal habitats such as dune systems (Dugan and Hubbard 2006).

Less studied are effects of coastal armouring on ecological connectivity (Bishop et al. 2017). Effects of structures on ecological connectivity, at both large and small scales, are of concern,

because they have the potential to propagate impacts beyond the site of structure placement. It is known that modification of the landscape contributes to habitat fragmentation (Fischer and Lindenmayer 2007). However, the way in which coastal structures modify ecological connectivity by fragmenting coastal habitats not been as well studied as other pathways of impact (see chapter 2; Bishop et al. 2017). Some research has investigated how shoreline infrastructure, including coastal armouring, can act as stepping-stones for biological invasions (Floerl et al. 2009; Dong et al. 2016), and a few studies have begun to consider how coastal armouring modifies the transfer of organic matter between adjacent habitats (i.e. land and sea, see chapter 4), but overall the extent to which coastal armouring modifies ecological connectivity, and the resulting ecological impacts are topics that need further research (Chapter 2).

The impacts to connectivity and ecological processes arising from the introduction of coastal armouring will vary according to the environmental conditions at the site at which they are placed (Airoidi et al. 2005; Bulleri 2005), the position of placement and design of the structure (Engelhardt et al. 2004; Tait and Griggs 1990), as well as the species composition and dispersal potential of the local species pool (Lechner et al. 2013; Rivero et al. 2013). Understanding how impacts vary with environmental context and interact with those of other stressors is critical to developing management strategies. While artificial structures may, in some instances, provide habitat for threatened or commercially important species (Briones-Fourzán et al. 2007; Martins et al. 2010; Perkol-Finkel et al. 2012), in other instances, such as when they are constructed in heavily modified port environments that are often hot-spots for non-native species, they may facilitate spread and proliferation of invasive and opportunistic species that are a detriment to ecosystem integrity (Mineur et al. 2012; Airoidi et al. 2015). Therefore, determining specific environmental contexts under which they produce positive and negative effects on biodiversity and ecosystem function should be a goal of future research.

Understanding the estuarine processes that are modified by coastal armouring, and the conditions under which these changes are most severe, will assist environmental managers in developing mitigation strategies that are aimed at minimising impacts to estuarine ecosystem functioning. These strategies can be facilitated by incorporating ecological principles into structure design (ecoengineering, Strain et al. 2018) or by using alternative approaches, such as restoration of natural habitat forming species such as vegetation or reef forming invertebrates (often termed living shorelines; Gittman et al. 2016), in place of shoreline stabilisation using hard engineering. Additionally, understanding the mechanisms by which impacts of coastal structures arise might help to identify scenarios in which construction of artificial structures will lead to particularly deleterious outcomes and should be avoided.

Impacts of seawalls on detrital subsidies

Detritus, non-living particulate organic matter that is available for uptake or chemical transformation (*sensu* Odum and de la Cruz 1963), is an important source of food and habitat to estuarine organisms (Robertson and Lenanton 1984). In estuaries, detritus accumulating at the high-tide mark is termed wrack, and is typically supplied by a variety of sources, including both terrestrial and marine origins (Canuel and Hardison 2016). Some estuarine habitats, with abundant primary producers such as mangroves, seagrass or saltmarsh, produce large quantities of wrack (Hyndes et al. 2014), and a subset of this wrack is retained within the source habitat, but some may be transported across habitat boundaries by wind, waves and currents to spatially subsidise adjacent systems (Hyndes et al. 2014; Polis and Hurd 1996). Habitats with scant or no macrophytes can be net recipients of spatial subsidies of wrack and phytoplankton produced elsewhere to provide a source of nutrients and carbon (Colombini et al. 2003; Orr et al. 2005; Polis et al. 1997).

The production, transport and stranding of wrack are spatially and temporally dynamic processes (Canuel and Hardison 2016; Middleburg and Herman 2007). Factors that influence the type and amount of wrack accumulating on a shoreline include: (1) the identity of proximate wrack sources, and their distance from the shoreline (Colombini et al. 2003; Heck et al. 2008), (2) weather events (i.e. storms, strong winds) and seasonal leaf shedding of macrophytes that generate detritus (Guntenspergen et al. 1995; Gómez et al. 2013; Yamazaki 2012), (3) patterns of wind and water movement that transport material and influence where it accumulates (Polis et al. 1997) as well as (4) structural features of the shoreline which determine whether arriving wrack is retained or washed away (Orr et al. 2005). The fate of wrack accumulating on a shoreline will depend on its chemical and physical properties (Colombini et al. 2003), as well as abiotic and biotic characteristics of the receiving environment (Hyndes et al. 2014; Moore et al. 2004; Polis et al. 1997). For example, at sites with abundant populations of leaf shredders, wrack may be rapidly decomposed. Conversely, at sites with high rates of sedimentation, wrack may be rapidly buried and stored in anoxic sediments where it contributes to blue carbon stores (Dugan et al. 2011; Duong and Fairweather 2011). Traits of wrack which are particularly important in influencing its decomposition rate include nitrogen and phosphorus content, with which decomposition rate is positively correlated, and lignin content and leaf mass per area, with which decomposition rate is negatively correlated (Cornwell et al. 2008). The lignin content and other secondary metabolites that act as chemical defences also reduce decomposition rate as they affect the palatability of wrack as a food source (Lastra et al. 2015; Rodil et al. 2015).

Seawalls may affect detrital dynamics by eliminating the high intertidal zone where wrack accumulates (Mellbrand et al. 2011, Heatherington and Bishop 2012; Harris et al. 2014),

modifying decomposition rates (Harris et al. 2014), and/or modifying the composition of wrack subsidies (Higgins et al. 2005). Whereas previous studies have assumed that seawalls will reduce terrestrial subsidies to aquatic environments by replacing or removing supratidal vegetation (Higgins et al. 2005), it is also possible that in some instances they may increase terrestrial subsidies to mid and low intertidal habitats by eliminating the high intertidal zone, thereby increasing proximity between terrestrial and aquatic habitats. In providing a novel substrate for organismal attachment (Connell and Glasby 1999; Bulleri and Chapman 2010), seawalls may also promote primary producers that can act as a new source for detrital input. Studies examining effects of seawalls and/or other coastal armouring structures on wrack subsidies have primarily focused on unvegetated shorelines. It is unclear how wrack cycling is modified where the seawall is constructed in biogenic habitat that is a net producer of wrack. Changes in wrack subsidies are of interest due to the important habitat and food resource they represent to terrestrial and aquatic invertebrates (Ince et al. 2007).

Impacts of seawalls on invertebrate communities of sedimentary shorelines

Invertebrates play an important role in determining the structure and function of coastal food webs, acting as a trophic link between primary producers or detritus (Colombini et al. 2003; Moore et al. 2004) and higher-level consumers (Ortega-Cisneros and Scharler 2015), as well as acting as ecosystem engineers (Mermillod-Blondin and Rosenberg 2006). In estuaries, the ecosystem services to which they contribute can include provision of raw materials, coastal protection, fisheries support, nutrient cycling, and carbon sequestration (Barbier et al. 2011; Prather et al. 2013). Marine invertebrates are a source of bioactive compounds used in the pharmaceutical, food, and polymer industries (Hayes 2012; Ibañez et al. 2012; Shahidi and Kamil 2001). Oysters are a food source and they build structures that can act as breakwaters enhancing coastal protection and providing habitat for commercially important species (Scyphers et al. 2011). Invertebrates can transform nutrients and sequester carbon through uptake, which may be a transitory carbon pathway, and excretion, where waste carbon is pelletised and may be buried for longer timeframes (Anderson et al. 2017).

Artificial structures represent novel habitats in estuarine environments, that modify invertebrate community structure (Bilkovic and Mitchell 2013; Heerhartz et al. 2016; Sobocinski et al. 2010). Coastal structures, such as seawalls, may modify the invertebrate communities of sedimentary shorelines directly by displacing them and indirectly by modifying environmental conditions (Heery et al. 2017). The loss of habitat from the introduction of coastal armouring may not only reduce invertebrate diversity through habitat fragmentation (Fahrig 2003), but also through modification of wrack quality and quantity in the intertidal (Bishop and Kelaher 2008; Olabarria

et al. 2010), a vital food source and niche space for estuarine invertebrates.

The response of invertebrates may, like their response to other disturbances (Hinchey et al. 2006), vary according to their functional feeding group, mobility and habitat. Scrapers, or grazers, feed on periphyton (Horne et al. 1994) which, within estuaries, can be found on trees, root structures, or pneumatophores in mangrove forests, as well as on the hard substrates of rocky shorelines. Where seawalls remove, through their destruction of natural habitats, or enhance, through their introduction of artificial structure, substrates for periphyton growth, they may be expected to alter the abundance of scrapers and grazers (Miserendino et al. 2008). Filter-feeders, that remove fine particulate detritus from the water column may, by contrast, be most affected by seawalls and other coastal armouring structures where they modify flow (Rubenstein and Koehl 1977). Shredders and detritivores, which are common where wrack accumulates on mangrove forests, beaches, and mud flats may respond most strongly where seawalls produce changes in wrack abundance and composition (Romanuk and Levings 2003). The invertebrates of sedimentary shorelines are often classified as infauna or epifauna. Infauna, living in sediments, may respond particularly strongly to any changes in sediment properties such as grain size and organic content (Strayer et al. 1997; Taghon et al. 2017). Epifauna, living on the surface of sediments or hard substrates, by contrast, may conceivably be most influenced by changes in the availability of hard substrate and the complexity of the habitat it forms (Glasby 2000; Jackson 1977; Kuklinski et al. 2006).

While it is understood that seawalls contribute to habitat loss, changes to sedimentology and hydrology, and in the case of sedimentary shorelines, introduce hard substrate that is not commonly present (see chapter 2), and that coastal armouring affects invertebrates on sedimentary shorelines (see Dethier et al. 2016, Heerhartz et al. 2016, Sobocinski et al. 2010), more research is needed to identify the specific mechanisms that lead to changes in invertebrate community structure. The mechanisms by which seawalls modify the ecology of unvegetated sedimentary shorelines and mangrove forests, and the context-dependency of effects, are the focus of this thesis.

Thesis aims and structure

Sedimentary shorelines may be particularly vulnerable to coastal development as the introduction of coastal structures can modify the sediment and hydrodynamic processes of these naturally geologically and morphologically dynamic systems. In order to avoid deleterious impacts to the ecological structure and function of sedimentary ecosystems, coastal structures should be designed and placed with ecological values in mind. Comparisons of how

environmental and biological processes differ between otherwise similar sedimentary shorelines with and without a seawall can assist in building the required knowledge of how seawalls modify ecosystems, which is needed for the development of mitigation strategies. This thesis applies a whole-system view of coastal habitats to address the question of how sedimentary ecosystems are modified by coastal armouring, examining impacts on invertebrate communities, habitat structure, and the processing of detrital subsidies. It has a particular focus on urban mangrove forests that have received little previous investigation with respect to their responses to coastal armouring, but in many parts of the world are increasingly threatened by coastal change.

The following chapter of this thesis (chapter 2) acts a review of the current literature, identifying the known effects of coastal armouring on the physical environment, clarifying specific environmental changes that occur, describing known and expected changes to biological communities and connectivity from direct and indirect effects of coastal armouring, and concluding with a discussion of implications for coastal management.

Chapter 3 addresses how seawalls influence sedimentary characteristics of largely unvegetated shorelines and, as a result, benthic community structure, and how such effects vary according to environmental context. Effects are compared between sandy and muddy shorelines. It was predicted that sites with a seawall would have coarser sediment and less wrack and vegetation than sites without a seawall, with resultant effects on the composition of benthic invertebrate communities. It was hypothesised that the greatest differences in benthic communities, benthic cover, and sedimentary characteristics would be proximate to the seawall and the equivalent height on shore without a seawall, as this is where the largest change in morphology occurs, with a decrease in differences lower along the intertidal gradient, further from the seawall. Effects were expected to be greatest along sandy shorelines, that are more wave exposed, than muddy shorelines that are more sheltered.

Chapter 4 examines how seawalls may modify the mechanisms and processes that control the composition and fate of detrital subsidies to urban mangrove forests. The cover, composition, decomposition rate and retention of wrack is compared among natural (unarmoured), armoured, and constrained shorelines (unarmoured shorelines of reduced width), to assess how seawalls modify detrital pathways, and whether any effects are simply due to lowering of the terrestrial-marine interface, or also due to the physical presence of a seawall. It was predicted that wrack accumulations would be smaller on armoured and constrained than natural shorelines due to loss of the high intertidal wrack accumulation zone, and contain proportionately more terrestrial litter due to enhanced proximity between the terrestrial and intertidal zone. It was expected that wrack at the armoured and constrained sites would be more readily washed away, and decompose faster due to mixing of terrestrial and marine litter sources.

Following on from chapter 4 which evaluates the differences in wrack dynamics between mangrove forests with and without a seawall, chapter 5 addresses how differences in wrack subsidies and structural attributes between mangrove forests with and without a seawall alter epifaunal invertebrate communities. Descriptors of habitat structure include measurements of tree circumference and density, pneumatophore height and density, algal and barnacle cover on trees and the seawall, forest widths, and an estimation of the area of intertidal mangrove trunks available for growth. Epifaunal communities are delineated as those that inhabit wrack and those that are on substrate itself. It was hypothesised that greater densities of pneumatophores would be found at sites with than without seawalls, leading to greater densities of macrofauna at the former. However, reduced shoreline widths at sites with seawalls were expected to reduce the total habitat available for macrofauna. It was also expected that the sites with a seawall would, due to the reduced distance between terrestrial and marine habitats, have a higher faunal diversity which includes more terrestrial species, than sites without seawalls due to increased spillover from the terrestrial environment.

The final chapter of this thesis, chapter 6, summarises the results of the experimental chapters, paying particular attention to the context-dependency of results. This chapter includes suggestions for management options for urbanised sedimentary shores, as well as a section on potential research directions. As a final note in this thesis, additional literature outputs to which I contributed during my PhD are attached. Considering the projected increases in human population and the development of the coastal zone, the results presented in this thesis contribute to a growing set of literature that can be used to develop management plans aimed at minimising detrimental effects of coastal development.

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2. Ecological impacts of seawalls: beyond the site scale

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Abstract

Seawalls are built to reclaim land, reduce erosion, and protect coastal infrastructure from the effects of climate change, such as sea-level rise and storm surge. While seawalls are generally built with protection of infrastructure in mind, there are ecological consequences to their use. Research has found that seawalls modify the physico-chemical environment of adjacent habitats by introducing new hard substrate, altering habitat complexity, changing the local light regime, impeding shoreline migration and, where they are situated below the high water mark, by constricting or eliminating the intertidal zone, acting as a barrier to tidal currents, and reflecting wave energy. Understanding the mechanisms by which seawalls impact ecosystems is needed if management strategies are to be developed that minimise their impact or enable multiple uses. Through identifying the direct changes to the ecology of habitats that result from the introduction of coastal armouring, the indirect impacts can be reasoned and issues with larger scale connectivity can be evaluated. With knowledge gaps regarding the ecological impacts of coastal armouring identified, directions for future research are suggested and considerations for improving coastal infrastructure design, which consider ecological responses, are proposed.

Introduction

People have been living alongside and modifying shorelines and water-ways since the beginnings of civilization (Charlier et al. 2005). Originally, shoreline modification was conducted to reclaim land and drain it to facilitate agriculture or urban settlements (Volker 1982). Current modification efforts also involve introducing hard structures, referred to as coastal armouring, to protect infrastructure and property from rising sea-levels and storm-surge (Dugan et al. 2011; Finkl 2013). As the world's coastal population continues to increase and sea-levels continue to rise by an estimated 26 – 98 cm between 2014 and 2100 (Wong et al. 2014), the demand for coastal armouring is set to increase. Without adaptation, 0.2–4.6% of global population is expected to be flooded annually by 2100 (Hinkel et al. 2014).

Coastal armouring can take an array of hard engineering forms, from parallel onshore and parallel offshore to perpendicular to shore constructions (Sorensen 2006), and can be identified by a number of nomenclatures, including “low-crested coastal defence structures” (Moschella et al. 2005). However, in this paper, structures constructed onshore and parallel to the shoreline are the focus and will be collectively termed ‘seawalls’. Seawalls are a common feature of ports, marinas, and highly urbanised areas (Floerl et al. 2009; Firth et al. 2013a), and in some estuaries and coastlines cover in excess of 50% of the shoreline (Dugan et al. 2011; Dafforn et al. 2015). Seawalls can be placed either above or below the high-water mark, be constructed of concrete, stone, steel, wood or any other material that can withstand repeated and intense wave action, and have a vertical or sloping face (Sorensen 2006; Nordstrom 2013). Over the past decade there has been increasing interest in how seawalls modify the ecological structure and function of coastal and estuarine ecosystems (Bulleri and Chapman 2010). Seawalls provide a novel habitat, create a static barrier to the movement of materials and energy between the land and the water, and modify the quality and availability of existing natural habitats (Bulleri and Chapman 2010; Dugan and Hubbard 2010; Dugan et al. 2011; Bishop et al. 2017). A mechanistic understanding of how seawalls modify the ecology of a diversity of habitats will enable seawall design to be appropriately modified to minimise ecological impacts and possibly assist estuarine and coastal ecosystems adapt to climate change by maintaining ecological functioning.

This paper reviews the existing knowledge of the physico-chemical and ecological impacts of seawalls, as well as likely but unquantified, effects. This review starts by summarising the observed and expected physico-chemical changes produced by the placement of seawalls. It then considers the direct effects of seawalls and the indirect effects, arising from physico-chemical and biological changes, to flora and fauna. Observed and predicted modifications of biota by seawalls are described by trophic level and functional feeding group, as this approach allows for greater generality than descriptions of the responses of individual taxa. By identifying key

knowledge gaps, directions for future research and implications for the design of coastal armouring are identified.

Impacts of seawalls on the physico-chemical environment

The extent to which seawalls modify the physico-chemical environment will be dependent on: (1) whether seawalls replace sedimentary or rocky shoreline; (2) the tidal elevation at which seawalls are constructed; (3) characteristics of the local- and meso-scale environment, such as wave-exposure, hydrology, sedimentology, aspect, and proximity to other seawalls; and (4) characteristics of the seawalls, such as whether they are vertical or sloping, impervious or permeable, or even their size (Kraus 1988). Nevertheless, and irrespective of where and how they are built, seawalls add new substrate and modify shoreline profile (Table 1; Fig. 1).

Depending on where they are constructed, seawalls may enhance or reduce the availability of hard substrate (Table 1). For instance, in unvegetated sedimentary environments where hard substrate is generally limited, they tend to enhance this resource, however, when constructed over natural rock reefs or in mangrove forests, the area of artificial substrate provided by seawalls may be insufficient to offset the loss of natural hard substrate. Considering, natural rocky reefs are dominated by horizontal surfaces and are of high heterogeneity and complexity and seawalls are predominantly vertical in orientation and, similarly to breakwaters, are of lower heterogeneity and complexity (Moschella et al. 2005), the replacement of predominantly horizontal with vertical surfaces can constrict tidal elevation zones (Chapman 2003; Fig. 1). Further, depending on their aspect, vertical surfaces may alter shading of the adjacent sedimentary or rocky shore environment (Fig. 1). This will influence light availability for primary producers and potentially also decrease the temperature of remnant intertidal habitats, particularly during midday low tides (Table 1). However, at larger scales, the actual construction and placement of the seawall may remove vegetation that formerly would have provided shading (Dugan et al. 2011). This coupled with the heat-absorption properties of dark-coloured rock-seawalls may, in some instances, lead to local enhancement of temperature along armoured shorelines (Morley et al. 2012).

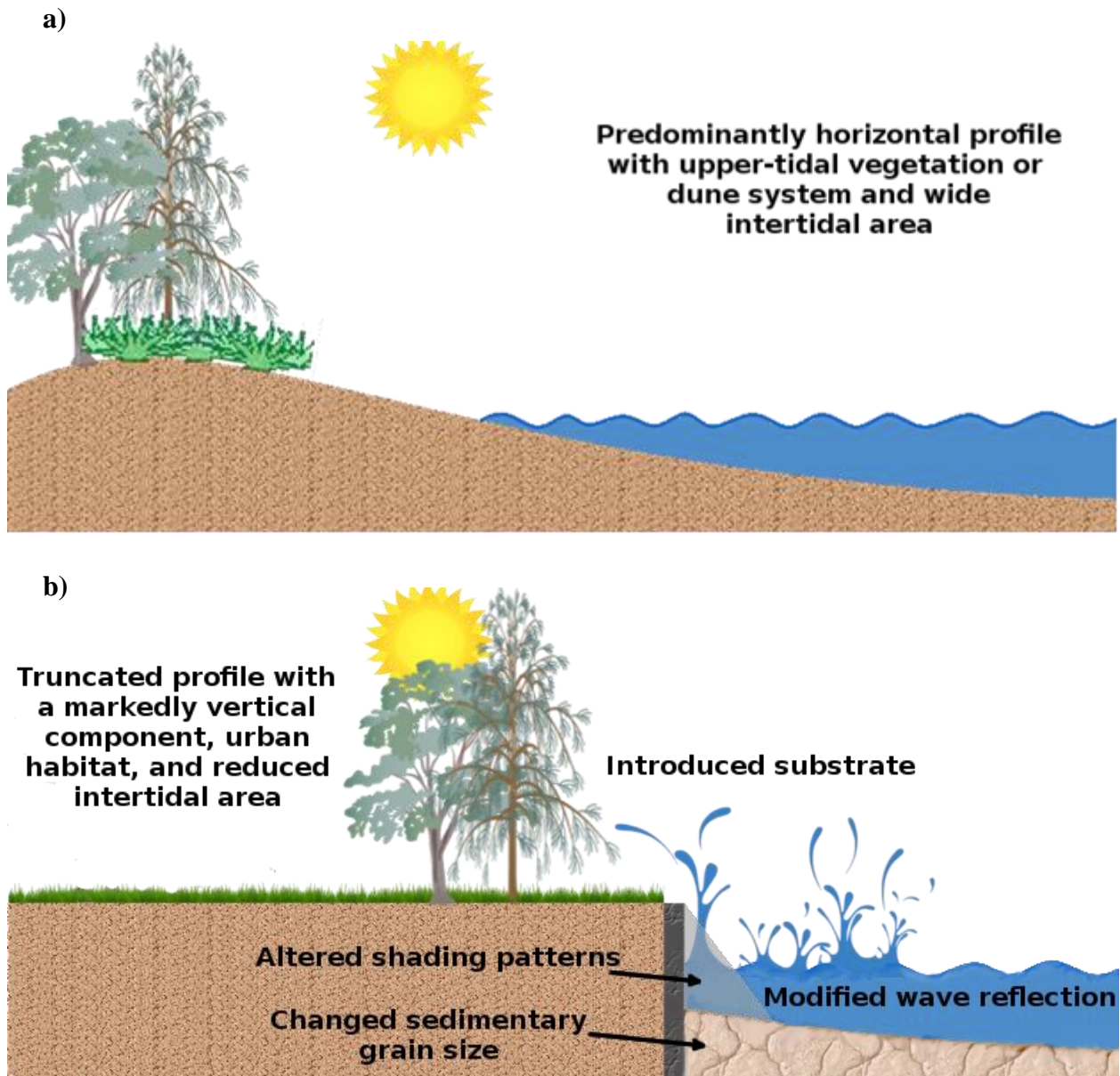


Figure 1; Conversion of shorelines from a) unarmoured to b) armoured introduces artificial substrate, causes habitat loss, and modifies the proximity of terrestrial and aquatic habitats. Additionally, seawalls may cause shading of adjacent substrate and may modify patterns of wave energy, leading to altered grain size of adjacent sediments from resuspension.

Natural sedimentary shorelines accrete and erode on daily, seasonal, yearly, and across geologic time scales (Cowell and Thom 1994) and have sloping gradients that are determined by (and affect) wave intensity (Wright and Short 1984; Cowell and Thom 1994; Short 2006). By introducing a static barrier, seawalls prevent natural shoreline migration, can displace natural sediment reserves such as dune systems on open coasts, and in many instances exacerbate erosion (Table 1; Pilkey and Wright 1988; Griggs 2005; although see Barkwith et al. 2013 for an example of where seawalls led to accumulation of sediments on their up-drift side).

The effects of seawalls on shoreline profile are particularly dependent on the tidal elevation at which seawalls are built, and tend to be greatest where seawalls are constructed in the breaker-zone of sandy beaches (Kraus 1988; Fig. 2). Seawalls may modify shoreline profile as a

consequence of placement loss, active loss, and/or passive loss (Pilkey and Wright 1988; Griggs 2005). In addition, seawalls can contribute to loss of intertidal and shallow subtidal habitats through 'coastal squeeze', which refers to the loss of habitat caused by hard structures, such as seawalls, restricting the ability of the shoreline to migrate landward in response to sea-level rise (Doody 2013; Pontee 2013). The presence of coastal armouring is known to coincide with a narrowed intertidal zone (Hall and Pilkey 1991; Fletcher et al. 1997; Dugan and Hubbard 2010) and combined with the processes that cause coastal squeeze has the potential to completely eliminate the intertidal zone over time.

Along exposed shorelines where the construction of seawalls leads to active loss of sediments, changes in the properties of adjacent sediments may also result (Table 1; Fig. 1). Resuspension of fine sediments by reflected waves can coarsen grain size, and increase sediment porosity (Reimers et al. 2009; Fagherazzi et al. 2014). In addition, organic particles may be eroded with sediments (Leipe et al. 2011), leading to a reduction in the organic content of sediments adjacent to seawalls. Initially, following construction of a seawall, the resuspension of fine particles from reflected waves increasing the concentration of suspended particulate materials in the water may be expected to decrease water quality, through increased turbidity and reduced light attenuation, and in areas with a history of industry, the resuspension of sediments may also increase the concentration of metals in the water column, as many are bound to fine particles (Knott et al. 2009). However, over time as fine materials are successively flushed from the sediments and hence are no longer present to be resuspended, water quality would, presumably, recover. Nevertheless, enhanced erosion and longshore transport of sediments in front of seawalls may continue even many years after seawall construction (Kraus 1988).

Most studies have considered impacts of seawalls on physico-chemical factors at relatively local scales. However, along shorelines where multiple seawalls are present they may have complex interactive effects that lead to changes in sediment transport processes at larger scales (Barkwith et al. 2013). Furthermore, where construction of seawalls leads to changes in key estuarine habitats, it may indirectly modify physico-chemical conditions of entire embayments via loss of ecosystem services. For example, loss of saltmarsh, that plays an important role in sediment accretion, may cause wide-spread changes in sediment transport and water quality (Li et al. 2014)

Seawalls may also modify the physico-chemical environment by providing a physical barrier to the transport of materials, such as organic matter and reproductive propagules (e.g. seeds), between land and sea, and, where seawalls squeeze the intertidal zone, by enhancing the proximity of terrestrial and aquatic habitats (Hall and Pilkey 1991; Bozek and Burdick 2005, Heatherington and Bishop 2012; Table 1). Where the construction of seawalls results in

conversion of intertidal to supratidal wetlands, major changes in the characteristics of sediments landward of the seawall can result. In Laizhou Bay China, the barrier-effect of seawalls was observed to replace gradients in soil salinity and pH from sea to land with abrupt transitions from one side of the seawall to the other (Bi et al. 2014). These effects are more fully discussed in the section on connectivity.

Table 1. Direct and indirect effects on ecological communities from the introduction of coastal armouring.

Type of effect	Terrestrial communities			Benthic fouling communities			Benthic sedimentary communities			Fish	Turtles
	Primary producers (e.g. coastal vegetation)	Invertebrates	Birds	Primary producers (e.g. microalgal biofilms; macroalgae)	Sessile invertebrates	Mobile invertebrates	Primary producers (e.g. saltmarsh, mangrove, seagrass)	Epifaunal invertebrates	Infaunal invertebrates		
DIRECT											
Introduction of new substratum				↑ - where seawall replaces unvegetated sedimentary shoreline, habitat area for fouling organisms is increased and connectivity between hard surfaces may be enhanced, facilitating biological invasion by providing 'stepping stones'; ↓ - where seawall replaces more complex rocky reef, habitat area and quality for fouling organisms is reduced						↑ - if seawall enhances abundance of macroalgae/ invertebrate prey resources, or makes these more accessible to predators by removing microhabitat refuges, higher trophic levels may benefit	
Destruction of natural habitat	↓ - where construction of seawall occurs within supratidal zone			↓ - where construction of seawall replaces natural rocky reef			↓ - where construction of seawall replaces biogenic habitat		↓ - where construction of seawall is in a previously sedimentary habitat	↓ - reduction/loss of key nursery habitats, such as seagrass, saltmarsh and mangrove	↓ - where construction of seawall reduces high intertidal/ supratidal area for nesting
Fragmentation of natural habitat	↓ - reduction in species due to loss of area, and habitat quality; decreased connectivity of habitat patches										
Reduction in / loss of intertidal zone		↓ - reduction in intertidal wrack accumulations that provide food/habitat	↓ - reduction/loss of low-tide foraging grounds of shorebirds	↓ - where seawall replaces largely horizontal surfaces of natural rocky reef with vertical surface, tidal elevation gradients are compressed			↓ - reduced intertidal area reduces species abundance and leads to decreased species richness			↓ - area of productive intertidal foraging grounds, accessed at high tide, is reduced	↓ - decreased availability of nest sites in high intertidal
Physical barrier between land and sea		↓ - reduction in wrack accumulation on high shore reduces food/habitat	↓ - reduction in invertebrate prey resources has cascading impacts						↓ - reduction in spatial subsidies of terrestrially-derived organic matter to sand-/mud-flat communities	↓ - access to high intertidal marshes may be prevented	↓ - access to supratidal zone for egg-laying impeded

Type of effect	Terrestrial communities			Benthic fouling communities			Benthic sedimentary communities			Fish	Turtles
	Primary producers (e.g. coastal vegetation)	Invertebrates	Birds	Primary producers (e.g. microalgal biofilms; macroalgae)	Sessile invertebrates	Mobile invertebrates	Primary producers (e.g. saltmarsh, mangrove, seagrass)	Epifaunal invertebrates	Infaunal invertebrates		
INDIRECT											
Sediment erosion							↓ -where sediment erosion deepens the area in front of seawalls, intertidal area is lost; sediment-dwelling organisms may be eroded with sediments				
Increased turbidity and suspended particulates				↓ - decreased light availability for subtidal species	↓ - fine particles can clog gills/feeding structures of filter-feeders, reducing growth rates and in some instances inducing mortality		↓ - decreased light availability for submerged aquatic vegetation, such as seagrass	↓ - fine particles can clog gills/feeding structures of filter-feeders, reducing growth rates and in some instances inducing mortality; pollutants, such as metals, buried in sediments may be exposed		↓ - decreased foraging efficiency of visually-feeding fishes	
Coarsening grain size							↔ - coarsening grain-size will benefit suspension feeders but negatively impact deposit feeders; the community composition of benthic primary producers may shift				
Locally enhanced shading				↓ - decreased light availability for photosynthesis	↑ - may lead to diminished desiccation/heat stress at low tide		↓ - decreased light availability for photosynthesis	↑ - may lead to diminished desiccation/heat stress at low tide			
Enhanced wave action				↓ - may lead to dislodgement, damage, and/or changes in morphology to combat dislodgement	↓ - may lead to decreased time available for foraging; may lead to dislodgement, damage, and/or changes in morphology to combat dislodgement		↓ - may lead to dislodgement, damage, and/or changes in morphology to combat dislodgement	↓ - may lead to decreased time available for foraging; may lead to dislodgement, damage, and/or changes in morphology to combat dislodgement			

Direct effects of seawalls on ecological communities

Some of the most well studied ecological impacts from the introduction of seawalls are the direct effects arising from the introduction of new substrate for attachment (Connell and Glasby 1999; Bulleri and Chapman 2010) and, where seawalls are constructed in the intertidal zones, the loss of supratidal and high-intertidal habitats (Dugan and Hubbard 2006; Dugan et al. 2008; Table 1). Regardless of whether they are built on rocky or sedimentary shorelines, seawalls introduce new substrate for colonisation.

The identity of taxa colonizing seawalls may depend on the timing of their construction, the materials from which they are constructed, and the proximity of seawalls to sources of colonists (Vaz-Pinto et al. 2014). Some opportunistic taxa may be able to colonise year round, however, the colonization of others may depend on whether the season at which new substratum becomes available coincides with their seasonal reproductive events (Underwood and Anderson 1994). Non-native species may be among the taxa that dominate the early successional communities of seawalls (Glasby et al. 2007; Dafforn et al. 2012; Megina et al. 2013; Fig. 3), especially where they are constructed adjacent to ports, marinas, and harbours which can serve as sources of propagules of non-native species (Floerl and Inglis 2005; Floerl et al. 2009).

The communities of seawalls typically contain a greater abundance of opportunistic and non-native species (Bulleri and Airoidi 2005) and fewer large grazers and predators (Chapman 2003), and are of lower biodiversity (Chapman 2003) to natural rocky reefs. Instead, they support communities that are more similar in composition to those of other artificial structures (Airoidi et al. 2005; Pinn et al. 2005; Burt et al. 2011). Even many years after construction, seawalls continue to support distinct communities to natural rocky shores (Bulleri and Chapman 2010; Dugan et al. 2011).

The differences in community composition between seawalls and rocky reefs may stem from a number of fundamental differences between the two habitats. Where seawalls have a smaller surface area than rocky shores, they may be expected to have reduced species richness as a result of the species-area relationship (Connor and McCoy 1979). Additionally, the communities that develop on seawalls may differ from those that develop on natural rocky shores as a result of differences in the chemistry and surface microtopography of artificial surfaces as compared to natural substrates (Walters and Wethey 1996; Connell and Glasby 1999). Some materials from which seawalls are constructed, such as concrete, can release compounds that are recognised by certain species as settlement cues (e.g. Anderson 1996). Any shading caused by the vertical orientation of artificial substrates may decrease space occupancy by primary producers and thereby increase occupancy by fouling animals as a consequence of reduced competition for space (Glasby 1999; Blockley 2007). Non-native invertebrates may benefit from lower rates of

sedimentation and reduced cover of algae on artificial structures as opposed to natural rocky shorelines (Glasby 1999; Miller and Etter 2008). On artificial surfaces built over sedimentary substrates, organisms may experience a refuge from predators that are common on natural rocky reefs (Dumont et al. 2011) but instead may experience greater predation from more mobile fishes (Munsch et al. 2014). Finally, seawalls lack microhabitats, such as rockpools and crevices, which are common on rocky shores and protect algae and soft-bodied invertebrates from desiccation at low tide (Firth et al. 2013b) and may offer some protection from predators (Chapman and Blockley 2009).

When hard structures, such as seawalls, are constructed in sedimentary environments, such as sandy beaches, mudflats, mangrove forests, or saltmarshes, they may increase habitat heterogeneity at the site-scale, adding new niches (Airolidi et al. 2005; Table 1). This can enable species previously absent from sites to colonise. In mangrove forests, where the availability of hard substratum for attachment and grazing can be limited (Branch and Branch 1980), the construction of seawalls might lead to enhanced abundances of species such as grazing gastropods otherwise limited to trunks and root structures (Fig. 3), potentially followed by a reduction in algal abundance. In environments where natural substrate has been degraded, artificial structures may facilitate populations of fouling organisms, such as oysters and corals (Ng et al. 2012; Drexler et al. 2014), and their ecosystem functions (Layman et al. 2014). However, where seawalls replace complex habitat, such as oyster reef or saltmarsh, they may reduce heterogeneity, leading to reduced abundances and diversities of nekton (Bilkovic and Roggero 2008). Moreover, on larger and longer scales seawalls reduce heterogeneity by creating uniformity between adjacent habitats and loss of site-specific variability, in a similar manner as general urbanisation (McKinney 2006).

Where seawalls are constructed below the high-water mark, supratidal and/or high intertidal habitat may be eliminated, even prior to active and passive losses or coastal squeeze (Table 1). Species normally present in the supralittoral zone either need to translocate, or if conditions do not permit shifting location, adapt or be lost (Fig. 3). Species that are able to migrate to lower tidal elevations may experience enhanced competition for resources such as space and food due to increased densities of organisms in a smaller area. For instance, the use of sandy beaches by shorebirds for foraging and roosting is less on beaches with than without armouring, both as a consequence as the reduced availability of intertidal area and a reduction in prey availability (Dugan and Hubbard 2006; Dugan and Hubbard 2010; Fig. 3). Similarly, ghost crabs, which typically burrow on the supratidal and high intertidal beaches, are often absent from beaches with intertidal seawalls due to a reduction in habitat availability (Lucrezi et al. 2009; Lucrezi et al. 2010; Noriega et al. 2012) and fewer turtles nest on beaches with than without seawalls

(Mosier 1998; but see Herren et al. 2007 for an example of where nesting was not affected; Fig. 3).

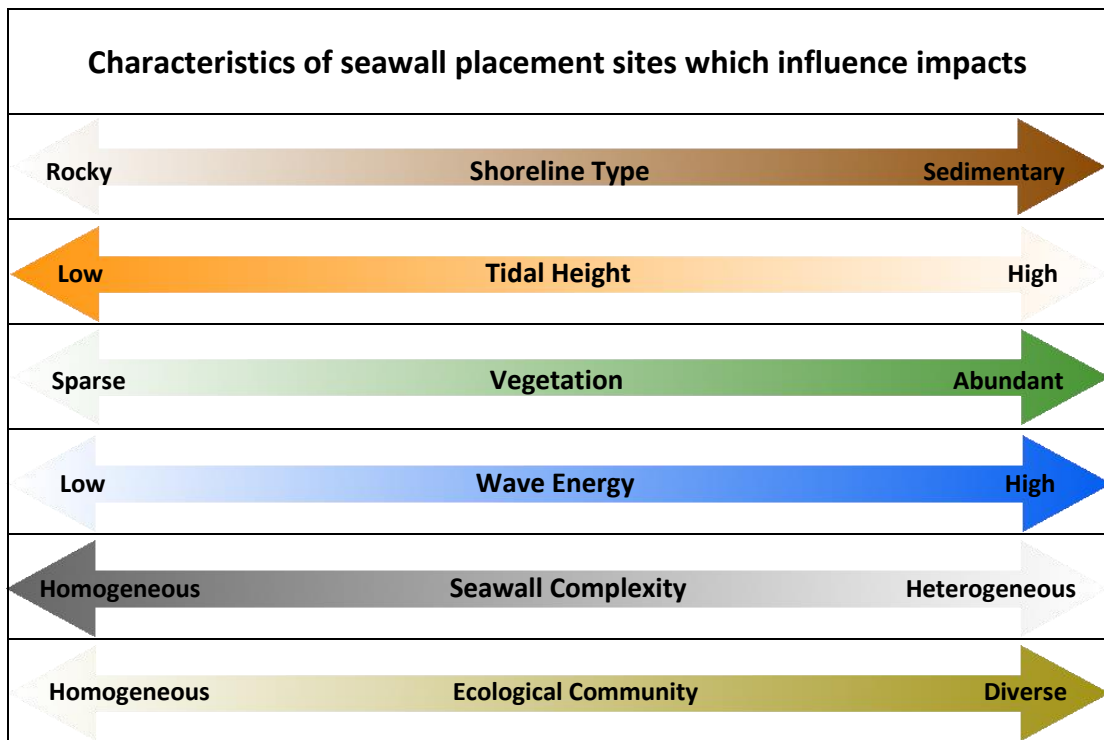


Figure 2; Characteristics of seawall placement site that influence ecological impacts. Lighter colour intensities represent weaker impacts from coastal armouring and deeper colour intensities, stronger impacts. The greatest ecological impacts of seawalls are expected to occur on sedimentary shorelines that have an abundance of vegetation with diverse ecological communities being replaced by a seawall of low complexity constructed at a low tidal elevation, and at sites of high wave action.

Indirect effects of seawalls on ecological communities

In addition to directly affecting biological communities by determining habitat availability, coastal structures, such as seawalls, may indirectly affect communities through their modification of abiotic conditions (Table 2) and biological interactions. However, fewer studies have considered these indirect effects of coastal armouring on ecological communities, particularly those occupying adjacent sedimentary ecosystems. Therefore, in this section we not only describe the indirect effects of seawalls that have been observed, but also those that are predicted based on the known physical, chemical (Fig. 1), and biological mechanisms that affect coastal communities.

Table 2. Predicted effects of seawalls on key aspects of the biotic and abiotic environment.

Environmental variable	Impact (-) Neg, (0) Neutral, (+) Pos.	Description
Vegetation	-	Seawalls may result in loss of vegetation from their site of placement, and typically provide a smaller area for growth of aquatic macrophytes than the natural substrates they replace. Additionally, where they cause significant shading of adjacent substrates they may reduce light levels below that required to sustain vegetation.
Temperature	+/-	Temperature is expected to increase where construction of the seawall results in loss of vegetation that previously provided shading or where seawalls are constructed of materials that are darker and absorb more heat than natural substrates; temperature is expected to decrease where seawall causes shading at a previously unvegetated site
Light	+ / -	Light is expected to increase where construction of the seawall results in loss of vegetation that previously provided shading; light is expected to decrease where seawall causes shading at a previously unvegetated site
Wave Energy	+ / 0	Where the seawall is situated above the high-water mark, it will have no influence on wave energy; when situated below the high-water mark seawalls reflect waves, increasing wave energy in their vicinity
Sediment Grain Size	+ / 0	Where the seawall is situated above the high-water mark, it will have no influence on sediment grain size; where seawalls situated below the high-water mark enhance wave energy, they may be expected to erode fine sediments, coarsening grain size

Just as the impacts of seawalls on physico-chemical variables depend on the tidal elevation at which they are built, and their environmental context, indirect effects of seawalls on biological variables also vary according to seawall placement. In general, greater indirect effects of seawalls are predicted for those situated below mean high water (Fig. 2). For example, where seawalls intercept wave action, the waves reflected by seawalls may influence the morphology of benthic organisms and/or the structure of the communities they form by modifying the physical forces experienced, the capacity of filter-feeding organisms to feed and by influencing boundary layers (Table 1).

Waves and currents exert drag and lift forces on rhizomes and hold-fasts of benthic macrophytes, and on the attachment points of sessile and mobile invertebrates. On wave exposed rocky shores, algae typically have stronger holdfasts and smaller blades with decreased roughness than on more sheltered shores (Shaughnessy et al. 1996; Pratt and Johnson 2002; Fowler-Walker et al. 2005; D'Amours and Scheibling 2007), mussels have greater attachment strengths, mediated by higher densities of byssal threads (Babarro and Carrington 2011; Garner and Litvaitis 2013), and sessile and mobile epibenthic molluscs are of reduced size, and flattened morphology, to minimize lift and drag forces (Akester and Martel 2000; Babarro and Carrington 2013). Consistent with an indirect effect of seawalls reflecting waves, invertebrates with tall spires and

algae with long thalli are typically absent from seawalls at wave-exposed locations (Bulleri and Chapman 2004; Bulleri and Airoidi 2005; Blockley and Chapman 2008).

Furthermore, where seawalls modify the hydrodynamic forces experienced by organisms in adjacent habitats, they may also modify the structure and function of organisms resident within these habitats. For example, seagrass is typically stunted (La Nafie et al. 2012) with patchier distributions (Fonseca and Bell 1998; Frederiksen et al. 2004; Nishihara and Terada 2010) in wave exposed locations, influencing the communities of fish and invertebrates that they sustain (Bell and Westoby 1986; Hovel 2002). Consequently, shifts in benthic community structure are often apparent across wave exposure gradients (Underwood 1981).

In sedimentary environments in which seawalls are built below the high-water mark, the reflection of wave energy by seawalls may modify the habitat for benthic, sediment-dwelling, communities by eroding sediments and associated organic particles and by coarsening mean sediment particle size (Table 1). Where wave reflection leads to resuspension of fine particles, turbidity plumes may form in adjacent waters, that decrease the light available for photosynthesis by benthic macro- and micro-autotrophs and phytoplankton. These fine particles might clog the gills and palps of filter feeders, hindering their feeding, and, by enhancing turbidity reduce the foraging-efficiency of visually orientated predators. Although these putative effects of seawalls remain to be tested, such biological responses have been seen following other disturbances that enhance turbidity (Manning et al. 2014).

Over the longer term, as fine particles that are resuspended are flushed, the coarsening of sediments adjacent to seawalls may lead to shifts in the community structure of sediment-dwelling flora and fauna. In particular, deposit feeding taxa, which are generally associated with muddy, organic-rich sediments may be negatively affected (Seitz et al. 2006). On sandy beaches, the coarsening of sandy beach sediments may influence the behaviour of swash-riding invertebrates. The burrowing time of the surf clam, *Donax* spp., lengthens with increasing grain size, rendering the bivalves more susceptible to erosion and to predators (McLachlan 1996; Nel et al. 2001; de la Huz et al. 2002; Marcomini et al. 2002). Additionally, where sediment movement is exacerbated by reflected waves, sediment-dwelling organisms may be eroded or buried and autotrophs, such as foliose macroalgae and seagrass that are sensitive to sand-scour (Airoidi 2003), may decrease in abundance. Reduced abundances of meiofauna in front of seawalls have been attributed to erosion and long-shore transport of animals along with sediments (Spalding and Jackson 2001). Further, seawalls have been found to exacerbate the impacts of storms on sandy beach organisms, such as ghost crabs, by accentuating sediment loss (Lucrezi et al. 2010).

Where seawalls shade adjacent habitat, they may induce changes in benthic community structure, by reducing light available to photosynthesisers and by modifying the adjacent microclimate (Table 1). Although the effects of altered patterns of shading by seawalls have not explicitly been examined, other artificial structures such as pontoons and pilings, that have shaded surfaces, typically have reduced macroalgal cover as compared to adjacent natural rocky reefs (Glasby 1999). Further, seawalls shaded by adjacent wharves have reduced cover of algae as compared to those that are unshaded (Blockley 2007). Shading of adjacent substratum by seawalls may also reduce their maximum temperature, potentially reducing heat and desiccation stress to intertidal species at low tide, many of which live under conditions close to the thermal limits (Stillman and Somero 2000; Somero 2005). However, where vegetation is cleared in the construction of the seawalls the reverse pattern of increases in substrate temperatures adjacent to coastal armouring may be observed (Rice 2006; Morley et al. 2012). Although elevated temperatures at armoured sites may not be problematic for highly mobile species, such as fish, that are able to migrate out of locally unfavourable conditions, they may have a negative effect on sessile organisms or less-mobile life-history stages that are vulnerable to temperature stress (e.g. Rice 2006; Jackson et al. 2008a).

The indirect effects of seawalls on biological communities might arise not only from their modification of the physico-chemical environment, but also through their modification of species interactions. Heterotrophic community structure is closely tied to the availability of food resources, as well as the availability of complex habitat, often provided by foundational species. Fouling communities of algae and sessile invertebrates that establish on seawalls built below the high-water mark provide a food resource for mobile grazers and predators. Due to the low complexity of seawalls, and the paucity of microhabitat refugia, invertebrate and algal communities, especially those with little structural or chemical defence, are particularly susceptible to visually feeding predators, including residents of seawalls (Jackson et al. 2008b) or fish and crustaceans, which can forage on the seawall at high tide (Munsch et al. 2014). Greater rates of foraging have been observed among fish at seawalls than at adjacent shorelines (Munsch et al. 2014), and seawalls have, in some instances, been observed to support greater numbers of juvenile fish than natural habitats, raising the possibility that they may in some contexts serve as nurseries (Pastor et al. 2013).

When, however, seawall construction results in large areas of habitat being lost, either directly, or indirectly through coastal squeeze, the resource base provided to predators and grazers by fouling communities on the seawall may be insufficient to offset the loss of foraging area. For example, the replacement of natural rocky reef with seawalls can decrease the area of hard substrate for growth of fouling organisms. This may negatively affect abundances of small mobile heterotrophs, such as gastropods and limpets, not only by reducing food resources, but

also the coverage of complex biogenic habitat, which in turn moderates competitive and predatory interactions (Klein et al. 2011).

Meso-predators, such as crabs and shrimp, may, like fouling organisms, suffer greater rates of predation on relatively structureless seawalls, than on natural shorelines. This effect may be particularly apparent where seawall construction results in loss of their complex natural habitats, such as oyster reef and marsh, in which rates of predation are much lower (Long et al. 2011). The net effect is that meso-predator abundances are sometimes diminished along modified, as opposed to natural, shorelines (Seitz et al. 2006). Nevertheless, in some instances, where seawalls are spatially removed from key natural habitats of predators, predation may be reduced on artificial surfaces (Dumont et al. 2011).

In modifying benthic community structure, seawalls may also indirectly affect ecosystem services that influence ecological communities over broader habitat areas. For example, Geraldini et al. (2014) found that by supporting different species of alga to natural hard substrate (in their case, oyster reef), seawalls were associated with greater denitrification than natural substrates. In removing nitrogen from the system, this service may have flow-on effects to surrounding benthic and pelagic organisms.

Effects of hard structures on connectivity

In addition to directly and indirectly modifying the ecology at the site of construction, seawalls can modify the ecology of spatially removed areas through their effects on landscape and trophic connectivity. Terrestrial and aquatic food webs are linked by the transfer of organic matter and nutrients across habitat boundaries (Duarte and Cebrián 1996; Polis et al. 1997; Melville and Connolly 2003; McLachlan and Brown 2006; Fig. 3). This results in aquatic primary producers contributing to terrestrial food webs, and terrestrial primary producers influencing aquatic food webs.

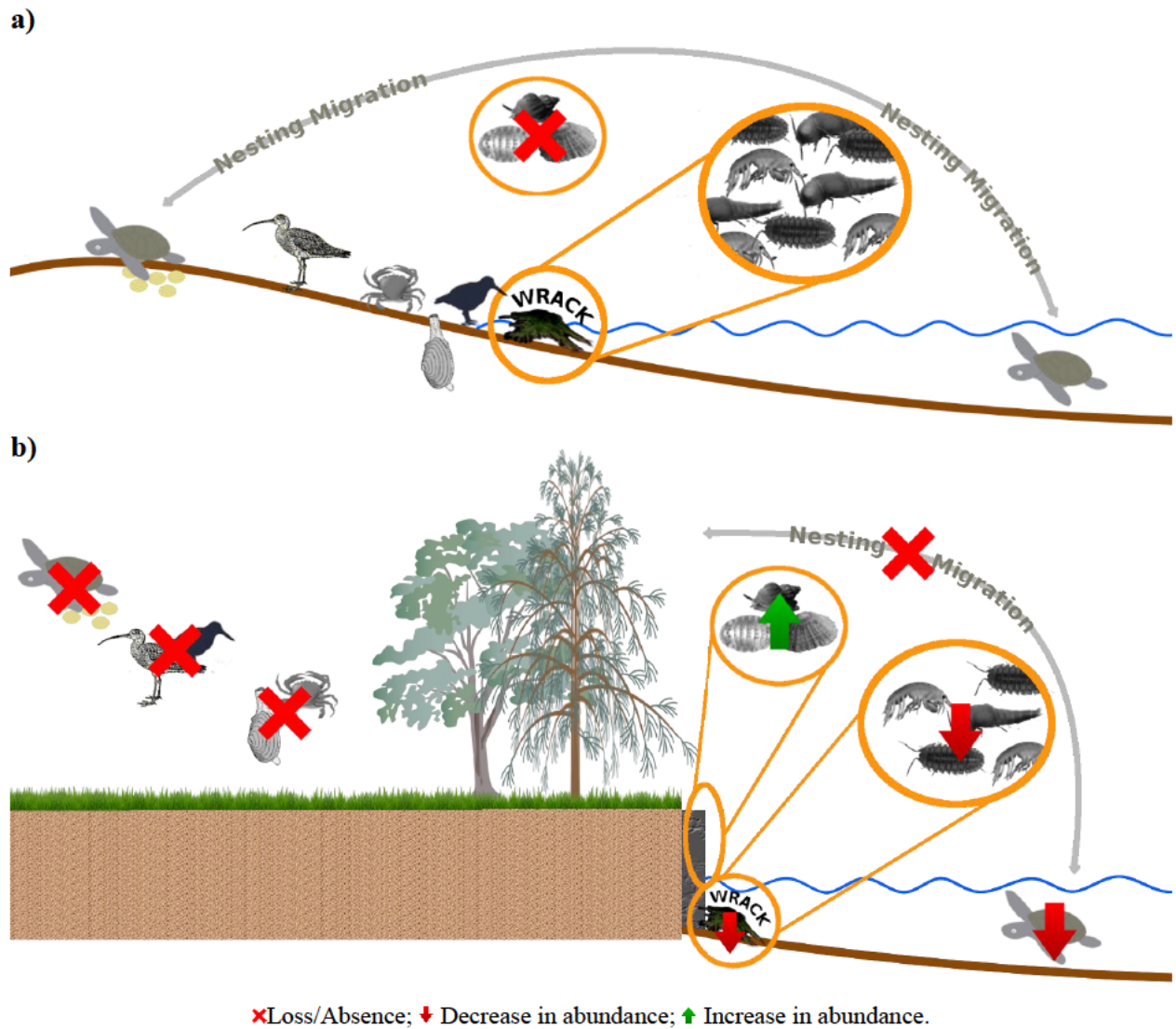


Figure 3; A comparison of ecological communities on sandy beaches a) unarmoured and b) armoured by seawalls. Unarmoured beaches can be important nesting sites for turtles, and sites of accumulation for wrack, which fuels invertebrates, and, ultimately, shorebirds. Seawalls constructed below the high water mark prevent turtle migration onto the supratidal beach for nesting, and reduce wrack retention, resulting in reduced abundances of invertebrates. Instead the artificial structure of seawalls may facilitate non-native taxa and grazing gastropods.

Seawalls may modify organic matter transport between land and sea by forming a physical barrier to movement of materials, by modifying the distribution and abundance of key primary producers and the physical environment for decomposition, and, where seawalls are built below the high-water mark, by eliminating or reducing the high intertidal zone where wrack would naturally accumulate (Mellbrand et al. 2011; Heatherington and Bishop 2012; Harris et al. 2014; Table 1; Fig. 3). Replacing gradually sloping shorelines with vertical transitions, seawalls, presumably, reduce the movement of organic matter from marine to terrestrial environments. However, where intertidal squeeze results in semi-terrestrial mangroves over-hanging the landward side of seawalls, estuarine leaf-litter inputs to terrestrial sediments may be locally enhanced (Fig. 4, see Chapter 4). Reduced accumulation and retention of wrack has been observed on the high shore of armoured coastal, estuarine, and riverine sites as compared to natural shorelines (Mellbrand et al. 2011; Harris et al. 2014; Heerhartz et al. 2014; Fig. 3). Further, faster break-

down rates of wrack have been observed on armoured than natural shorelines, perhaps because of greater physical disturbance in the former (Harris et al. 2014). The net effect is altered invertebrate communities at armoured as compared to natural sites (Seitz et al. 2006; Harris et al. 2014; Lawless and Seitz 2014; Heerhartz et al. 2016; Fig. 3). Among infauna, deposit feeders appear to be particularly negatively affected, consistent with a reduced allochthonous input of carbon (Seitz et al. 2006).

In general, transport of materials from the terrestrial to marine environments may, due their down-hill direction of movement, be less inhibited by seawalls than sea to land transport. Significant reductions in terrestrial resource subsidies to the marine environment may, nevertheless, occur where armouring is accompanied by the replacement of riparian vegetation with lawns on the landward side (Higgins et al. 2005). Alternatively, in instances where the riparian zone remains but the intertidal zone is squeezed, there may be reduced accumulation of terrestrial litter in the high-mid intertidal zone (Heerhartz et al. 2014) and, instead, increased terrestrial litter input to low intertidal and subtidal sediments as a result of their increased proximity to the site of terrestrial plants and their litterfall (Fig. 4). Although some types of terrestrial leaf litter are readily broken down in coastal waters, other more recalcitrant types cannot be readily assimilated by aquatic systems (Guenet et al. 2010; Bianchi 2012) and the benefits of any increase in terrestrial leaf litter input to marine environments remain unclear.

At smaller scales, structures that provide substrate for the growth of macroalgae and invertebrates can enhance production of detritus and its deposition in adjacent sedimentary environments (Airoldi et al. 2010). The accumulation of biological debris at the base of the structures may modify local seabed communities (Boehlert and Gill 2010), attracting scavengers such as flatfish (Pleuronectiformes), mobile crustaceans, and echinoderms, and enriching communities within the soft sediment (Coates et al. 2012).

Seawalls may also form a physical barrier to movement of live organisms between marine and terrestrial environments. For example, seawalls placed at or below the high tide mark can prevent species such as sea turtles and terrapins, which spend most of their time in the water, from reaching the supratidal zone to lay their eggs (Roosenburg 1990; Witherington et al. 2011; Fig. 3). At sites with seawalls, these species may construct their nests lower on the shoreline, where they are more susceptible to inundation (Roosenburg 1990; Witherington et al. 2011) and erosion due to passive losses in front of seawalls during storms (Rizkalla and Savage 2011). Alternatively, they may avoid nesting along armoured shorelines, potentially eliminating entire breeding colonies or increasing crowding in, and competition for, suitable nest sites (Roosenburg 1990; Rizkalla and Savage 2011). Similarly, it has been seen that estuarine terrapins associate less with armouring than natural marsh habitats (Idsell et al. 2015), suggesting coastal armouring

reduces niche space for terrapins. Further, dependent on tidal elevation at which the seawall is placed, there may be an effect on environmental conditions that support the use of shallow estuarine habitats for mating and gestation by stingrays (Jirik and Lowe 2012).

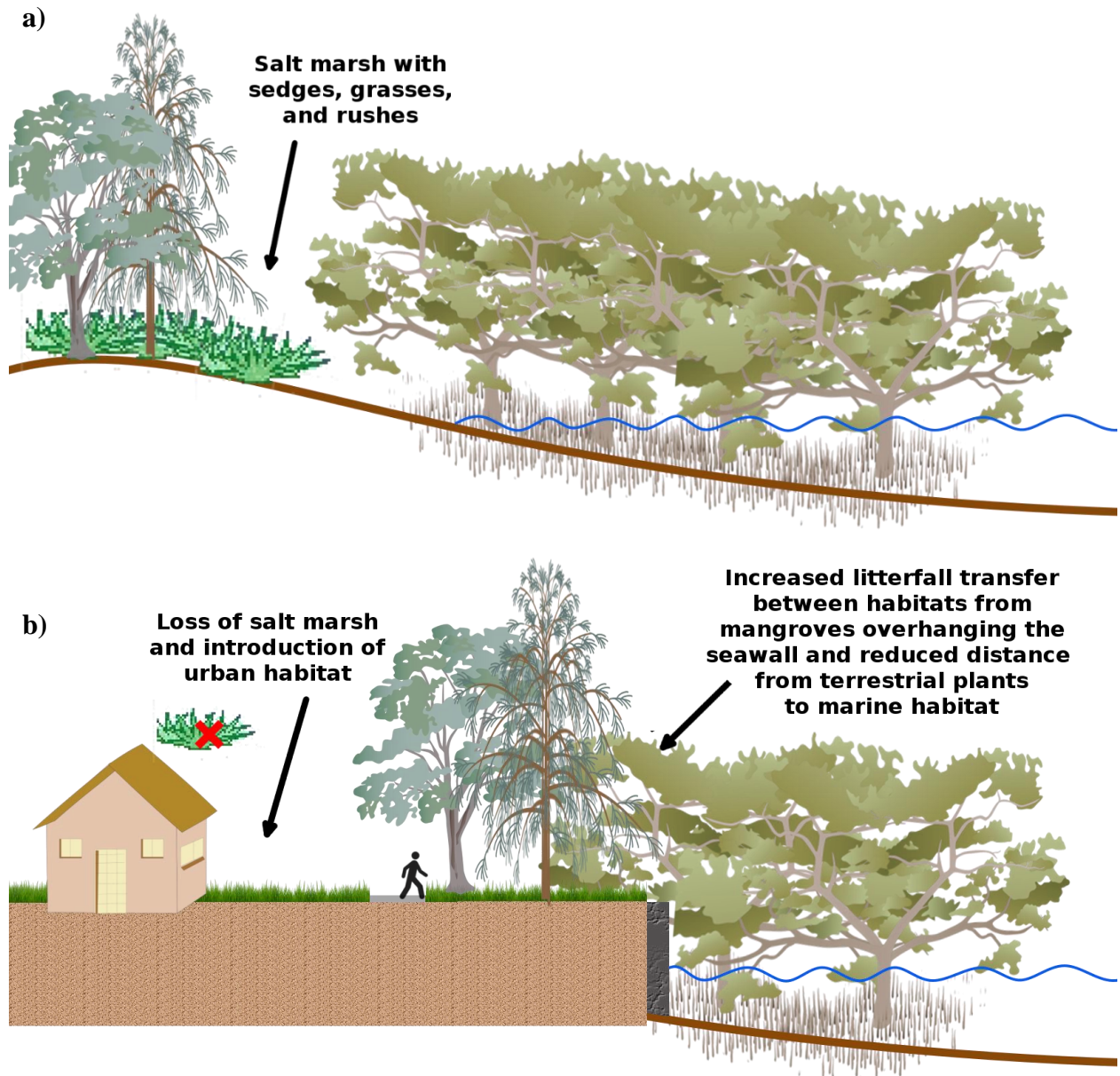


Figure 4: A comparison of estuarine wetland communities found along a) unarmoured and b) armoured shorelines. Seawall placement in the mid intertidal zone truncates mangrove forests and results in loss of saltmarsh. Proximity of terrestrial and semi-aquatic vegetation may be increased as the result of loss of the high intertidal zone. Connectivity between terrestrial and aquatic ecosystems may be enhanced where branches overhanging seawalls lead to increased litterfall of mangroves into terrestrial communities, and terrestrial vegetation into mangrove forests. ✗ Loss/Absence.

In addition to modifying land-sea connectivity, seawalls may also affect long-shore connectivity of aquatic plant and animal species. Seawalls can act as ‘stepping stones’ for marine invaders between ports and marinas, where vector densities are high (Glasby et al. 2007; Floerl et al. 2009). Both the establishment and spread of the limpet *Littorina saxatilis* in Belgian waters (Johannesson and Warmoes 1990) and the green algae *Codium fragile* ssp. *tomentosoides* in the north Adriatic Sea (Bulleri and Airolidi 2005) are thought to have been facilitated by seawalls

acting as stepping stones. Additionally, in environments where hard substrate is scarce, or are separated by large intervening stretches of sedimentary environment, seawalls may facilitate the dispersal of native rocky shore organisms over larger distances. This effect of seawalls may be particularly great for species that lack a pelagic larval stage or have a very short larval duration. Populations of *Patella caerulea* associated with artificial habitats are less genetically diverse than those in natural habitats (Fauvelot et al. 2009), perhaps due to greater connectivity in areas with substantial coverage of artificial habitat. In fragmenting natural habitat patches, seawalls may, however, in some instances decrease the connectivity of these habitats, resulting in changes to their community composition (Goodsell et al. 2007; Goodsell 2009). As the length of shoreline armoured by seawalls continues to increase, the effects of seawalls on connectivity will be increasingly important. Seawalls are becoming ubiquitous on shorelines and the connectivity issues associated with them are likely to have drastic impacts for coastal ecosystems and diversity.

Future research needs

The demand for coastal structures that protect property and infrastructure and provide renewable energy will increase in response to changes to the global climate regime and rising coastal populations (Thompson et al. 2002). This paper describes the known and expected ecological effects arising from the placement of seawalls in estuarine and coastal environments. The review identifies a growing literature quantifying the extent to which coastal armouring, such as seawalls, provide intertidal and subtidal fouling communities with equivalent habitat to natural rocky reef. However, the review also identifies relatively few studies investigating effects of coastal armouring on the sedimentary environments in which they are often constructed, or on higher trophic levels or highly mobile species, such as fish. As utilisation of seawalls in the coastal environment continues to grow, a mechanistic understanding of how seawalls modify ecological communities, particularly in sedimentary environments, and when and where their impacts are greatest is needed in order to develop strategies for enhancing the ecological sustainability of seawalls (Table 3).

Studies have primarily been focused at small scales (i.e. patches or site), and have primarily come from highly urbanised coasts (e.g. Sydney Harbour, the Mediterranean) where biological diversity has already been reduced by a history of industry, overfishing and pollution. Few studies (but see Wijnberg 2002; Pinn et al. 2005), have attempted to quantify the cumulative impacts of seawalls at larger spatial or temporal scales. This is despite urban seascapes increasingly being dominated by artificial structures, as opposed to natural shorelines, and the potential for seawalls to modify patterns of connectivity of native and invasive species. Studies

are needed that ascertain the mechanisms by which the fragmentation of landscapes by seawalls alters the communities of remnant natural habitats (Table 3). It would be useful to know the threshold lengths of seawalls required to produce state changes to the ecosystems of embayments and coastlines, a question that may be addressed by a combination of empirical research and modelling (Table 3). Furthermore, how the replacement of natural shorelines with artificial structures influences key ecosystem functions, and modifies provisioning, regulating, and cultural services is a key research need.

Table 3. Key research gaps and directions for future research

Impacts of seawalls on larger scales	Spatial Temporal
Impacts at alternate sites to prevalent literature	Less degraded sites Sedimentary shorelines
Effects on ecological processes	Predation Competition Facilitation Trophic pathways
Effects on exchange between adjacent systems	Organisms Propagules
Changes in sedimentary environment	Predation Competition
Design modifications to mimic sedimentary shorelines	Use of 'living' seawalls
Verification of the setting that produces the greatest impact	Sedimentary or rocky shores Tidal elevation Local- and meso-scale environment, i.e. wave-exposure, hydrology, sedimentology, aspect, proximity to other seawalls Seawall characteristics, i.e. imperviousness, slope, size
Quantification of magnitude of environmental impact	Terrestrial Marine

With studies on effects of seawalls being conducted primarily at already highly degraded locations, it is unclear the full extent of their impacts along less degraded shorelines. Increasingly, seawalls are not only being used to protect the infrastructure of key global cities, but also small settlements as well. Studies assessing impacts of seawalls constructed to protect settlements of moderate size, along coastlines with a more recent history of development, and fewer co-occurring stressors, are needed (Table 3). Furthermore, as urbanization of our coastlines continues, studies are needed to assess how the construction of seawalls interacts with other activities of humans that fragment or degrade ecosystems.

Early studies comparing the ecological role of seawalls and natural rocky reefs primarily focused on quantifying differences in epibenthic community structure between the two (Chapman 2003; Bulleri and Chapman 2004). More recently studies have begun to investigate the ecological processes underlying these structural differences, for example differences in rates of recruitment, predation, and the prevalence of competitive and facilitative interactions between the two (Bulleri 2005; Moreira et al. 2006; Jackson et al. 2008b; Klein et al. 2011; Murani 2013; Cacabelos et al. 2016). Nevertheless, studies investigating differences in the structure and function of food webs between seawalls and natural rocky reefs remain rare, with most studies focusing on a single trophic level, and not one study using the isotopic techniques required to understand trophic connectivity. Furthermore, very few studies have considered how seawalls influence meta-population dynamics, the implications of this for food web structure, and the genetic structure and viability of populations. More studies are needed that explicitly consider effects of seawalls on trophic and landscape connectivity by using population genetics and tracking techniques (Table 3). Improved knowledge of the scales at which seawalls influence connectivity could contribute to marine spatial planning that considers not just economic and social objectives, but ecological objectives as well.

Although seawalls are more commonly built along sedimentary shorelines, including sandy beaches, mudflats, mangroves, saltmarshes, seagrass and/or oyster reefs, than rocky shorelines, this review revealed that impacts of seawalls on sedimentary environments have received surprisingly little research attention. The little research on sedimentary environments has primarily come from sandy beaches and saltmarshes in the USA, and primarily in the last 5 years (Witherington et al. 2011; Morley et al. 2012; Bilkovic and Mitchell 2013; Toft et al. 2013; Drexler et al. 2014; Munsch et al. 2015). While the structure and function of rocky shore communities is largely driven by competition for space on the two-dimensional surface of the substrate, in the three-dimensional environment of sediments, competition for space is rare (Peterson 1991). Hence, whereas on rocky reefs impacts of seawalls primarily arise from the reduction in habitat complexity increasing competitive and predatory interactions, in sedimentary environments the mechanisms of impact are likely to be quite different. Engineering studies have documented changes in sediment grain size, shoreline profile and patterns of flow adjacent to seawalls constructed on sedimentary shorelines (see section on *Physico-chemical impacts*). This review suggests some testable hypotheses of how these changes may be expected to modify sedimentary ecosystems, based on well-established relationships between sediment-grain size, flow and shoreline type, and community composition. Empirical studies are now needed to evaluate these hypotheses. As the ecological understanding generated by concentrated research effort on the similarities and differences in the habitat provided by seawalls and natural rocky

reef has led to tangible management outcomes, this level of understanding has not been attained for sedimentary ecosystems (Table 3).

Not only is a more concerted research effort required to understand how seawalls modify ecological patterns and process on sedimentary shorelines, but also to enhance our understanding of when and where, along both sedimentary and rocky shorelines, seawalls have the greatest impacts (Table 3; see also Fig. 2). The tidal elevation at which seawalls are built may range from the subtidal to the supratidal. Furthermore, seawalls are constructed in environments ranging from wave-exposed coastlines to sheltered embayments of estuaries. Although it might be predicted that seawalls may have greatest impact where they are built at low elevation on wave exposed coastlines, due to the combined effects of placement loss and passive loss, this is not necessarily the case. Seawalls built in the supratidal may have greater impact on terrestrial ecosystems, both by reducing their area and modifying their connectivity to marine environments. Furthermore, although seawalls may have less of an impact on wave energy in sheltered environments, the habitats, such as seagrass beds, found in these systems may be more sensitive to environmental change. Carefully designed studies contrasting the impacts of seawalls across environmental gradients may help to address these research gaps, and provide guidelines as to where ecosystems will be particularly sensitive to coastal armouring.

Understanding the changes to the environment caused by the introduction of a seawall will allow developers and managers to protect coastal resources as well as coastal property. The finding that the low structural complexity of seawalls supports less biodiversity of fouling organisms and mobile epibenthic species than more complex natural rocky reefs has led to design modifications of seawalls to include more complex structures (Chapman and Underwood 2011; Firth et al. 2014). Pilot projects, in which the structural complexity of seawalls has been enhanced, for example by adding drill holes or fins, have demonstrated positive effects of these modifications on biodiversity (Martins et al. 2010; Toft et al. 2013). Similarly, the inclusion of flower pots or other water-retaining structures on the surface of intertidal seawalls has enabled species that are specific to rock pools and otherwise absent from seawalls to colonise artificial substrates (Chapman and Blockley 2009; Browne and Chapman 2011; Firth et al. 2013). Greater understanding of how sedimentary ecosystems are modified by seawalls may enable the design of seawalls used in these environments to also be modified to minimise their impacts. This may include use of habitats, such as mangroves and oyster reefs, with natural wave-buffering capacities as living seawalls, as has been done in the United States with salt marsh as a buffer (Bilkovic and Roggero 2008; Bilkovic and Mitchell 2013; Bilkovic et al. 2016; Gittman et al. 2016). It is acknowledged that while artificial habitats can be modified in such ways to better mimic natural conditions, they are not replacements (Chapman and Blockley 2009; Toft et al. 2013).

Historically, the protection of human settlements and coastal infrastructure from inundation and erosion has come at a considerable cost to ecological systems. Over the past few decades, a rich body of research has greatly enhanced our understanding of how seawalls modify the structure and function of ecological communities at small scales. However, in order to design seawalls that minimize ecological impacts and preserve, if not enhance, ecosystem services, a greater understanding of how seawalls modify the structure and function of ecosystems at the landscape-level is needed. Several studies have started to address the larger scale impacts of seawalls. As such efforts increase, our capacity for embarking on green engineering (i.e. ecologically sustainable seawalls) at the estuary and coastline scale will increase.

Summary

Seawalls are increasingly common along estuarine and coastal shorelines, replacing and modifying natural habitats. This paper examines the mechanisms by which seawalls may directly and indirectly affect ecological systems, at scales ranging from the site at which the seawall is constructed to scales of 10s of kilometres, as a consequence of changes in trophic and landscape connectivity, and identified remaining research gaps.

The nature of physico-chemical impacts of seawalls is dependent on the habitat which the seawall is constructed, for instance, the amount of wave exposure or type of substrate (i.e. sedimentary/rocky), and the features of the seawall itself, as in either the materials (i.e. concrete/sandstone) or the aspect, which can contribute to modified shading patterns and hydrodynamics. With the direct effects of seawalls on ecological communities arising from the addition of novel habitat, and the loss of habitat at the site of seawall construction, it has been seen that seawalls typically support lower diversity than natural rocky shores because of their relatively featureless surface, and their compressed tidal zonation. Therefore, to mitigate losses to biodiversity, design modifications have attempted to increase complexity via artificial rock pools or adding relief to the seawall. However, this does not necessarily appease diversity goals as seawalls also typically contain high proportions of non-native species as compared to many natural substrates. Sources of recruits and the hydrodynamic patterns that mobilise them should factor into seawall placement strategies. This will address concerns with the spread of NIS and reduce the ability of seawalls to act as stepping stones in the biological invasion process.

While many of the direct effects of seawalls come from the placement of a novel substrate and the features of the artificial substrate, or lack of features, indirect effects of seawalls on adjacent habitats follow from their modification of physico-chemical conditions and the changes resulting from the direct impacts. Essentially, these indirect ecological effects arise from altered patterns

of shading, differences in habitat complexity, changes to sediment properties, and hydrodynamic conditions, as well as the modification of trophic interactions. For example, their vertical surface may make algae and invertebrates more accessible to consumers such as fish, but reduce predation by whelks and other predators associated with rocky reefs, resulting in altered species assemblies. Where possible, design of coastal armouring should include features that mimic natural conditions or, better, maintain the natural structure of the shoreline, including using natural materials and features, i.e. living shorelines.

Although most research has focussed on site-scale ecological impacts of seawalls, impacts may propagate over much larger spatial scales where seawalls modify landscape or trophic connectivity. Considering that coastal habitats are the interface between two environments, changes to connectivity has major implications for ecosystem functioning, as ecological processes rely on transfer of resources across habitat boundaries. Not only do populations in coastal systems rely on recruits from adjacent habitats, much of the food sources are from allochthonous inputs. Designing coastal armouring to account for this alteration of connectivity has been lacking as most studies have focused on impact assessment at the site scale. As increasing lengths of shoreline are armoured, it is important to understand the cumulative impacts to ecological systems of constructing additional seawalls at the scale of estuaries, and coastlines. Further, while mechanistic understanding of how seawalls modify fouling communities has allowed innovative eco-engineering approaches to be developed to enhance their ecological value, mechanistic understanding of impacts to sedimentary habitats lags behind. Only with such mechanistic knowledge will it be possible to develop appropriate eco-engineering techniques that target the maintenance of biodiversity in adjacent sedimentary environments.

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3. Spatial variation in infaunal communities between sedimentary shorelines with and without seawalls.

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Abstract

Seawalls are an increasingly conspicuous component of coastal seascapes, yet their effects on the sedimentary ecosystems in which they are frequently built remains poorly understood. In addition to producing loss of habitat at their site of construction, seawalls may modify adjacent habitat through their effects on physical and biological processes. The magnitude and nature of such effects may vary spatially according to environmental conditions at the site of placement, the local species pool and characteristics of the seawall itself. We assessed how differences in infaunal communities between shorelines with and without seawalls vary spatially with tidal elevation, and among locations, according to variation in environmental conditions. Infaunal communities and key sediment variables were compared between pairs of otherwise similar sites with and without seawalls at five locations within Brisbane Waters, Sydney Australia. Contrary to the prediction that differences in faunal communities between sites with and without seawalls would be greatest at the high intertidal elevations at which seawalls were placed, we found greater differences at mid-intertidal elevations. At muddy sites, characterised by high faunal abundance and richness, the abundance of mid-intertidal invertebrates was less at sites with than without seawalls. By contrast, at sandy sites, which were characterised by low invertebrate abundance and richness, the reverse pattern was seen, with more invertebrates, of more taxa at sites with than without seawalls. Although the structure of faunal communities were correlated to sediment variables, sediment grain size and organic content did not display clear patterns of difference between sites with and without seawalls across the locations. Instead, differences in the community of species present at sandy and muddy locations, or differences in the way seawalls modify hydrodynamics may account for the differing direction of effects between these places. An understanding of how seawalls modify sedimentary communities, and where impacts are greatest, is needed so that engineered designs and placement can be modified to minimise ecological impacts.

Introduction

Seawalls are a common feature of urbanised shorelines and have been used for decades to stabilise reclaimed land, and to protect infrastructure from erosion and storm surge (Sorensen et al. 1984; Pope 1997; Pope and Curtis 2005; Harman et al. 2013). Already, over 50% of the shoreline of some urbanised estuaries in Australasia, Asia, America and Europe is armoured by seawalls and other coastal defence structures (Dafforn et al. 2015) and the number of heavily armoured shorelines is set to increase as sea-levels rise (Church et al. 2013; Meehl et al. 2012) and coastal populations grow (Neumann et al. 2015). While the purpose of seawalls is to stabilise shorelines, they often have large unintended ecological impacts (Airoidi et al. 2005; Bulleri and Chapman, 2010; Dugan et al. 2017). Many studies have examined the extent to which seawalls replicate the habitat provided by rocky shores, their closest natural analogue (Bulleri et al. 2005; Chapman and Bulleri 2003). By contrast, relatively few studies have examined their impact on the sedimentary ecosystems in which they are typically built (see Heery et al. 2017).

Where studies have considered impacts of seawalls on sedimentary shorelines, the focus has typically been on geomorphological impacts, such as changes in beach width, profile and erosion/accretion (Kraus 1988; Pilkey and Wright 1988; Plant and Griggs 1992; Miles et al. 2001; Griggs 2005; Saitoh and Kobayashi 2012; Doody 2013; Pontee 2013). Such changes in shoreline width and profile have implications for ecological communities where they influence habitat availability (Defeo et al. 2009; Heatherington and Bishop 2012; Manca et al. 2013), in some instances causing loss of coastal dunes (Lucrezi et al. 2009) and supratidal or high intertidal vegetation (Morley et al. 2012; Heerhartz et al. 2016). Loss or narrowing of shorelines may also modify availability of other resources. For example, wrack (dead organic matter) accumulation and retention may be reduced in areas where the high intertidal zone is lost, or shorelines are narrowed (Dugan and Hubbard 2006; Harris et al. 2014; Sobocinski et al. 2010). Changes in wrack availability has implications for invertebrates that use this resource as food and as habitat (Dethier et al. 2016; Heerhartz et al. 2016).

Additionally, seawalls may modify other environmental conditions of sedimentary shorelines such as sediment temperature, through the provision of shading (Morley et al. 2012), and, where built below the mean high tide mark, sediment grain size (Ahn and Choi 1998; Bozek and Burdick 2005). Temperature is an important aspect of the ecological niche of many organisms, and has large direct and indirect effects on intertidal organisms (Southward 1958). Sediment properties such as grain-size have long been established to be key factors in influencing the community structure of infauna (Gray 1974; Ysebaert and Herman 2002), and may be influenced by seawalls if these modify patterns of wave reflection and sediment erosion (Ahn and Choi 1998; Bozek and Burdick 2005). Despite the documented effects of seawalls on the

sedimentary environment, few studies have followed their impacts through to dependent infauna (but see Dethier et al. 2016; Rolet et al. 2015). The comparatively few studies on the effects of seawalls on the ecology of sedimentary shorelines have primarily focussed on their impacts to predators such as shorebirds (Dugan et al. 2003), fish (Munsch et al. 2015a; Toft et al. 2007), and ghostcrabs (Lucrezi et al. 2009; Noriega et al. 2012; Schlacher et al. 2016), with fewer studies examining effects of armouring on infauna (but see Ahn and Choi 1998; Sobocinski et al. 2010; Dethier et al. 2016; Heerhartz et al. 2016). Understanding impacts to invertebrates is important given their role in fuelling higher trophic levels, remineralising detritus, recycling nutrients, and oxygenating and stabilizing sediments (Bouma et al. 2009; Graf and Rosenberg 1997; Snelgrove 1999; Waldbusser et al. 2004).

The way in which seawalls modify sedimentary communities is likely to be a function of the environmental context and species pool at the site of their placement, as well as the design of the seawall itself (see Chapter 2, Heery et al. 2017). Seawalls placed below the high-water mark are expected to have greater impacts on sedimentary habitats than those placed in the supratidal, both as a consequence of placement loss and their greater potential to modify hydrodynamics and sediment transport through wave reflection (see Chapter 2; Heery et al. 2017). Among seawalls placed below the high-water mark, effects may be greater at wave-exposed than sheltered locations (Heery et al. 2017), on shorelines where their construction results in loss of intertidal vegetation (Morley et al. 2012), or at locations where the species pool is diverse, or dominated by species sensitive to stress (see Chapter 2; Heery et al. 2017). Of the studies examining sedimentary community response to coastal armouring, the majority have focused on coastal sandy beach ecosystems (Lucrezi et al. 2010; Morley et al. 2012; Munsch et al. 2015b; Rice 2006). Estuarine ecosystems differ biologically, morphologically, and physico-chemically from coastal marine ecosystems, so may be expected to respond differently to seawall placement. Further, within estuaries, the high spatial and temporal variability in physico-chemical conditions may lead to variation in the effects of seawalls on sedimentary ecosystems among locations (Dethier et al. 2016).

This study assessed differences in sediment invertebrate communities between intertidal estuarine shorelines with and without seawalls. We predicted that overall, sedimentary shorelines with seawalls would have coarser sediments with less wrack and vegetation, than those without seawalls, and would consequently support different invertebrate communities. We expected that differences in sediment variables, and hence invertebrate communities between sites with and without seawalls would be greatest at high intertidal elevations, proximate to the base of the seawall, and would diminish with decreasing elevation due to the increasing distance from the seawall. We also predicted that across locations sampled, the nature of differences between sites

with and without seawalls would vary according to the composition of the resident community, and local geophysical conditions.

Methods

Study Sites

Sampling was conducted in Brisbane Waters (33.52 S, 151.34 W), approximately 80 km north of Sydney, New South Wales, Australia (Fig. 1). Brisbane Waters is a wave-dominated barrier estuary with semi-diurnal tides of approximately 1.5-2 m. Five sampling locations were selected within 1 km of the mouth of the estuary (two at Wagstaffe on the south side, and three at Ettalong on the north side; Fig. 1), each of which contained paired sites approximately 100 to 200 m apart that were largely similar but with and without seawalls in the high-intertidal zone. Previous studies suggest that this approach is adequate for the detection of ecological differences, attributable to seawalls (Heatherington and Bishop 2012). At each location, the seawall had been constructed just below mean high water, such that it is regularly wetted for short periods (< 3 hours) during diurnal high tides. The ages of the seawalls differed, with those at locations 1 and 2 being decades old and those at locations 3, 4, and 5 being only one year old, at the time of sampling. Land-use adjacent to each of the sampling locations was residential interspersed with urban parkland.

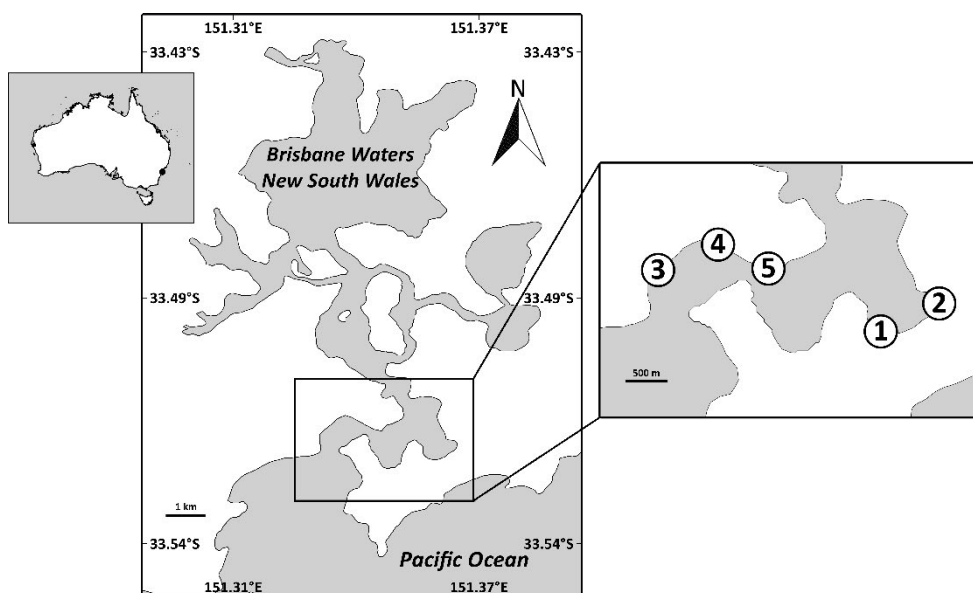


Figure 1; Map showing study locations in Brisbane Waters, to the north of Sydney, New South Wales, Australia. Stars indicate sampling locations, at Wagstaffe (1, 2) and Ettalong (3, 4, 5).

Sampling

Invertebrates and environmental variables at each of the study sites were sampled over five days in October and November 2014 (i.e. the Australasian spring). Timing of these sampling events coincided with a relatively developed community as it was felt that autumnal and winter sampling would have naturally reduced abundances and richnesses, making identifying differences problematic. To test the hypothesis that differences in sediment communities between paired sites with and without seawalls would be greater at high intertidal elevations close to the base of the seawall than at lower intertidal elevations, sampling was conducted at high, mid and low intertidal heights. The high intertidal elevation was set at the wrack line (~1.6 m above the Lowest Astronomical Tide [LAT]), which corresponded to the base of the seawall at the armoured sites. The low intertidal elevation corresponded to the average spring low tide mark (~0.3 m above LAT), while the mid intertidal elevation was half way in between the high and low tide marks (i.e. ~0.9 m above LAT). The width of the shoreline did not detectably differ between sites with and without seawalls, at any of the locations.

To assess differences in sediment characteristics between sites with and without seawalls, replicate ($n = 3$) 2.5 centimetre (cm) diameter by 10 cm deep cores were taken at each tidal height of each site for each of grain size and organic/mineral content analysis. Sedimentary chlorophyll was sampled by coring the top 2 cm of sediment at each of the intertidal heights ($n = 7$) with a 1.5 cm diameter, 10 ml polypropylene centrifuge tube, to give approximately 2-3 g of sediment. Upon collection, tubes of sediment for chlorophyll extraction were immediately put on ice, in a darkened cooler, until transfer to a -30° C freezer within 4 hrs.

Grain size was determined by drying sediments at 60° C until they reached a constant weight, then calculating the proportion by weight of dried sediments retained on nested sieves ranging by half phi (ϕ) gradations from -1 to 4, and the proportion of sediments falling through the 4 ϕ sieve. Sedimentary mean grain size, mud and sand content were calculated using Gradistat v8 (Blott and Pye 2001), while sedimentary organic content was determined using a modification of the loss on ignition method (Heiri et al. 2001). Briefly, the sediment samples were pre-dried to a constant weight at 60° C, cooled to room temperature in a desiccator to ensure no moisture contamination, weighed, and then combusted at 450° C for four hours, with organic content calculated as the percent weight loss between drying and combustion. Sedimentary chlorophyll was assessed by a modified trichromatic method (APHA 2012) where approximately 2 grams of sediment were immersed in 10 ml of 90% acetone for 36 hours. The sediment/acetone mixture was agitated three times over the 36 hours and left to settle for 12 hours before measurement of light absorbance at 630, 647, 664, and 750 nm using a Shimadzu UV-mini 1240 spectrophotometer (Shimadzu; Sydney, Australia). Chlorophyll-*a* concentrations (per unit

volume of sediment) were calculated from these absorbances using the equations of Jeffrey and Humphrey (1975), with absorbance at 750 nm first subtracted from each value to control for the effect of any suspended particles in the samples.

Benthic cover at each field site was surveyed using replicate ($n = 7$) 0.5 x 0.5 m quadrats, placed haphazardly at each of the designated tidal heights of each study site. The quadrats were evenly strung with 10 by 10 strings to form 100 intersection points (Meese and Tomich 1992), under which we scored the % of primary cover including: (1) organic debris, (2) sediment (particles < 1 cm in diameter), (3) rock (particles > 1 cm in diameter), (4) live vegetation (e.g. seagrass, grass, sedges), and (5) anthropogenic litter (e.g. plastic, glass). Infauna were sampled in 10 cm diameter sediment cores depressed to a depth of 10 cm ($n = 7$ per tidal elevation, per study site). Sample cores were processed in the lab by wet sieving through a 500 micron mesh and preserving the remaining sediment/fauna in 10% formalin until fauna could be sorted. Once sorted, infauna were placed in 70% ethanol, enumerated, and identified to Family. Species identified through SIMPER analysis were further identified to species level.

Statistical Analysis

Differences in environmental and biological variables between sites with and without seawalls were assessed using 3-way univariate PERMANOVAs (Anderson et al. 2008) with the factors armouring (2 levels: fixed; seawall vs no seawall), location (5 levels: random), and height (3 levels: fixed; high, low, mid intertidal). The multivariate analysis was of the invertebrate community data set. Separate univariate PERMANOVAs were run on each of the total abundance and richness of invertebrates per sample, taxa identified by SIMPER (similarity percentages routine, PRIMER; Clarke 1993) as key discriminators in faunal communities between armouring treatments, as well as sediment and benthic cover variables that were identified by DistLM as best explaining benthic community structure (see below). The multivariate PERMANOVA, run on the invertebrate community data set, used Bray Curtis dissimilarity measures calculated from untransformed data, to which a dummy variable of 1 had been added to allow for the analysis of null abundances (Clarke and Gorley 2015). Univariate analyses used Euclidean distances calculated between untransformed data. P-values were interpreted as significant following adjustment using the Benjamini-Hochberg procedure, which corrects for the inflated false discovery rate associated with conducting multiple tests. All analyses were conducted in PRIMER v7 with PERMANOVA+ add-on (PRIMER v7: Clarke and Gorley 2015; PERMANOVA: Anderson et al 2008).

PERMDISP analyses were conducted prior to each analysis to determine if there were significant differences in multivariate dispersion among treatments (Clarke et al. 2014). These revealed significant differences in dispersion among locations and heights, but not between sites with and

without seawalls (Table 1). Hence, within levels of the other factors, any effect of armouring could be interpreted as not simply an effect of heterogeneity. Where PERMANOVAs detected significant main effects of or interactions involving armouring, full PERMANOVAs were followed by pairwise *a posteriori* tests assessing sources of effects.

Table 1; PERMDISPs testing for heterogeneity in the dispersion of invertebrate (a) abundances and (b) richness, as well as (c) multivariate environmental data, including benthic cover and sediment characteristics (i.e. Chlorophyll-a, grain size, and organic content), among levels of the factors location, height, and armour.

	F	df1	df2	p(perm)
<i>Abundances</i>				
Location	24.46	4	145	0.001
Height	12.46	2	147	0.002
Armour	0.29	1	148	0.71
<i>Richness</i>				
Location	10.83	4	145	0.001
Height	12.05	2	147	0.001
Armour	3.10	1	148	0.158
<i>Environmental</i>				
Location	23.66	4	205	0.001
Height	27.28	2	207	0.001
Armour	5.74	1	208	0.069

The SIMPER procedure assessed the average percent contribution of individual taxa to the Bray Curtis dissimilarity in infaunal communities between armoured and unarmoured sites. Those taxa with the greatest dissimilarity to standard deviation ratio were considered key discriminators (Clarke 1993). A distance based linear model (DistLM) of community abundance patterns with environmental data (sediment and cover variables) as the predictor variables was used to determine the suite of environmental variables (McArdle and Anderson 2001), identified using a corrected Akaike Information Criterion (AICc), that best explained spatial variation in benthic community structure among the sites. Draftsman's plots were run prior to the DistLM analysis and, for correlated variables, only one of them was included in the analysis.

Results

The five locations varied in sediment properties and benthic cover (Table 2). Locations at Wagstaffe were generally characterised by higher variability in mean grain size, a greater organic and mud content, and a greater cover of organic debris and live vegetation than locations at Ettalong (Table 2). Overall, 89 taxa were identified in this study, 72 of which were found at the Wagstaffe locations and 44 of which were found at the Ettalong locations, with 27 species shared between the two areas. At Wagstaffe, the dominant phyla were Annelida and Mollusca,

accounting for 57.9 % and 27.8 %, respectively, of total abundance. At Ettalong, Arthropoda dominated, accounting for 70.2 % of total abundance.

Table 2; Summary of sediment properties and benthic cover at each sampling location. $n = 9$ for sediment variables (excluding chl-*a*); $n = 21$ for chl-*a* and for benthic cover. Sand and mud grain size are between 0 and 3 ϕ (ϕ) and greater than 3 ϕ , respectively.

	Location 1	Location 2	Location 3	Location 4	Location 5
<i>Sediment</i>	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE	Mean \pm SE
Organic Matter (%)	1.3 \pm 0.2	1.4 \pm 0.1	0.6 \pm 0.1	0.4 \pm 0.0	0.5 \pm 0.0
Chlorophyll- <i>a</i> (mg/m ³)	1.1 \pm 0.1	1.4 \pm 0.2	1.7 \pm 0.3	0.4 \pm 0.0	0.5 \pm 0.1
Sand (%)	87.9 \pm 4.3	66.2 \pm 6.4	98.3 \pm 0.5	99.0 \pm 0.0	100.0 \pm 0.0
Mud (%)	2.6 \pm 0.3	4.5 \pm 0.9	0.2 \pm 0.1	0.0 \pm 0.0	0.0 \pm 0.0
Grain Size (μ m)	354.0 \pm 64.8	616.1 \pm 115.4	295.3 \pm 12.2	317.6 \pm 8.4	259.2 \pm 5.7
<i>Benthic Cover</i>					
Bare Sediment (%)	82.4 \pm 5.3	70.6 \pm 5.9	95.9 \pm 1.6	96.0 \pm 1.1	93.1 \pm 1.8
Organic Debris (%)	8.3 \pm 3.3	6.0 \pm 2.8	1.0 \pm 0.2	2.7 \pm 0.7	6.9 \pm 1.8
Live Vegetation (%)	6.4 \pm 2.2	2.5 \pm 1.0	0.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
Rock (%)	0.0 \pm 0.0	21.0 \pm 5.1	2.9 \pm 1.7	0.0 \pm 0.0	0.0 \pm 0.0
Anthropogenic litter (%)	2.9 \pm 1.3	0.0 \pm 0.0	0.2 \pm 0.1	1.4 \pm 1.0	0.0 \pm 0.0

Benthic infaunal community structure, total abundance and richness each displayed three-way interactions between location, tidal height and armouring (Table 3). At the high-intertidal elevation, significant differences between sites with and without seawalls were apparent in invertebrate abundance at locations 1 and 2, and richness at locations 1 and 3 only ($p_{\text{perm}} < 0.05$, *a posteriori* tests), with differences inconsistent in direction (Fig. 2 a, b). At the mid-intertidal elevation, abundance displayed significant differences between sites with and without seawalls at locations 2, 3, and 4, and richness at locations 3 and 4 ($p_{\text{perm}} < 0.05$, *a posteriori* tests). Whereas at the muddier locations, 1 and 2, mid-intertidal abundance was generally less at sites with than without seawalls, at the sandier locations, 3, 4, and 5, the opposite pattern was apparent, with both mid-intertidal abundance and richness generally greater at sites with than without seawalls (Fig. 2 c, d). At the low intertidal elevation, significant differences in invertebrate abundance between sites with and without seawalls were apparent at location 4 and in richness at locations 3 and 5 ($p_{\text{perm}} < 0.05$, *a posteriori* tests), but as with differences displayed in the high intertidal, the direction and magnitude of these differences was spatially variable (Fig. 2 e, f).

Table 3; Results of 3-way PERMANOVAs testing for differences in (a) invertebrate community composition, (b) abundance and (c) richness between armoured and unarmoured sites (Ar), at each of 5 locations (Lo), and 3 intertidal heights (He). Significant terms (at $\alpha = 0.05$) are shown in bold. The outcome of a posteriori tests are shown on Figure 2.

Factor	Community Structure				Abundance			Richness		
	df	MS	F	<i>p</i> (mc)	MS	F	<i>p</i> (mc)	MS	F	<i>p</i> (mc)
Lo	4	23394.0	15.5	< 0.001	19696.0	35.6	< 0.001	19476.0	64.8	< 0.001
He	2	24184.0	2.6	0.003	28373.0	4.1	0.016	15208.0	6.4	0.007
Ar	1	6457.0	0.9	0.547	3101.9	0.7	0.538	768.7	0.3	0.740
Lo x He	8	9465.2	6.3	< 0.001	6855.0	12.4	< 0.001	2360.8	7.9	< 0.001
Lo x Ar	4	6955.0	4.6	< 0.001	4206.0	7.6	< 0.001	2303.3	7.7	< 0.001
He x Ar	2	6096.3	0.8	0.772	3074.9	1.1	0.401	1222.3	0.9	0.501
Lo x He x Ar	8	7541.1	5.0	< 0.001	2878.3	5.2	< 0.001	1381.2	4.6	< 0.001
Res	120	1505.1			553.2			300.5		
Total	149									

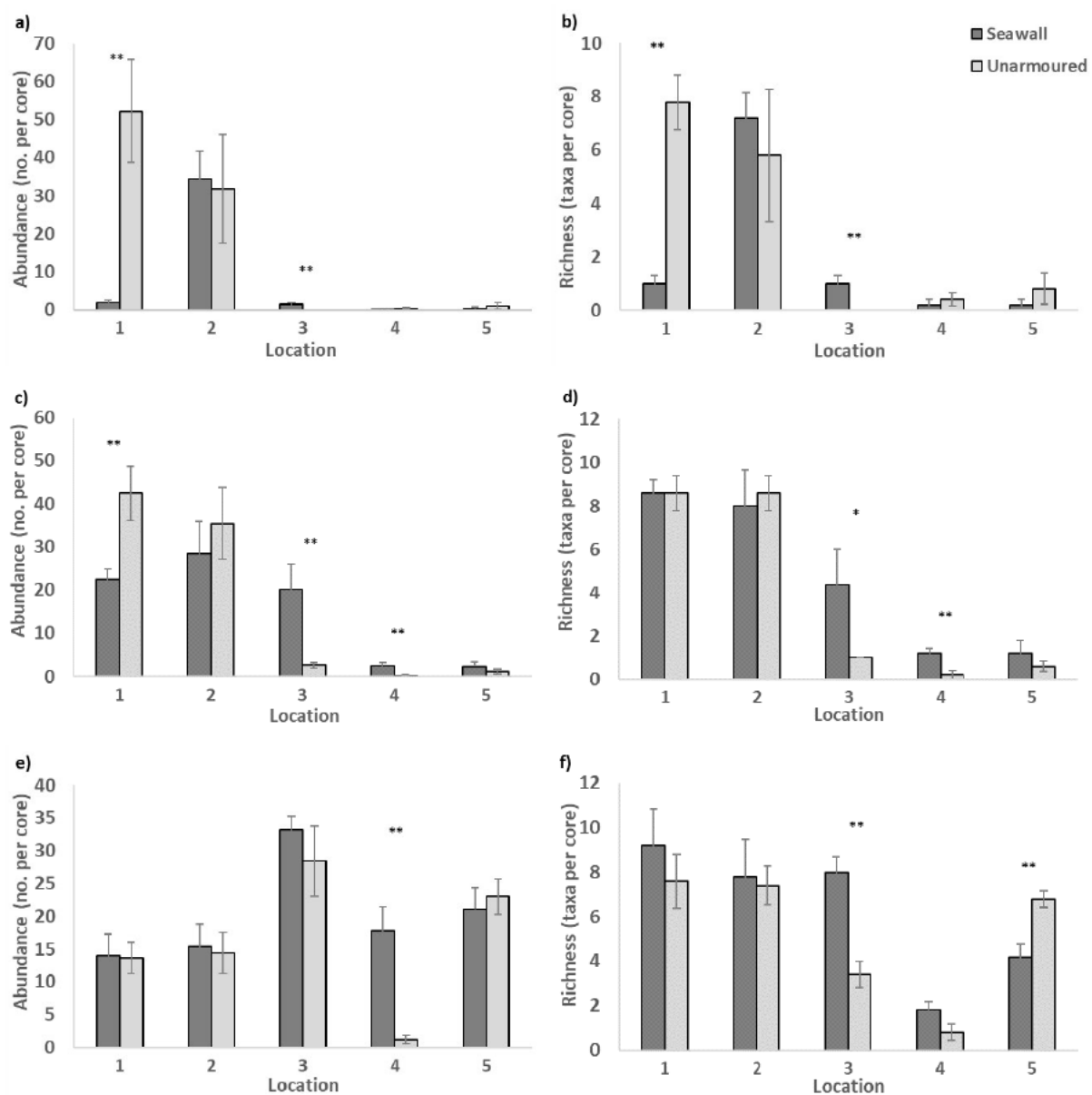


Figure 2; Mean (\pm SE) abundance and richness of invertebrates at high (a & b), mid (c & d), and low (e & f) elevations of sites with and without seawalls, at each of five locations of Brisbane Waters, NSW, Australia. Sites 1-2 were at Wagstaffe and 3-5 at Ettalong. Significant differences between sites with and without a seawall (PERMANOVA a posteriori pairwise tests) are marked (*: $p < 0.05$; **: $p < 0.01$). $n = 7$.

The DistLM analysis found that collectively, percent organic matter, percent of mud content, and the chlorophyll-*a* concentration of sediment best explained variation in faunal abundance, accounting for 30.3% of the variation and producing an AICc value of 238.91 (Fig. 3). Organic matter, mud, and chlorophyll-*a* each displayed significant three-way interactions between location, tidal height, and armouring (Table 4). While the most striking differences seen for the organic matter and mud content were between locations, with higher content at Wagstaffe locations (1,2) than Ettalong locations (3,4,5) across all intertidal elevations (Fig. 4), there were also significant differences between sites with a seawall and without. There was significantly lower organic matter content with a seawall than without at all intertidal elevations for location 1, the mid-intertidal of location 4, and the low intertidal of location 5 ($p_{(\text{perm})} < 0.05$, *a posteriori* tests), but higher organic matter content with a seawall than without at the mid intertidal of location 5 ($p_{(\text{perm})} < 0.05$, *a posteriori* tests) (Fig. 4a,d,g). Mud content was significantly higher with a seawall than without at the high intertidal of location 2, the mid intertidal of locations 2 and 4, and the low intertidal of location 4 ($p_{(\text{perm})} < 0.05$, *a posteriori* tests), but lower mud content was seen with a seawall than without at the high intertidal of location 3, and the low intertidal of locations 2 and 5 ($p_{(\text{perm})} < 0.05$, *a posteriori* tests) (Fig. 4b,e,h). Chlorophyll-*a* concentrations were significantly higher with a seawall than without at all intertidal elevations of locations 2, 3, and 4 ($p_{(\text{perm})} < 0.05$, *a posteriori* tests), but lower chlorophyll-*a* concentrations were seen with a seawall than without at the mid intertidal of location 1 and the low intertidal of location 5 ($p_{(\text{perm})} < 0.05$, *a posteriori* tests) (Fig. 4c,f,i).

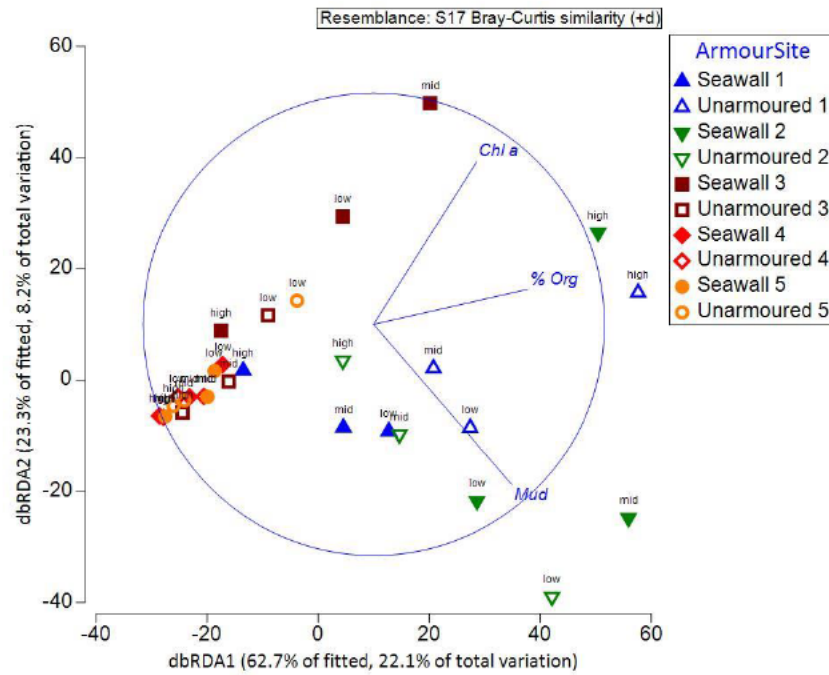


Figure 3; Distance based linear model (DistLM) of benthic community abundance patterns as a result of environmental parameters, overlay indicating predictor variables of the best model determined by AICc.

Table 4; Results of 3-way PERMANOVA testing for differences in (a) organic matter content, (b) mud content, and (c) chlorophyll-a content between armoured and unarmoured sites (Ar), at each of 5 locations (Lo), and 3 intertidal heights (He). Significant terms (at $\alpha = 0.05$) are shown in bold. The outcome of a posteriori tests are shown on Figure 4.

Factor	df	Organic Matter				Mud			Chlorophyll-a		
		MS	F	p(mc)		MS	F	p(mc)	MS	F	p(mc)
Lo	4	4.6	191.0	< 0.001		< 0.1	203.1	< 0.001	9.2	46.6	< 0.001
He	2	0.1	0.4	0.722		< 0.1	2.2	0.177	1.8	0.9	0.444
Ar	1	1.6	0.9	0.395		< 0.1	0.5	0.503	15.2	1.8	0.252
Lo x He	8	0.4	16.4	< 0.001		< 0.1	34.7	< 0.001	2.1	10.6	< 0.001
Lo x Ar	4	1.5	68.2	< 0.001		< 0.1	11.9	< 0.001	8.4	42.3	< 0.001
He x Ar	2	0.5	1.0	0.405		< 0.1	1.3	0.338	1.9	0.8	0.486
Lo x He x Ar	8	0.5	21.1	< 0.001		< 0.1	20.8	< 0.001	2.3	11.8	< 0.001
Res	180	< 0.1				< 0.1			0.2		
Total	209										

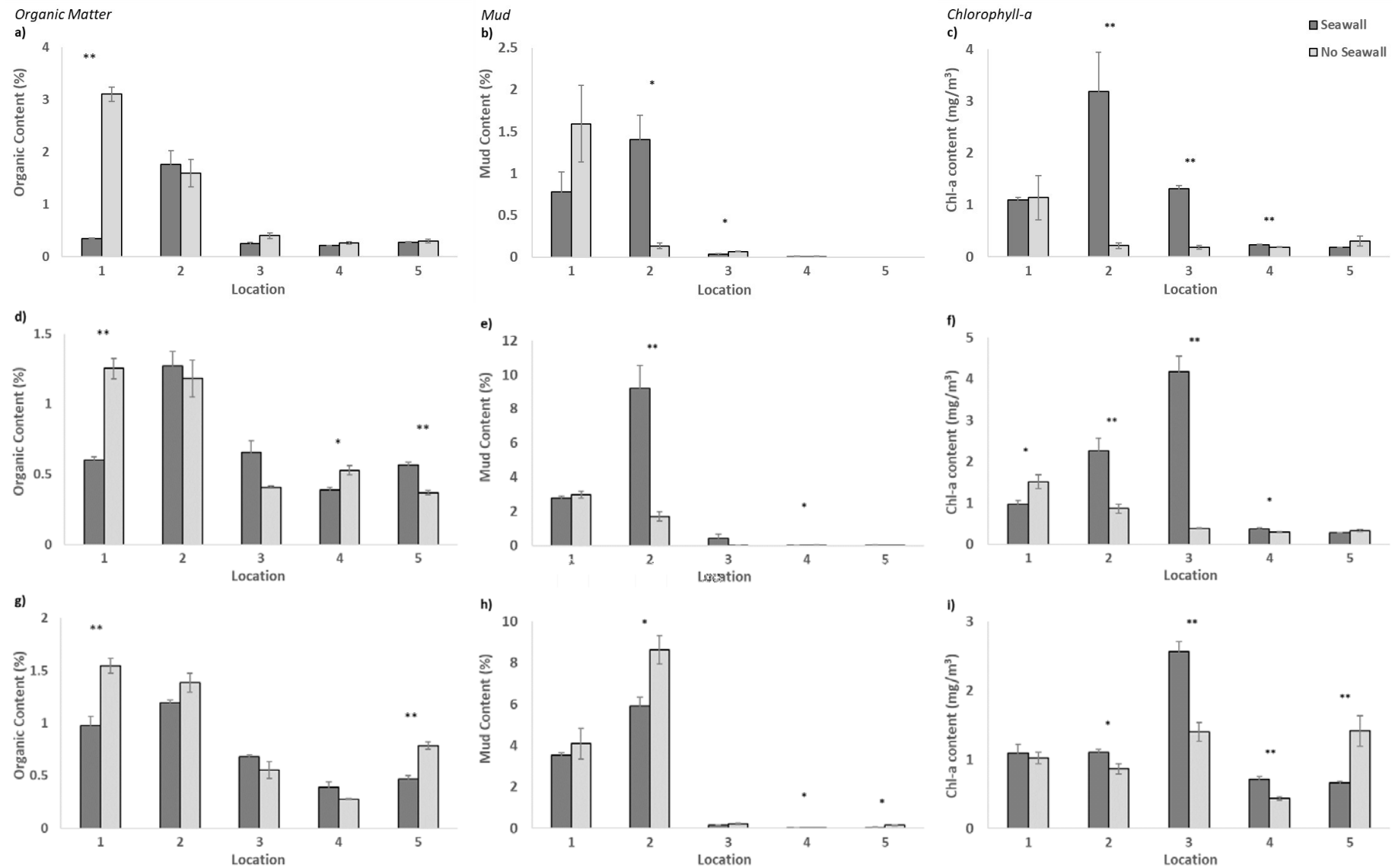


Figure 4; Mean (\pm SE) organic matter, mud, and chlorophyll-a content at high (a, b, c), mid (d, e, f), and low (g, h, i) elevations of sites with and without seawalls, at each of five locations of Brisbane Waters, NSW, Australia. Sites 1-2 were at Wagstaffe and 3-5 at Ettalong. Significant differences between sites with and without a seawall (PERMANOVA *a posteriori* pairwise tests) are marked (*: $p < 0.05$; **: $p < 0.01$). $n = 3$.

SIMPER analysis indicated that at the Wagstaffe locations (1, 2), the nereid annelid *Australonereis ehlersi* and the mactrid bivalve *Spisula trigonella* contributed most to dissimilarity in faunal communities between sites with and without seawalls, while at the Ettalong locations, the exoedicerotid amphipod, *Exoediceros fossor* was the most important contributor. The abundance of each of these three taxa responded to a significant interaction between location, intertidal height, and armour (Table 5). At the mid- and low-intertidal elevations of the Ettalong (3,4,5) locations, where *Exoediceros fossor* was most typically found, the amphipod was generally more abundant at sites with than without a seawall (Fig. 5 d, g), although at the low-intertidal of location 3 the opposite pattern was apparent. *Australonereis ehlersi* and *Spisula trigonella*, by contrast, displayed spatially variable patterns with respect to seawalls (Fig. 5 b, c, e, f, h, i). While each of these taxa were more abundant at sites with than without a seawall at the high intertidal of the Wagstaffe locations (1, 2; Fig. 5 a,b), at the mid-intertidal elevation the reverse pattern was seen (Fig. 5 d, e) although this pattern was only significant for *A. ehlersi* at location 2, and at the low intertidal elevation, patterns of difference between sites with and without seawalls were variable (Fig. 5 h,i).

Table 4; Results of 3-way PERMANOVAs testing for differences in the abundances *Australonereis ehlersi*, *Spisula trigonella*, and *Exoediceros fossor* between armoured and unarmoured sites (Ar), at each of 5 locations (Lo), and 3 intertidal heights (He). Significant terms (at $\alpha = 0.05$) are shown in bold. The outcome of a posteriori tests are shown on Figure 4.

Source	<i>Australonereis ehlersi</i>				<i>Spisula trigonella</i>			<i>Exoediceros fossor</i>		
	df	MS	F	<i>p</i> (mc)	MS	F	<i>p</i> (mc)	MS	F	<i>p</i> (mc)
Lo	4	3764.5	9.69	< 0.001	4562.5	14.56	< 0.001	9010.7	36.61	< 0.001
He	2	2528.9	0.87	0.493	1284.3	0.39	0.806	10295.0	3.99	0.023
Ar	1	315.7	0.25	0.810	536.2	0.33	0.751	4721.2	2.06	0.181
Lo x He	8	2921.5	7.52	< 0.001	3329.9	10.63	< 0.001	2577.4	10.47	< 0.001
Lo x Ar	4	1272.0	3.27	0.003	1639.4	5.23	< 0.001	2290.4	9.30	< 0.001
He x Ar	2	2181.5	0.96	0.44	3405.4	1.50	0.248	721.8	0.16	0.972
Lo x He x Ar	8	2272.2	5.85	< 0.001	2270.8	7.25	< 0.001	4656.0	18.92	< 0.001
Res	120	388.4			313.28			246.2		
Total	149									

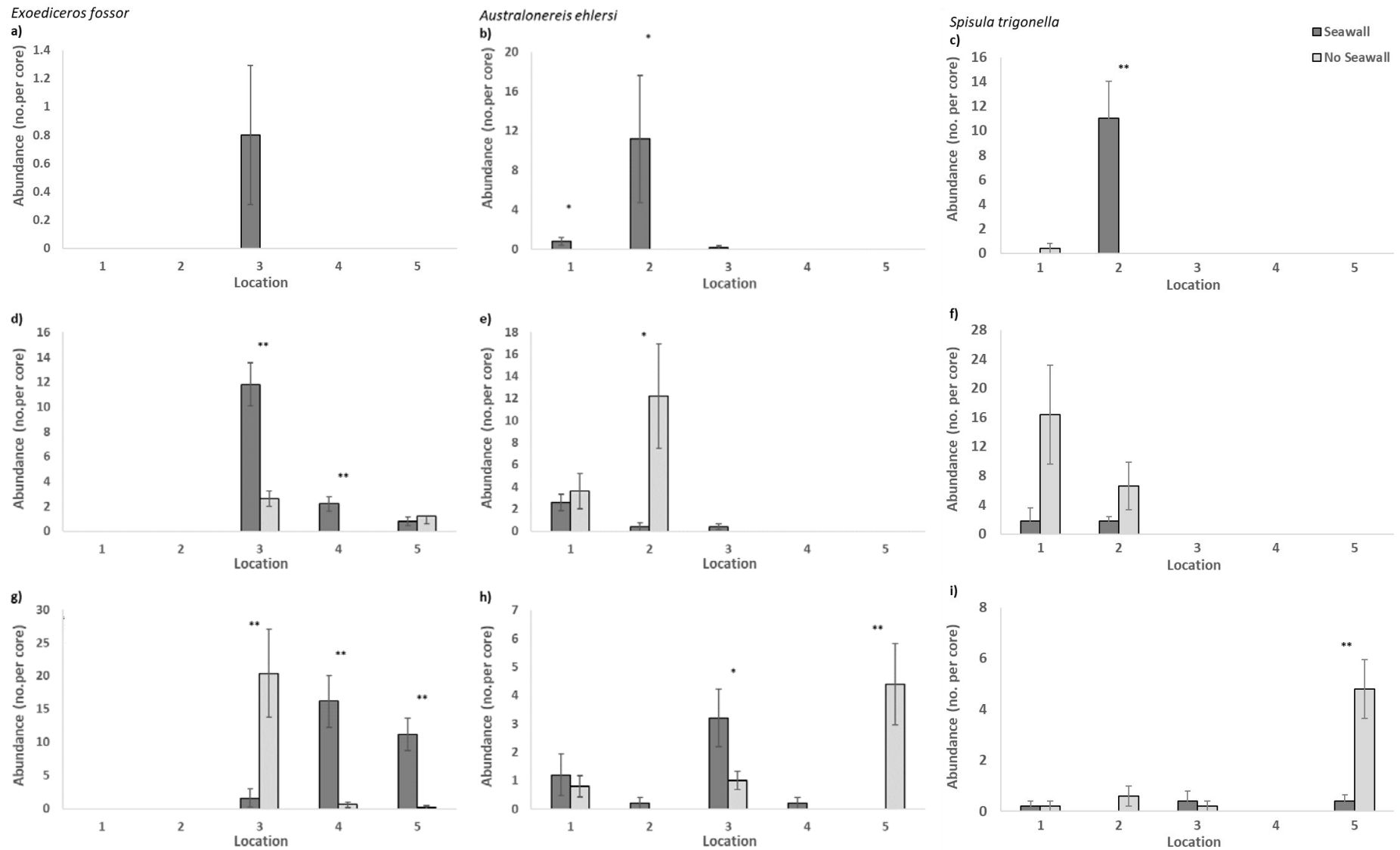


Figure 5; Mean (\pm SE) abundance of *Exoediceros fossor*, *Austalonereis ehlersi*, and *Spisula trigonella* at high (a, b, c), mid (d, e, f), and low (g, h, i) elevations of sites with and without seawalls, at each of five locations of Brisbane Waters, NSW, Australia. Sites 1-2 were at Wagstaffe and 3-5 at Ettalong. Significant differences between sites with and without a seawall (PERMANOVA a posteriori pairwise tests) are marked (*: $p < 0.05$; **: $p < 0.01$). $n = 7$.

Discussion

Coastal armouring and the resultant habitat modification is an increasing threat to ecological communities, and the key ecosystem services they support (Bishop et al. 2017; Dugan et al. 2017; Heery et al. 2017). Here we found differences in infaunal communities between shorelines with and without seawalls which varied spatially, in magnitude and direction, among locations and tidal elevations. Despite predictions that differences would be most apparent at high intertidal elevations, where habitats are most proximate to the artificial structures, the most spatially consistent effects of seawalls were apparent at mid intertidal elevations. Whereas invertebrate communities displayed weak and idiosyncratic patterns with respect to seawalls at the high and low intertidal elevations, at the mid-intertidal elevation spatially consistent effects were evident across locations of similar sediment characteristics. At muddy sites, mid intertidal invertebrates were generally less abundant at sites with than without seawalls. By contrast, at sandy sites, mid intertidal invertebrates were more abundant and richer in the presence than the absence of seawall.

The greater difference in invertebrate communities between sites with and without seawalls at mid than high or low intertidal elevations is likely to reflect an interaction between the proximity of habitat to seawalls and traits of the resident biotic communities that influence their susceptibility to perturbation. The high intertidal zone which, in this study, was most proximate to seawalls, supported invertebrate communities that were more species poor compared to those lower on the shore, and that were presumably dominated by stress-tolerant species that are able to withstand the longer emersion time (Peterson 1991; Jaramillo et al. 1993). Prevailing stress may select for organisms that have enhanced resistance to local stressors and so are able to withstand further disturbance (Sanford and Kelly 2011) and in previous studies, these high intertidal communities have been demonstrated to display a high degree of resistance to perturbations (e.g. Schlacher and Thompson 2012). The mid intertidal zone, although further from seawalls, supported a more diverse invertebrate community potentially comprised of species more susceptible to perturbation, while the low intertidal zone, which was situated 16-40 m from the base of seawalls may simply have been too far away to be affected by disruptions from the seawalls themselves.

Spatially variable responses of infaunal communities to seawalls may be attributable to differences in local abiotic conditions, the local species pool and/or the design of seawalls and their date of construction (Heery et al. 2017). Here, the key predictor of how invertebrate communities differed between sites with and without seawalls appeared to be whether the

location had muddy or sandy sediments. The pattern displayed by invertebrate abundance at muddy locations was consistent with previous studies, which have generally found reduced abundances and richness of invertebrates at armoured than unarmoured sites (Dethier et al. 2016; Heerhartz et al. 2016; Rolet et al. 2015). These studies have attributed such negative effects of armouring to a reduced shoreline width, which reduces the available space for wrack subsidies to accumulate (Harris et al. 2014; Heerhartz et al. 2016; Sobocinski et al. 2010). Here, however, shoreline width was similar between pairs of shorelines with and without seawalls, and we did not find differences in wrack volumes between these stretches, presumably because the seawalls were placed just below the mean high-water mark. Although it is often assumed that at wave exposed sites, rebound of waves by seawalls may coarsen sediments, and lower organic matter resources (Bozek and Burdick 2005), our study, like others (e.g. Dethier et al. 2016) did not find any consistent effect of armouring on these variables at either the muddy or sandy locations. At the sandy locations, which were low in sediment organic content, positive effects of seawalls on abundance and richness may instead result from seawalls enhancing organic subsidies to sediments through their provision of a substrate for algal growth (Bishop and Kelaher 2007; Rossi and Underwood 2002). Higher chlorophyll content of the sediment was found at sites with than without a seawall at 3 of the 5 locations in this study. Alternatively, seawalls may enhance abundances of invertebrates by lowering desiccation stress through enhanced moisture retention of sediments through shading (Kon et al. 2010). However, we did not measure moisture retention or shading effects. It is also possible that the differing ages of the seawalls contributed to differences in their impact at sandy as compared to muddy sites. Shallow subtidal infauna display localised responses to seawall construction, that disappear rapidly with time (Bilkovic and Mitchell 2014).

The differing patterns spatial patterns at sandy and muddy locations may reflect differences in the species pool that is present at each location. Consistent with paradigms about effects of sediment grain size on fauna (Gray 1974; Sanders 1958), we found marked differences in the invertebrate communities of sandy and muddy sites. Whereas the sandy sites were dominated by amphipods such as the exoedicerotid *Exoediceros fossor*, the muddy sites were dominated by annelids and molluscs such as the nereid *Austalonereis ehlersi* and the mactrid bivalve *Spisula trigonella*. At the mid-intertidal elevation at which each of these taxa were more abundant, *Exoediceros fossor* was more abundant at sites with than without a seawall, while the nereid and mactrid displayed the opposite pattern. In general abundances and the richness of fauna were much lower at sandy than muddy sites, suggesting a stronger abiotic filter selecting for those species that can tolerate the conditions (Jaramillo et al. 1993; McLachlan 1996, Brazeiro 2001; Strayer et al. 2012).

As this mensurative study did not include the before-after-control-impact design (Underwood 1991) necessary to causally attribute differences in the community structure of paired sites to seawalls, other factors may have contributed to the spatial differences observed in invertebrate communities between sites with and without seawalls. For example, even at the scale of tens of metres, stretches of shoreline may differ in their exposure to wind and boat waves, adjacent land use, and recreational pressures (Bilkovic et al. 2006; Bishop and Chapman 2004; Bozek and Burdick 2005; Schlacher et al. 2008). This can result in spatial variation in faunal communities that is just as great, if not greater, at scales of tens of metres as tens of kilometres (Morrissey et al. 1992). Particularly for the low intertidal elevation, which was 16 m (Ettalong locations) to 40 m (Wagstaffe locations) from the base of the seawall, other factors may be responsible for idiosyncratic differences seen between sites with and without seawalls. Unlike previous studies that demonstrate strong negative effects of seawalls on sedimentary communities, we did not find differences in the width of the intertidal zone between sites with and without seawalls (Heatherington and Bishop 2012; Heerhartz et al. 2016; Lucrezi et al. 2009; Manca et al. 2013).

Understanding when and where seawalls have the greatest impact on adjacent communities is critical to the development of strategies that minimise their ecological footprint. For example, if sites can be identified at which the biota is likely to be particularly sensitive to seawalls, alternative strategies for coastal protection, such as the establishment of living shorelines or beach nourishment may instead be prioritised (Bilkovic et al. 2016; Currin et al. 2010; Speybroeck et al. 2006). Alternatively, if the mechanisms by which negative impacts arise are understood, it may be possible to modify seawall design in such a way that reduces impact (Firth et al. 2016; Bishop et al. 2017). The results of this study suggest that the effects of seawalls on infaunal communities may display considerable among-location variation even within relatively narrow geographic areas. Establishing cause-effect relationships between seawalls and changes to biota, and the environmental factors that mediate this, will be critical to the development of innovative strategies in the face of ongoing coastal urbanisation.

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4. Comparison of wrack dynamics and habitat structure between natural and seawall modified mangrove forests

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Abstract

Wrack, dead organic matter that naturally accumulates at the high-water mark of intertidal shorelines, underpins coastal food webs through its provision of food and habitat to invertebrates, and is an important carbon store. Coastal armouring may modify wrack deposits on shorelines by truncating the intertidal zone, or modifying the physical and biological processes that deliver and remove wrack. An initial survey of wrack deposits on shorelines of the Parramatta River, Sydney, Australia, armoured and unarmoured by seawalls, revealed that seawalls eliminated the high-water wrack accumulation zone, limiting wrack deposits to mid and low intertidal elevations. By comparison to the high-shore wrack deposits of natural shorelines, the mid-shore wrack deposits on armoured shorelines were sparse. These mid-shore deposits contained a much greater terrestrial wrack component, dominated by *Casuarina* spp., than equivalent tidal elevations on unarmoured shores. Experiments tracking the fate of marked wrack on armoured and unarmoured shorelines revealed that the smaller wrack deposits on armoured than unarmoured shores were in part due to the lower retention of wrack on the former. Decomposition experiments suggested that the smaller wrack deposits on armoured than unarmoured shorelines may also be due to *Casuarina* litter accelerating the decomposition of the dominant wrack component, mangrove leaves, at armoured sites. The smaller wrack deposits, and faster turnover of these, on armoured shorelines has major implications for the terrestrial and marine food webs that depend on these as a source of nutrients and carbon. As a key mechanism for the smaller wrack deposits on armoured shorelines was the more rapid rate at which they were washed away, and wrack retention increases with habitat structure. Eco-engineering strategies that add structure to armoured sites may assist in mitigating impacts of seawalls to food webs dependent on wrack.

Introduction

Most primary production is not consumed by herbivores, but instead enters the detrital pathway (Cebrian and Lartigue 2004; Moore et al. 2004). In providing structural habitat for organisms, and a source of carbon and nutrients, detritus plays a major role in determining the composition of communities and the structure of food webs (Moore et al. 2004). Although some detritus is retained close to the source of its production, much of it is highly mobile and is transported large distances by wind and water to fuel food webs far removed from its source (Polis et al. 1997; Baring et al. 2018). For example, some estuarine mudflats are dependent on terrestrial ecosystems as a key carbon source (Cook et al. 2004). Conversely, marine seagrass and macroalgae can accumulate on the supratidal of sandy beaches (Dugan et al. 2003; Heck et al. 2008; Mellbrand et al. 2011). On estuarine and coastal shorelines, organic matter that accumulates at the high tide mark is referred to as wrack (Orr et al. 2005). The spatio-temporal dynamics (i.e. when and where it washes onshore, how long it persists), of wrack is a critical factor influencing the ecosystem functioning of coastal habitats (Dugan et al. 2003; Bishop and Kelaher 2007; Heck et al. 2008; Mellbrand et al. 2011).

Wrack dynamics are determined by the supply of organic matter to coastal shorelines, as well as its subsequent fate. Of the wrack arriving on shorelines, some will be retained across tidal cycles by structural elements of the environment, such as shoots, roots and cobbles, whilst a fraction is quickly dispersed away (Harris et al. 2014; Orr et al. 2005; Strain et al. 2018). For the wrack retained, traits of the wrack itself, environmental conditions, and the local decomposer community determine how quickly the wrack is decomposed, and hence its impact on the local benthic community (Ainley and Bishop 2015; Nicastro et al. 2012). Labile detritus, with a low carbon to nitrogen ratio, and a low fibre content, is generally more rapidly decomposed than more refractory detritus, with a high carbon to nitrogen ratio and a high fibre content (Enríquez et al. 1993; Melillo et al. 1982). The presence of secondary metabolites may determine the palatability of wrack to decomposer communities (Alongi 1987; Hättenschwiler and Vitousek 2000). Whereas small quantities of labile wrack may fuel benthic systems, large quantities can negatively impact productivity by triggering sediment anoxia through over stimulation of bacterial metabolism (Bolam et al. 2000; Norkko and Bonsdorff 1996; Thrush 1986).

Decomposition rates of wrack are not only determined by traits of individual litter components, but also the composition of the litter mix (Blair et al. 1990; Moore and Fairweather 2006; Wardle et al. 1997). Decomposition rates may display large non-additive effects of litter-mixing as a result of spillover of decomposition-enhancing nutrients or microbes from one component to another (Gartner and Cardon 2004; Hättenschwiler et al. 2005). Environmental conditions such as wind, temperature, and water motion can influence decomposition by influencing reaction

rates, and rates of physical wrack fragmentation (Hammann and Zimmer 2014; Walse et al. 1998).

Urbanisation is increasingly modifying detrital pathways by altering wrack sources, patterns of wrack transport and accumulation, as well as decomposition (Bishop et al. 2010; Harris et al. 2014; Heerhartz et al. 2014; Strain et al. 2018). Along many urbanised coastlines of Asia, America and Europe, seawalls now account for > 50% of the shoreline (Bacchiocchi and Airoidi 2003; Bulleri and Chapman 2010; Dugan et al. 2011; Lee and Li 2013). Seawalls can act as physical barriers to the cross-boundary transport of wrack (Bishop et al. 2017; Heerhartz et al. 2014) and, in modifying environmental conditions, may influence the retention and degradation of organic material (Harris et al. 2014; Strain et al. 2018). Stretches of shoreline armoured by seawalls and other coastal defences typically have a reduced width as compared to adjacent unarmoured stretches (Heatherington and Bishop 2012; Heerhartz et al. 2014), providing a reduced area for wrack accumulation (Heerhartz et al. 2014). The altered slope and habitat complexity of armoured shorelines can alter wrack retention and decomposition (Harris et al. 2014), whilst land-use changes at armoured sites can result in altered wrack composition (Heerhartz et al. 2014).

In urbanised south-east Australian estuaries, seawalls are increasingly being constructed to separate housing developments from mangroves. These seawalls truncate the width of the mangrove forest, and can alter the density of key structural elements, such as pneumatophores and saplings (Heatherington and Bishop 2012). These structural changes to mangrove forests may influence supply, retention and decomposition of wrack on these shorelines, ultimately influencing the structure and function of detrital food webs. Here, we ask the questions: (1) how does the type and amount of wrack accumulating in urban mangrove forests differ between armoured stretches of shoreline, with a seawall, and unarmoured stretches of shoreline, without a seawall; (2) how do differences in wrack retention and decomposition between armoured and unarmoured shorelines contribute to differences in their wrack deposits; and (3) what are the ramifications of an altered wrack composition at armoured as compared to unarmoured shorelines on decomposition processes? We hypothesise that, partially as consequences of reduced wrack retention and of accelerated decomposition, wrack deposits will be smaller on armoured than unarmoured shorelines. Where armouring results in the loss of the high intertidal zone of mangrove forests and increases the proximity of the mid intertidal zone to the terrestrial environment, we expect that there will be a greater subsidy of mangrove leaves to the terrestrial environment and of terrestrial wrack to the mid intertidal zone than on unarmoured shorelines. Where terrestrial wrack has a higher phenolic content and is more refractory than marine litter

sources in the mid intertidal zone, it is expected to slow their decomposition through negative spillover effects.

Methods

Study area

The study was conducted within two urbanised estuaries of New South Wales, Australia: Parramatta River (-33.84° S, 151.19° E), the major tributary of Sydney Harbour; and Brisbane Waters (-33.52° S, 151.33° E), situated approximately 80 km north of Sydney. Within each estuary, we identified *Avicennia marina* mangrove forests (hereafter ‘locations’) in which there were adjacent stretches (separated by < 1 km) of shoreline armoured and unarmoured by vertical seawalls (hereafter, ‘sites’). Previous mensurative studies suggest that this distance between armoured and unarmoured shorelines is sufficient for effects of armouring to be seen (Heatherington and Bishop 2012). Unarmoured stretches of shoreline were either ‘natural’ where the mangrove forest width was uninhibited by reclamation works or ‘constrained’ where the mangrove forest width was limited by land reclamation works, though without hard armouring. The armoured sites each had a vertical seawall constructed at a mid-intertidal elevation. In total there were six mangrove forests within the Parramatta River, five of which were censused for wrack deposits (PR2-6), three of which were utilised for wrack mobility and decomposition studies (PR1-PR3) and one of which was utilised for an experiment examining the effects of *Casuarina* spp. litter on mangrove leaf decomposition (PR3, Fig. 1). Two mangrove forests in Brisbane Waters were utilised for wrack mobility studies only (BW1-2; Fig. 1). All locations were characterised by semi-diurnal tides with a range of ~1.5 m, and were adjacent to urban parkland.

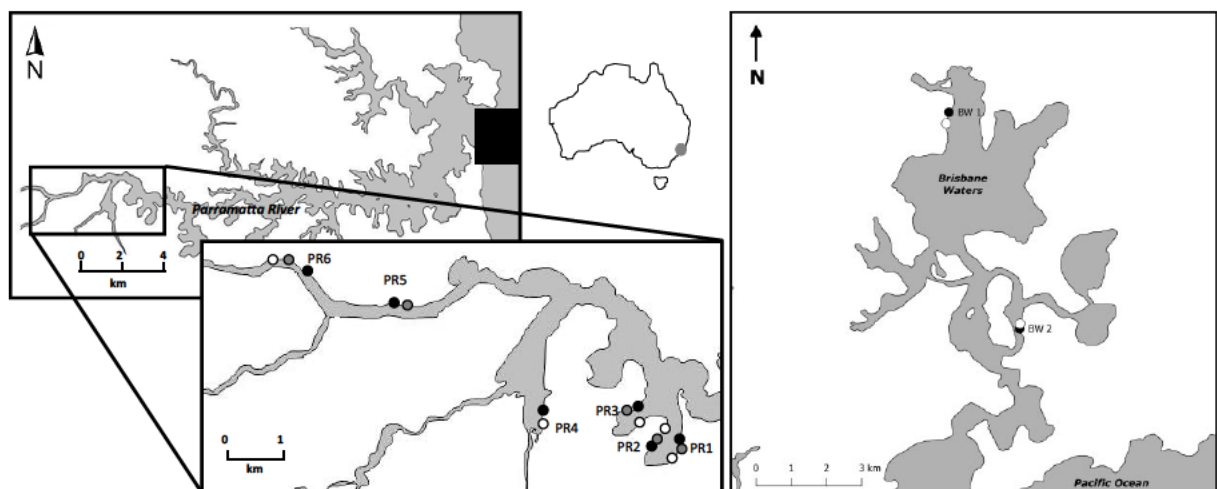


Figure 1; Map of the Parramatta River (left) and Brisbane Waters (right), NSW, Australia, showing the location of study sites. Along the Parramatta River, there were five locations, containing a stretch of shoreline armoured by a vertical seawall (armoured, black symbols) and one or more unarmoured stretches of shoreline at which the width of mangrove forest was either unconstrained by land-based infrastructure (natural, white symbols) or constrained, such that it was of similar width to the armoured stretch (constrained, grey symbols). In Brisbane Waters there were two locations, each containing an unarmoured shoreline (natural, white symbols) and a shoreline armoured by a vertical seawall (armoured, black symbols).

Wrack survey

To assess how the type and amount of wrack accumulating in urban mangrove forests vary as a function of armouring, a survey was conducted at five mangrove forests (PR2-6; Fig. 1) along the mid-upper Parramatta River in December 2013. Sampling was conducted in the Austral summer, as leaf shedding by *A. marina* in the Sydney region peaks at this time of year (Goulter and Allaway 1979). Each location contained at least one stretch of shoreline armoured by a seawall and one or more adjacent unarmoured stretches (Fig. 1). Where possible, both natural and constrained stretches of unarmoured shoreline were sampled adjacent to each armoured shoreline, but at two of the sites (PR4, PR5) this was not possible. The inclusion of both natural and constrained treatments in our design enabled us to disentangle whether any difference between places with and without a seawall was due solely due to a constriction in shoreline width (in which case, we expected [seawall = constrained] \neq natural) or due to effects of the seawall structure itself (in which case, we expected seawall \neq [constrained = natural]).

Within each site, sampling was done: (1) 1 m landward of either the seawall or the upper intertidal extent of the constrained or unarmoured mangrove forest (hereafter referred to as ‘supratidal’); (2) 0.5 m seaward of the seawall or at a corresponding elevation of the adjacent unarmoured stretches of shoreline (‘mid-intertidal’); and (3) 5 m seaward of the base of the seawall or at a corresponding elevation of the adjacent unarmoured stretches of shoreline (also, ‘mid-intertidal’). Additionally, at the natural sites we sampled: (4) 0.5 m seaward of the high intertidal limit of the mangrove forest; and (5) 5 m seaward of the high intertidal limit of the mangrove forest. This design allowed us to compare wrack deposits between equivalent tidal elevations of armoured, natural and constrained sites. It also enabled us to compare wrack deposits between the high intertidal wrack accumulation zone of natural sites and the mid-intertidal zone of the unarmoured and constrained sites, holding distance from the land-sea interface constant. At each position within each site, we censused the wrack assemblage using five haphazardly positioned 50 x 50 cm quadrats strung to produce 100 evenly spaced intersection points. Under each intersection point we recorded the presence or absence of wrack by type (species where possible or broad morphology – leaf, twig, branch – where this was not). For each shoreline type, at each location, we measured the width of the mangrove forest from the landward- to the seaward-most pneumatophore.

Wrack retention

At each of five study sites, three in the Paramatta River (PR1, PR2, PR3) and two in Brisbane Waters (BW1, BW2; Fig. 1), the retention of marked mangrove leaves was compared between armoured and unarmoured shorelines. In May 2016, for Parramatta River locations, and December 2016, for Brisbane Water locations, we placed marked leaves at four positions for

each location: (1) the high water line of unarmoured, natural sites (UH), where wrack naturally accumulates in the absence of a seawall; (2) the upper-most intertidal elevation (just below the seawall, in the mid-intertidal zone) of armoured sites (AM) where wrack accumulates in the presence of a barrier; and, to assess to what extent any difference in mobility of wrack between armoured and unarmoured sites is a function of the constriction of the intertidal zone alone versus additional effects of the seawall, (3) at a mid-intertidal elevation on unarmoured, natural, sites (UM), equivalent to the tidal elevation of wrack accumulation on armoured sites. At each elevation, five 25 x 25 cm plots were established at least 6 m apart. Each plot received 30 g (towel dried wet weight) of green to slightly yellowing, mature *A. marina* mangrove leaves (approx. 15 – 20 leaves), freshly collected from trees adjacent to the area, and spray-painted pink on one side with all-weather outdoor paint (British Paints Australia; neon pink, 81DM0159) to facilitate their identification from amongst other leaves. Spray paint was applied to leaves at least one hour before deployment. A control treatment, in which 30 g (towel dried wet weight) leaves were caged to facilitate their retention, revealed that they did not lose their paint over the experimental period of seven days. Seven days after deployment, a 2 m radius surrounding each experimental plot was thoroughly searched for marked leaves. Marked leaves found within the 2 m radius were dried to constant weight in a 60°C oven. The dry weight at 60°C of the control leaves after 7 days was also determined and used as a standard against which to calculate the proportion of leaves in each of the experimental plots that had been ‘retained’ (dry weight of experimental leaves/dry weight of control leaves).

Decomposition of mangrove leaves from a common source

To assess if armouring influences decomposition, and whether this is solely due to the constriction of the intertidal zone by the seawall, or also due to modification of other environmental conditions, a decomposition study was conducted using *A. marina* leaves from a common source. The experiment, replicated at three sites of the Parramatta River (PR1-3; Fig. 1), included the same three treatments as outlined for the wrack retention study, as well as an additional fourth treatment: (1) high tide wrack line of unarmoured, natural, sites (UH); (2) the upper-most intertidal elevation of armoured sites (AM); (3) a mid-tidal elevation of the unarmoured, natural, site (UM) that was comparable to that of treatment 2; and (4) a mid-tidal elevation of the unarmoured, constrained, site (CM) that was comparable to that of treatments 2 and 3.

The *A. marina* leaves used in the experiment were collected fresh from trees at a single study site, situated on Buffalo Creek, Boronia Park (33.82° S, 151.14° E), a tributary of Sydney Harbour, and were the oldest leaves, most likely to become detached from plants during storm events. Leaves were rinsed, towel dried and weighed into ~10 g quantities, with wet weights

recorded (to the nearest 1 mg) before deployment in 100 mm x 150 mm litter bags, constructed of 1 mm nylon mesh (Allied Filter Fabrics). This mesh size, commonly used in litter bag studies (e.g. Ainley and Bishop 2015), was chosen to allow small detritivores and leaf shredders (< 1mm) to enter bags, whilst minimizing loss of litter fragments through the mesh. Litter bags provide a standardised method with which to assess decomposition, with mass loss of litter in 1 mm mesh bags resembling that of loose, naturally entrained leaves in deposition zones (Cummins et al. 1980). Ten ~10 g samples of leaves were washed and dried, and then weighed before and after drying to constant weight at 60°C to determine the wet to dry conversion factor.

In July 2014, twenty litter bags per treatment were deployed within each site, at least 1 m apart, by pegging litter bags flat against the sediment surface using two diagonally positioned pegs. Previous research within the Sydney region indicates that leaves decompose rapidly at all times of year (Goulter and Allaway 1979). Five bags were collected from each treatment of each site after 2 weeks, 4 weeks, 2 months and 4 months. Upon collection leaves were gently washed over a 500 µm sieve to remove associated mud, and dried to constant weight at 60°C. The percentage of mass remaining in each litterbag was calculated relative to the mass deployed at the start of the experiment, using the wet to dry weight conversion factor to estimate dry weights at the start of the experiment.

The effect of Casuarina litter on mangrove decomposition

Among the differences between armoured and natural unarmoured sites was a higher biomass of *Casuarina* wrack at the former. To assess how *Casuarina* wrack might influence detrital pathways in armoured *A. marina* mangrove forests, we: (1) compared decomposition rates (as measured via mass loss), as well as C:N ratios and total phenolics, between *A. marina* leaves and *Casuarina* foliage (branchlets, comprising articles and leaves) and; (2) assessed how the presence of *Casuarina* foliage influences the mass loss, C:N ratio and total phenolics of *A. marina* when the two litter components are decomposed alongside. The experiment, conducted at a single location of the Parramatta River (PR3, Fig. 1), had six treatments: (1) 6 g mangrove leaves (M6; representing the scenario at unarmoured sites of mangrove leaves only); (2) 6 g mangrove leaves and 3 g *Casuarina* foliage (M6C3; representing the scenario of armoured sites, with moderate *Casuarina* inputs), (3) 9g mangrove leaves (M9; to control for the differing total litter biomass between treatments 1 and 2), (4) 6 g *Casuarina* foliage (C6; to assess how decomposition of *Casuarina* differs to mangrove leaves), (5) 3g mangrove leaves and 6 g *Casuarina* needles (M3C6; representing armoured sites with reduced mangrove and moderate *Casuarina* inputs), (6) 9 g *Casuarina* needles (C9; to match the M9 treatment in biomass). Litter was collected fresh from live *A. marina* mangrove and *Casuarina* trees so as to hold starting stage of decomposition constant, and was deployed in the 1 mm mesh litter bags described

above. As with the aforementioned *A. marina* decomposition experiment, ten 10 g samples of each litter type were used to determine the wet to dry weight conversion factor.

In September 2016, twenty-eight replicate litter bags of each of the six treatments (i.e. 168 in total) were deployed in groups of four haphazardly, at least 3 m apart, at the base of the seawall in the mid-intertidal zone. Litter bags were secured by pegging each flat to the sediment surface. Seven bags of each treatment were collected 7, 21, 42, and 77 days later. Upon collection, the contents of litter bags were emptied over 500 μm sieves, samples were rinsed, and the two litter components (i.e. *A. marina*, *Casuarina*) were separated from one another for drying at 60°C to constant weight. *Casuarina* and *A. marina* could easily be visually distinguished from one another based on distinct morphological features, even after the longest exposure time. The percentage mass loss of each litter component was calculated separately.

To assess: (1) differences between the two litter sources in their chemistry, and (2) the influence of litter mixing on the chemistry of each litter component, dried mangrove leaves from three randomly selected replicates of the treatments M6 and M6C3 and dried *Casuarina* foliage from three randomly selected replicates of the treatments C6 and M3C6 were ground to a fine powder for total phenolic and carbon, hydrogen, and nitrogen analysis. Total phenolic content was estimated using a modified Folin-Ciocalteu colorimetric assay (Ainsworth and Gillespie 2007; Singleton et al. 1999). Briefly, 4 – 4.5 milligrams (mg) of finely ground sample was added to 1 ml of 50:50 methanol and distilled water and incubated in the dark at 4°C for 24 h. Following incubation, 0.1 ml of the solution was added to 0.5 ml of Folin-Ciocalteu phenol reagent and 1.5 ml of 20 % sodium carbonate (Na_2CO_3) and further incubated in the dark for 2 h at room temperature. A standard curve was generated using the same process with various weights (0, 5, 10, 20, 30, 40, 50 mg) of Gallic Acid as the sample. The absorbances of the resulting solutions were determined at 765 nm using a spectrophotometer (UVmini-1240; Shimadzu Scientific Instruments (Oceania) Pty. Ltd., Australia), and the results are expressed in mg of Gallic Acid Equivalent units per g of dry leaf (mg GAE/g dry leaf). The carbon, hydrogen, and nitrogen was determined by running 2.5 – 3.5 mg of finely ground sample through a LECO CHN 900 analyser (LECO, USA), enabling the direct measurement of the percent content of nitrogen (%N), to a precision of $\pm 3\%$, and the estimation of the carbon-nitrogen ratio (C:N).

Statistical analysis

Paired t-tests assessed differences in the width of mangrove forests between: (1) armoured and natural; (2) armoured and constrained; and (3) natural and constrained shorelines.

Hypotheses about differences in wrack deposits and wrack retention between armoured, natural and/or constrained shorelines were tested using univariate permutational analyses of variance

(PERMANOVAs, Anderson et al. 2008). PERMANOVAs apply the traditional ANOVA partitioning procedure to a distance matrix, but use permutations to obtain P-values (Anderson et al. 2008). Consequently, unlike ANOVAs, PERMANOVAs do not have explicit assumptions about the underlying distributions of data and can use any distance matrix that is appropriate to the data. PERMANOVAs were used here because they allow interpretation of interaction terms within random factors (Anderson et al. 2008).

To test the hypothesis that at a supratidal elevation, there would be greater cover of mangrove leaves at armoured or constrained, than natural shorelines, two-way orthogonal PERMANOVAs with, the factors location (five levels, random) and shoreline type (3 levels, fixed; Natural, Seawall, Constrained) were run. To assess whether: (1) on armoured shorelines the mid-intertidal cover of mangrove leaves is less, but the mid-intertidal cover of terrestrial litter sources is greater than the high-intertidal wrack accumulation zone of armoured shorelines; (2) when tidal elevation is held constant there are differences in the cover of wrack constituents between armoured, natural and constrained sites; and (3) any differences between armoured and natural sites is solely a function of the reduced shoreline width, separate three-way PERMANOVAs, with the factors location, treatment (4 levels, fixed; natural high [UH], natural mid [UM], armoured mid [AM], constrained mid [CM]) and position (2 levels, fixed: 0.5 m vs 5 m below elevation of seawall or habitat margin) were run separately on each of mangrove leaves and total terrestrial wrack (which was dominated by *Casuarina* spp.). A 2-way PERMANOVA assessed differences in the retention of leaf litter among treatments (3 levels, fixed; AM, UH, and UM) and locations (5 levels, random).

PERMANOVAs were run on Euclidean distance matrices calculated from pairwise comparisons between arcsine-transformed proportionate wrack covers, with *p*-values calculated via Monte Carlo permutation of residuals under a reduced model. Prior to each PERMANOVA, the assumption of homogeneity of dispersion among treatments was evaluated using PERMDISP (Clarke et al. 2014) and unless otherwise reported was non-significant for levels of shoreline modification and tidal elevation. Where PERMANOVAs detected significant effects (at $\alpha = 0.05$) of factors of interest, *a posteriori* pair-wise PERMANOVAs assessed sources of differences. PERMANOVAs were run using the PERMANOVA+ add-on to the PRIMER 7 software (PERMANOVA, PRIMER v7.0.13; Anderson et al. 2008; Clarke and Gorley 2015).

For each of the two decomposition experiments, log-linear regressions assessed rates of litter mass loss for each treatment, at each site. Litter decay constants (*k*) were estimated from the slope of each regression line, with litter half-lives ($t_{1/2}$) calculated using the formula: $t_{1/2} = (\ln 2)/k$. We tested for significant differences in regression slopes (i.e. decay) among treatments using ANOVAs, followed by Tukeys post-hoc tests that examined sources of significant treatment

effects. For the experiment examining effects of armouring on mangrove leaf decay, a separate analysis comparing the four treatments (UH, UM, AM, CM) was run for each of the three study locations, due to the differing elevation of the seawall at each. For the experiment examining effects of litter mixing on decay rates, we conducted three ANOVAs. The first, comparing rate of mass loss among the four monospecific litter treatments (M6, M9, C6, C9) was to assess differences in mass loss between species (i.e. C vs M), and between litter volumes (i.e. 6 vs 9 g treatments). The second tested whether mass loss of mangrove litter differed between treatments with (M3C6, M6C3) and without (M6, M9) *Casuarina*, while the third examined how mass loss of *Casuarina* litter differed between treatments with (M3C6, M6C3) and without (C6, C9) mangrove leaves. For this second experiment, analogous analyses also assessed how litter mixing influences change through time in the total phenolic concentration, %N and C:N ratio of each litter component. Regression analysis and post-hoc testing was performed in R using the base package (R Development Core Team, 2013). Assumptions of the log-linear regressions were verified through visualization of fitted residuals and normality QQ plots.

Results

Wrack Survey

Overall, unarmoured, natural shorelines were significantly wider than armoured ($t = 4.4$, $df = 3$, $p = 0.011$) or unarmoured, constrained ($t = 4.8$, $df = 2$, $p = 0.021$) shorelines, the latter two of which did not significantly differ in width ($t = 0.8$, $df = 3$, $p = 0.242$; Fig. 2).

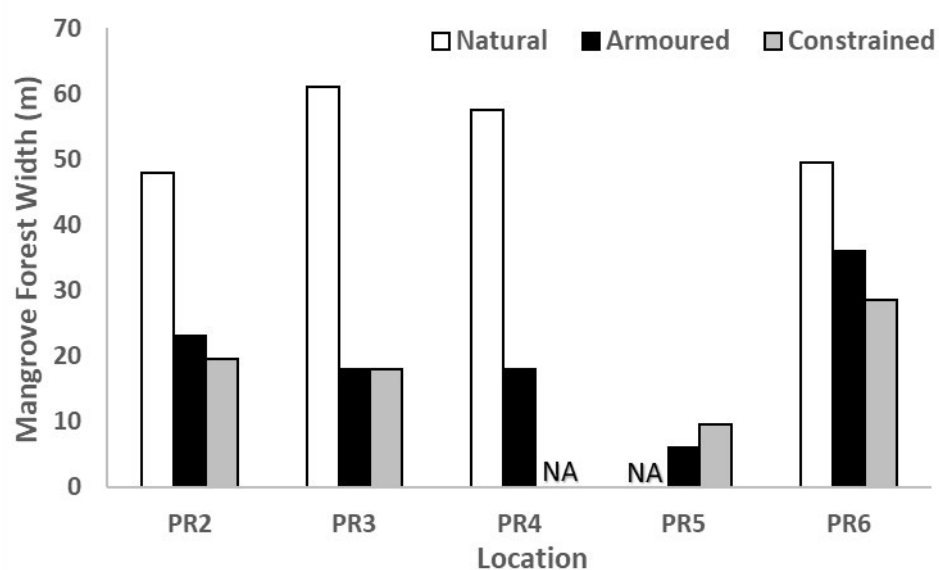


Figure 2; Widths in meters of natural (white), seawall-armoured (black) and constrained (grey) stretches of mangrove shoreline at each of five locations along the Parramatta River (see Fig. 1). NA = not available.

At the supratidal elevation, differences among shoreline types in the cover of mangrove wrack varied among locations (PERMANOVA, sig. shoreline type x location interaction; Pseudo- $F_{6, 52} = 10.4$, $p(\text{mc}) = 0.0001$; Fig. 3). At two of the four locations at which natural shoreline was sampled, the natural shoreline had a significantly smaller supratidal cover of mangrove leaves than the armoured shoreline (PR2: $t = 10.44$, $p(\text{mc}) = 0.0001$; PR4: $t = 2.95$, $p(\text{mc}) = 0.019$) with a similar, though non-significant trend evident at a third site (PR3: $t = 1.6$, $p(\text{mc}) = 0.151$). Of the three locations with natural shoreline that also had constrained shoreline, two had smaller wrack cover on the natural than constrained shoreline (PR3: $t = 3.52$, $p(\text{mc}) = 0.006$; PR6: $t = 2.86$, $p(\text{mc}) = 0.022$). One of the four locations with armoured and constrained shorelines had higher cover along the constrained than armoured shoreline (PR6: $t = 2.86$, $p(\text{mc}) = 0.019$). All other pairwise tests were non-significant.

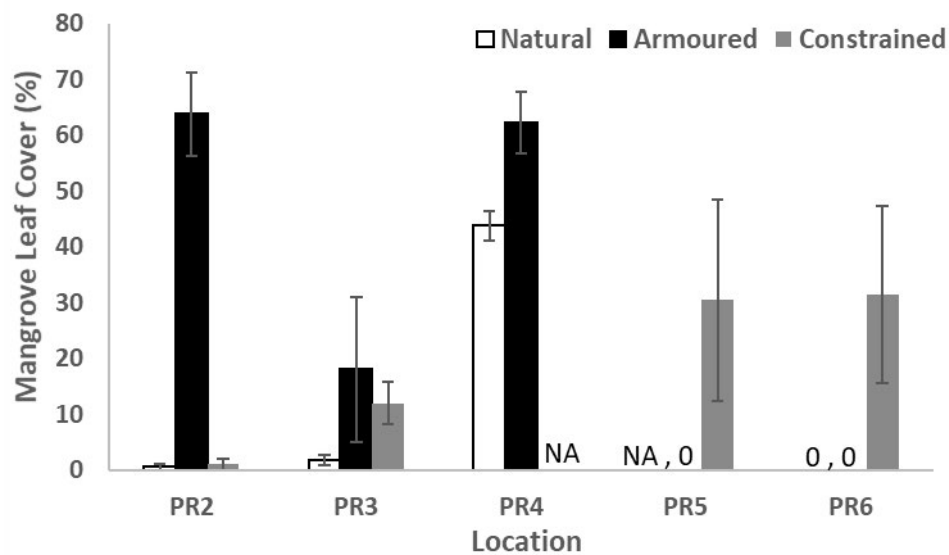


Figure 3; Mean (\pm SE) percent cover of mangrove leaves in the supratidal zone of natural (white bars), seawall-armoured (black) and constrained (grey) shorelines of mangrove forests. $n = 5$; NA = data not available; 0 = no wrack recorded.

In the mid-intertidal zone, the cover of terrestrial material, dominated by *Casuarina* foliage (which accounted for 93.3% of terrestrial litter cover), did not display any significant interactions or main effects of treatment or elevation (PERMANOVA: Pseudo- $F_{6, 104} = 0.90$, $p(\text{mc}) = 0.52$), however, a significant effect of location was seen (Pseudo- $F_{6, 104} = 10.81$, $p(\text{mc}) = 0.001$). Nevertheless, across all locations, terrestrial material was consistently absent from the mid intertidal zone of natural shoreline, only occurring in the mid intertidal of some seawall or constrained sites, among which considerable among- and within- site patchiness was seen (Fig. 4). While terrestrial material was evident at the high intertidal on the natural shoreline, two locations had a small amount of cover (PR3, PR2, 0.8 ± 0.4 %; PR4, PR2, 1.4 ± 0.6 %), and one location had extensive cover (PR2, 93.4 ± 0.4 %) which barred this location from being included in figure 3, as it would overwhelm the comparison of the mid intertidal. Dispersion of variances

consequently varied among locations (PERMDISP: $F_{4, 125} = 39.28$, $p(\text{perm}) = 0.001$) and treatments (PERMDISP: $F_{2, 127} = 3.46$, $p(\text{perm}) = 0.027$).

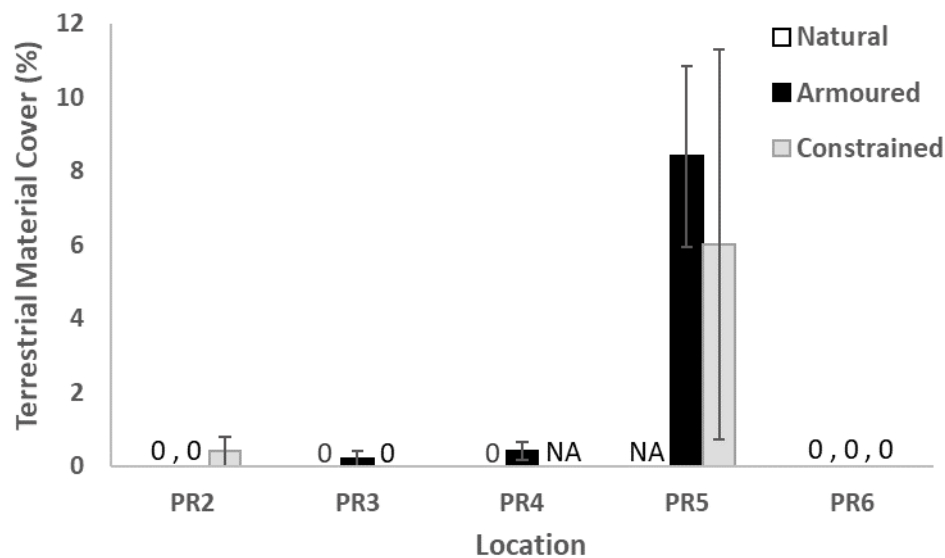


Figure 4; Mean (\pm SE) percent cover of terrestrial litter 0.5 m below the seawall or equivalent height in the mid intertidal zone of natural (white bars), seawall-armoured (black) and constrained (grey) shorelines of mangrove forests. $n = 5$. NA = data not available; 0 = no wrack recorded.

When mangrove litter deposits were compared between the high tide wrack accumulation zone of natural shorelines (0.5 and 5 m below the high tide mark) and the mid intertidal of natural, constrained, and armoured shorelines (0.5 and 5 m below the seawall or equivalent, or landward extent of the mangrove forest, in the case of constrained shorelines), a significant interaction between location, shoreline type (i.e. unarmoured mid, unarmoured high, seawall, constrained), and distance from the habitat margin was found (PERMANOVA: Pseudo- $F_{9, 136} = 5.79$, $p(\text{mc}) < 0.001$). Pair-wise *a posteriori* comparisons examined differences in shoreline type within each distance from the habitat margin, i.e. 0.5 m and 5 m, and location.

At the 0.5 m distance from the habitat margin, significantly higher cover of mangrove leaves were seen with armouring than the equivalent mid-intertidal of the natural shore at four locations (PR2: $t_8 = 4.72$, $p(\text{mc}) = 0.001$; PR3: $t_8 = 2.47$, $p(\text{mc}) = 0.040$; PR4: $t_8 = 3.84$, $p(\text{mc}) = 0.005$; PR6: $t_8 = 4.13$, $p(\text{mc}) = 0.003$) and the high intertidal of the natural shore at one location (PR2: $t_8 = 6.64$, $p(\text{mc}) < 0.001$). Similarly, there were significantly higher cover of mangrove leaves at the constrained shore than the equivalent mid-intertidal of the natural shore at three locations (PR2: $t_8 = 19.36$, $p(\text{mc}) < 0.001$; PR3: $t_8 = 3.43$, $p(\text{mc}) = 0.010$; PR6: $t_8 = 5.23$, $p(\text{mc}) = 0.001$) and the high intertidal of the natural shore at one location (PR2: $t_8 = 27.18$, $p(\text{mc}) < 0.001$). Conversely, significantly higher cover of mangrove leaves were seen at the high intertidal than the mid intertidal of the natural shoreline at two locations than the equivalent mid-intertidal of the natural shore at two locations (PR4: $t_8 = 2.88$, $p(\text{mc}) = 0.021$; PR6: $t_8 = 4.74$, $p(\text{mc}) = 0.001$),

but the mid intertidal of the natural shore had higher cover of mangrove leaves than the high intertidal of the natural shore at one location (PR2: $t_8 = 4.39$, $p(\text{mc}) = 0.001$) (Fig. 5b).

Differences in mangrove leaf cover were also seen at the 5 m distance from the habitat margin. Location PR6 had significantly lower cover on the constrained shore than, the armoured shore ($t_8 = 6.26$, $p(\text{mc}) < 0.001$), the high intertidal of the natural shore ($t_8 = 3.63$, $p(\text{mc}) = 0.006$) and the mid intertidal of the natural shore ($t_8 = 4.43$, $p(\text{mc}) = 0.003$). This location (PR6) also had significantly lower cover leaf cover at the mid intertidal than the armoured ($t_8 = 4.30$, $p(\text{mc}) = 0.002$) and high intertidal of the natural shore ($t_8 = 3.17$, $p(\text{mc}) = 0.013$). Additionally, there was significantly lower cover of mangrove leaves at the armoured shore than the high intertidal of the natural shoreline at two locations (PR2: $t_8 = 2.55$, $p(\text{mc}) = 0.036$; PR4: $t_8 = 2.51$, $p(\text{mc}) = 0.035$) and constrained at location PR2 (PR2: $t_8 = 3.47$, $p(\text{mc}) = 0.009$), while there was also lower cover at the mid intertidal than the high intertidal of the natural shore at location PR4 (PR4: $t_8 = 5.13$, $p(\text{mc}) = 0.001$) (Fig. 5b).

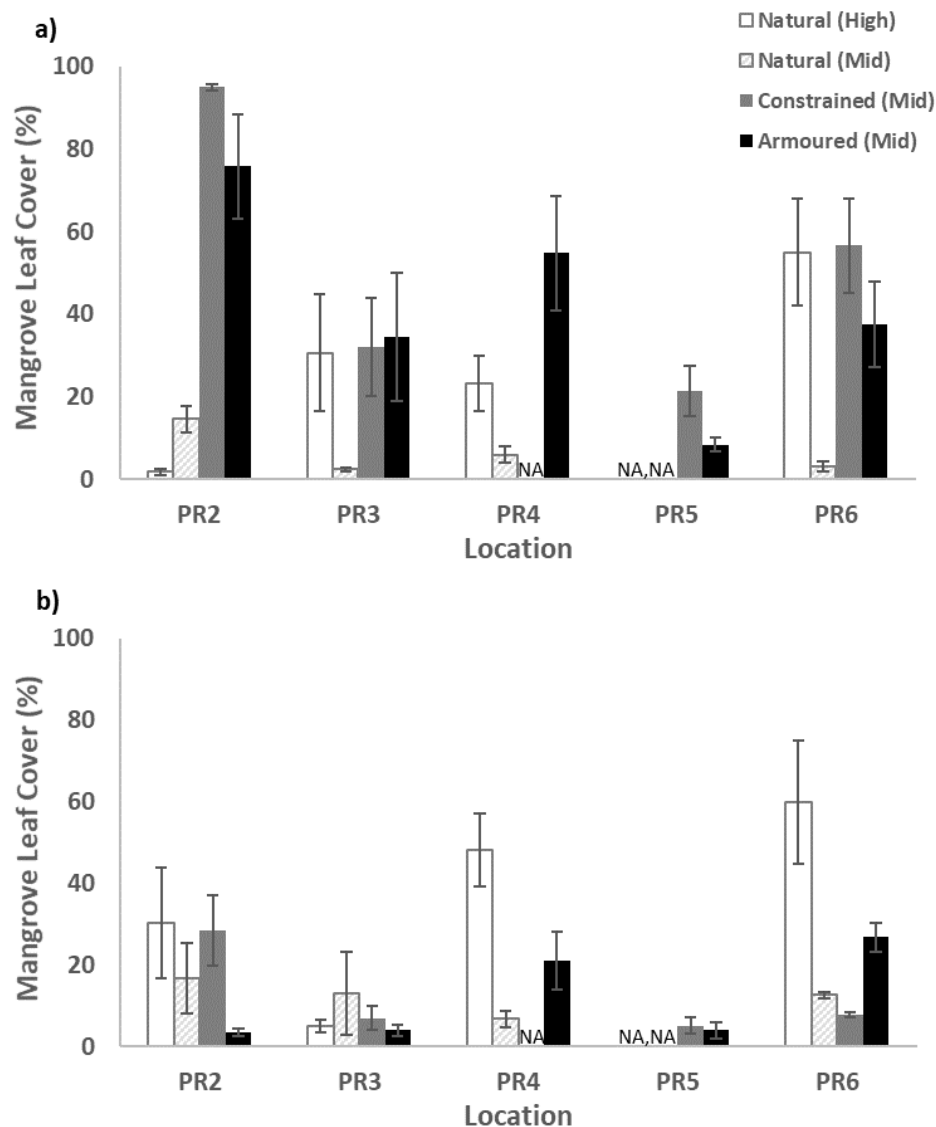


Figure 5; Mean (+SE) percent cover of mangrove leaves a) 0.5 m or b) 5m below the seawall (black bars) and at equivalent mid tidal elevations on the constrained (dark grey) and natural (white, patterned) shorelines, and at 0.5 or 5 m from the high intertidal extent of natural (white, no pattern) shoreline. $n = 5$. NA = data not available.

Wrack retention

Differences in wrack retention between armoured and unarmoured stretches of shoreline varied among locations (PERMANOVA, sig. Treatment x Location interaction; Pseudo- $F_{8, 61} = 3.21$, $p(\text{perm}) = 0.004$). At 2 of the 5 locations (PR2, BW1), a significantly smaller proportion of marked wrack was retained just seaward of the seawall (AM) than in the high-tide wrack deposition zone of adjacent unarmoured shoreline (UH; $p(\text{mc}) < 0.05$, *a posteriori* tests, sig. Treatment x Location) with no significant difference between these two treatments at the other locations (Fig. 6). Additionally, at 2 of the 5 locations (PR2, PR3), the proportion of wrack retained just below the seawall was smaller than at an equivalent tidal elevation of the natural shoreline (UM; $p(\text{mc}) < 0.05$, *a posteriori* tests, sig. Treatment x Location), with a similar, though non-significant (i.e. $p > 0.05$), trend at the other three locations (Fig. 6). Consequently, at 2 of the 5 locations (PR3, BW2) less wrack was retained at the higher (UH) than lower tidal elevation of the unarmoured shoreline (UM; $p(\text{mc}) < 0.05$, *a posteriori* tests, sig. Treatment x Location), with no significant difference between elevations at the other three locations (Fig. 6).

Table 3; Distance, in meters, from the mean low water mark to elevations on the shore, among which the retention of wrack was compared, at each of five locations (see Fig. 1). AM = armoured mid-intertidal; UM = unarmoured mid-intertidal; UH = unarmoured high-intertidal.

Location	Distance from mean low water (m)		
	AM	UM	UH
PR1	35	35	41
PR2	23	23	48
PR3	15	15	60
BW1	12	12	26
BW2	8	8	19

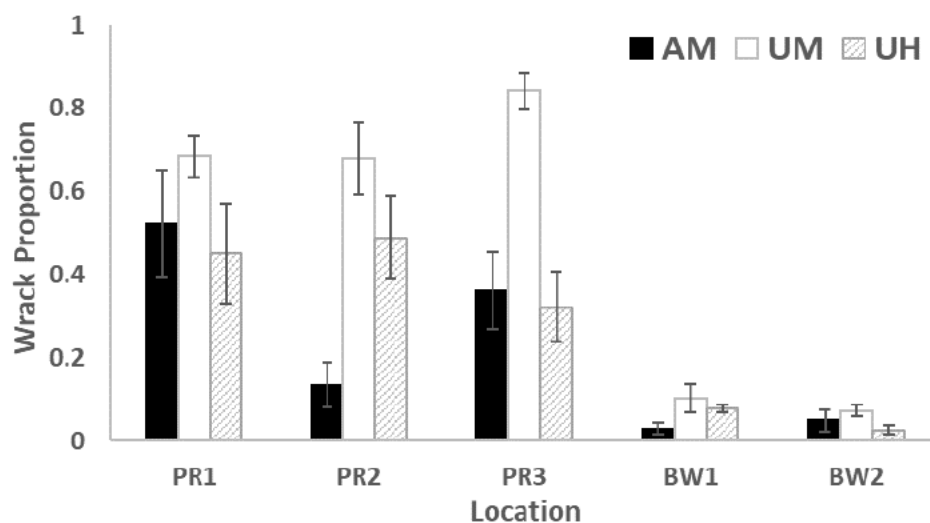


Figure 6; Mean (\pm SE) proportion by mass of marked wrack remaining within a 2 m radius of the placement location seven days after deployment. At each of five locations (PR1, PR2, PR3, BW1, and BW2), wrack was placed just below the base of a seawall (AM, black bars), at an equivalent intertidal elevation of adjacent armoured shoreline (UM, white) and at the high tide wrack line of adjacent unarmoured shoreline (UH, white with pattern), with $n = 5$ replicate plots.

Decomposition of mangrove leaves from a common source

Across shoreline treatments and locations, mangrove leaf decay constants ranged from 67-200 days (Table 2), with mass loss responding to the interacting effects of treatment, location, and time (ANOVA; $F_{17, 216} = 3.72$, $p < 0.001$). At two of the three locations at which mangrove litter bags were deployed, there was no significant effect of shoreline treatment on mangrove leaf decomposition (ANOVA; PR1: $F_{3, 73} = 2.14$, $p = 0.102$; PR2: $F_{3, 76} = 1.40$, $p = 0.2495$). However, at the third site (PR3), a significant effect of shoreline treatment was found (ANOVA; PR3: $F_{3, 75} = 12.184$, $p < 0.001$), with the rate of mangrove leaf decomposition significantly slower at the high intertidal elevation of the natural shoreline than at either the mid intertidal elevation of the natural ($t = 5.44$, $p < 0.001$) or the constrained shoreline ($t = 2.71$, $p = 0.041$). Additionally, at this location decomposition was significantly faster at the mid-intertidal elevation of the natural shoreline than, both, the armoured shoreline ($t = 4.87$, $p < 0.001$), and the constrained shoreline ($t = 2.676$, $p = 0.044$).

Table 2; The mean (\pm SE) decay constants (k), regression values (r^2), p -values, and litter half-life ($t_{1/2}$) of mangrove litter at each of three locations (PR1, PR2, PR3; Fig. 1). At each location, litter bags were deployed in the high intertidal wrack accumulation zone of natural, unarmoured stretches of shoreline (UH), at the base of seawalls (AM) or at equivalent mid intertidal elevations of adjacent natural (UM) or constrained (CM) unarmoured sites. Estimates of k and $t_{1/2}$ were obtained using log-linear regression.

LOCATION AND TREATMENT	r^2	k (d^{-1})	SE	$t_{1/2}$ (d)	p value
PR1					
UH	0.52	-0.008	0.002	82	< 0.001
UM	0.64	-0.003	0.001	200	< 0.001
CM	0.83	-0.007	0.001	93	< 0.001
AM	0.42	-0.008	0.002	83	0.001
PR2					
UH	0.81	-0.008	0.001	85	< 0.001
UM	0.82	-0.01	0.001	67	< 0.001
CM	0.64	-0.008	0.001	82	< 0.001
AM	0.58	-0.007	0.001	100	< 0.001
PR3					
UH	0.77	-0.004	0.001	161	< 0.001
UM	0.81	-0.008	0.001	90	< 0.001
CM	0.72	-0.007	0.001	97	< 0.001
AM	0.78	-0.005	0.001	128	< 0.001

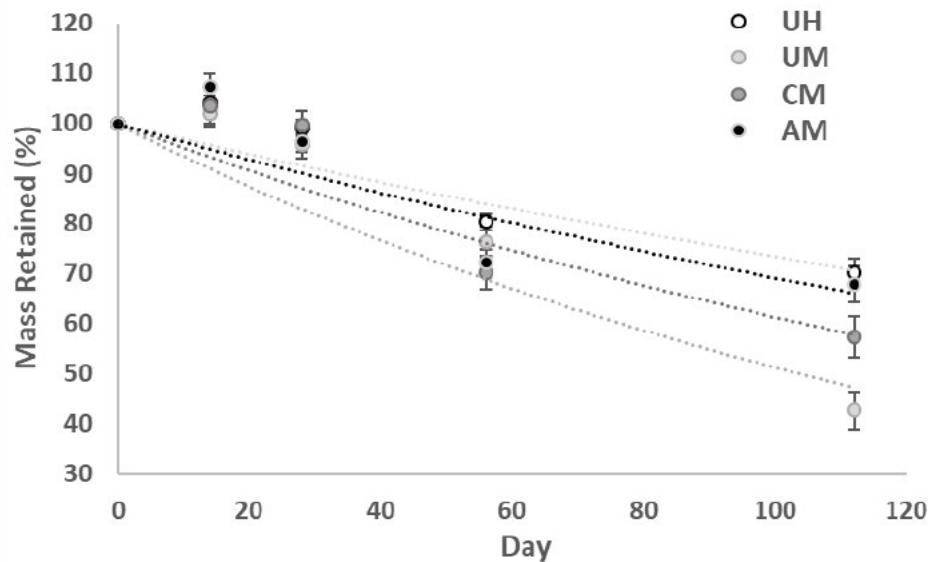


Figure 7; Mean (\pm SE) percent mass loss of mangrove leaves at location PR3 of treatments on natural shorelines (UH, white circles; UM, light grey), constrained (CM, dark grey), and armoured by a seawall (AM, black), $n = 7$.

The effect of Casuarina litter on mangrove decomposition

When decomposed independently of one another, the rate at which mangrove leaves lost mass was significantly faster than for the *Casuarina* foliage, but for neither litter type did decomposition rate vary as a function of litter volume (post-hoc tests, ANOVA: $F_{3,121} = 7.29$, $p < 0.001$, Table 3). Effects of litter mixing on decay rate were seen for mangrove ($F_{3,118} = 4.59$, $p = 0.004$; Table 3; Fig. 8a), but not *Casuarina* foliage ($F_{3,131} = 1.28$, $p = 0.295$; Table 3; Fig. 8b) with significantly faster mass loss of mangrove leaves in the presence than the absence of *Casuarina* foliage, regardless of *Casuarina* density (t-tests, $[M6 = M9] < [M3C6 = M6C3]$, Fig. 8a).

Table 3; The mean (\pm SE) decay constants (k), regression (r^2) and p -values, and litter half-life ($t_{1/2}$) of the mangrove (M) and *Casuarina* (C) components of litter in bags in which they were decomposed separately (M6, M9, C6, C9) or together (M6C3, M3C6). Estimates of k and $t_{1/2}$ were obtained using log-linear regression.

TREATMENT	MANGROVE					CASUARINA				
	r^2	k (d^{-1})	SE	$t_{1/2}$ (d)	p value	r^2	k (d^{-1})	SE	$t_{1/2}$ (d)	p value
M6	0.85	-0.011	0.001	65	< 0.001					
M9	0.92	-0.012	0.060	57	< 0.001					
M3C6	0.89	-0.018	0.064	39	< 0.001	0.87	-0.006	0.024	107	< 0.001
M6C3	0.89	-0.016	0.060	43	0.020	0.88	-0.007	< 0.001	105	< 0.001
C6						0.81	-0.006	0.024	107	< 0.001
C9						0.90	-0.008	0.024	87	< 0.001

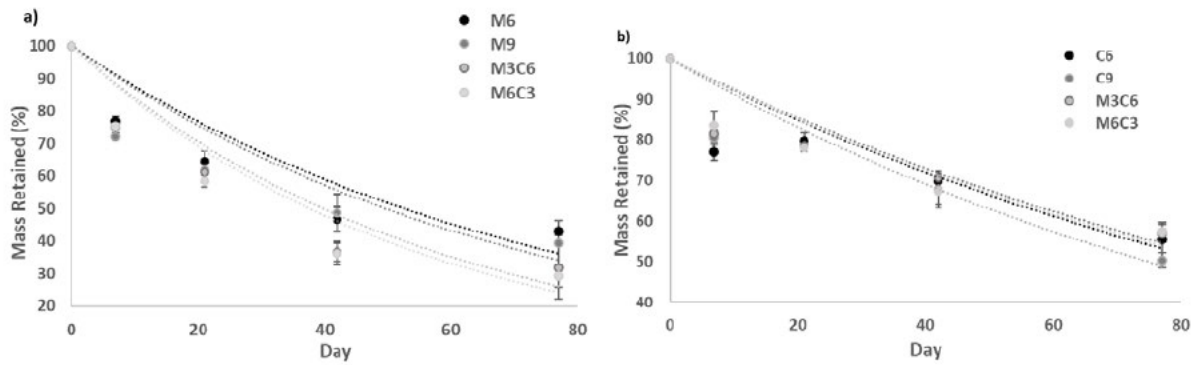


Figure 8; Mean (\pm SE) percent mass loss of a) mangrove leaves in treatments with (M3C6, M6C3) and without (M6, M9) *Casuarina* foliage, and b) *Casuarina* foliage in treatments with (M3C6, M6C3) and without (C6, C9) mangrove leaves with associated regression curves. Darker colours represent monospecific litter treatments, lighter colours represent mixed litter treatments, $n = 7$.

The mangrove leaves had a lower phenolic content, a lower C:N ratio and a higher %N than the *Casuarina* foliage at the start of the experiment (Table 4). Neither loss of phenols from the mangrove leaves, nor changes in their C:N or %N during decomposition was influenced by the presence of *Casuarina* foliage (phenols: $F_{1,26} = 0.50$, $p = 0.488$; C:N: $F_{1,26} = 2.09$, $p = 0.160$; %N: $F_{1,26} = 2.31$, $p = 0.105$; Figure 9a). Change in the C:N ratio and %N of the *Casuarina* foliage during decomposition were similarly not influenced by the presence of mangrove leaves (C:N: $F_{1,26} = 0.005$, $p = 0.405$; %N: $F_{1,26} = 0.323$, $p = 0.575$), but phenols were lost more rapidly from *Casuarina* foliage in the presence than the absence of mangrove leaves (phenols: $F_{1,26} = 30.335$, $p < 0.001$; Figure 9b, Table 5).

Table 4; Initial concentrations of phenolic concentrations, CN ratios and nitrogen contents of mangrove leaves and *Casuarina* foliage, prior to decomposition.

Litter type	Phenol (mg GAE/g dry leaf)	C:N Ratio	Nitrogen (%)
Mangrove leaves	26.73 ± 1.23	19.32 ± 1.53	2.37 ± 0.17
<i>Casuarina</i> foliage	35.41 ± 3.51	23.02 ± 0.28	2.08 ± 0.03

Table 5; The mean (\pm SE) decay constants (k), regression (r^2) and p -values, and half-lives ($t_{1/2}$) for the phenol content in mangrove (M) and *Casuarina* (C) components of litter in bags in which they were decomposed separately (M6, C6) or together (M6C3, M3C6). Estimates of k and $t_{1/2}$ were obtained using log-linear regression.

	r^2	k (d^{-1})	SE	$t_{1/2}$ (d)	p value
MANGROVE					
M6	0.40	-0.028	0.009	25	0.007
M6C3	0.16	-0.019	0.010	36	0.076
CASUARINA					
C6	0.81	-0.031	0.004	22	< 0.001
M3C6	0.89	-0.076	0.007	9	< 0.001

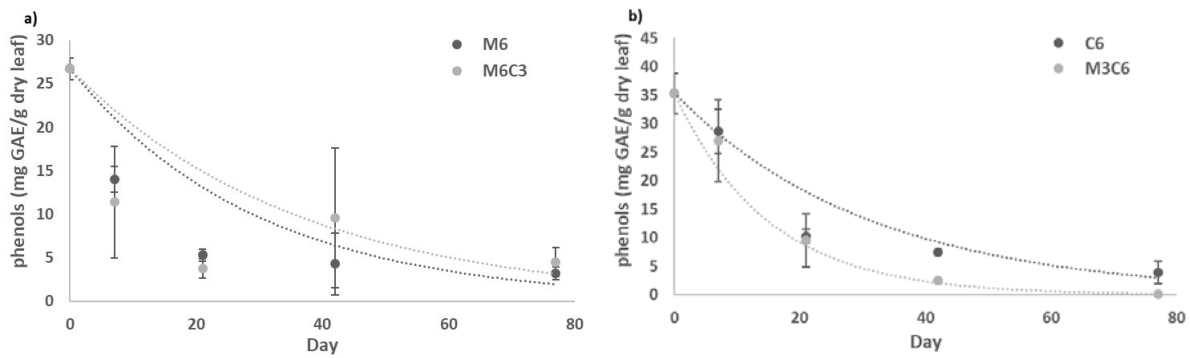


Figure 9; Mean (\pm SE) concentration of phenols in (a) mangrove leaves decomposed with (M6C3) and without (M6) *Casuarina* foliage and (b) *Casuarina* foliage decomposed with (C6M3) and without (C6) mangrove leaves, $n=3$.

Discussion

There is growing evidence that coastal armouring modifies wrack subsidies to adjacent shorelines (Bishop et al. 2010; Harris et al. 2014; Heerhartz et al. 2014; Strain et al. 2018), but the mechanisms by which such effects arise remain unclear. We found that in mangrove forests, as in other intertidal habitats (e.g. Dethier et al. 2016; Strain et al. 2018), armouring significantly truncated shoreline width, eliminating the high intertidal zone at which wrack naturally accumulates. Instead, on armoured shorelines, wrack deposits were greatest in the mid-intertidal zone, just seaward of the base of the seawall. Not only were the wrack deposits on armoured shorelines lower on the shore, but they were also smaller in size as compared to the high intertidal deposits on natural shorelines. Contrasts between armoured and constrained shorelines, of similar width but the latter without a seawall, revealed that the smaller wrack deposits on armoured shorelines were not just a function of a truncated shoreline, which presumably supports fewer mangrove trees. The mid intertidal wrack deposits of constrained (but unarmoured) shorelines were of similar to size to the high intertidal wrack deposits of natural shorelines, and in some instances larger than the mid intertidal deposits of armoured shorelines. These results suggest that on armoured shorelines, the physical structure of the seawall itself also negatively influences wrack accumulation.

A reduced retention of wrack on armoured shorelines appeared to be at least partially responsible for the pattern seen. The experiment tracking the fate of marked wrack revealed that the presence of seawalls negatively influenced the retention of wrack in the mid-intertidal zone when compared to natural shorelines, without seawalls. This pattern may reflect hydrodynamic differences between armoured and unarmoured sites at high tide, when the mangrove forest is inundated. Seawalls can enhance wave reflection as compared to unarmoured shorelines (e.g. Kraus and McDougal 1996; Miles et al. 2001), potentially resulting in enhanced mobilisation of

deposited wrack as well as sediments. Alternatively, or additionally, the greater rate of flushing of wrack at armoured sites may reflect structural differences in the habitat of armoured and unarmoured sites. The size and density of key structural elements influences the trapping, retention and accumulation of wrack on intertidal shorelines (Orr et al. 2005; Bishop and Kelaher et al. 2013). Although densities of pneumatophores (mangrove peg roots) are generally greater in armoured than unarmoured mangrove forests and tree densities do not display consistent patterns of difference (Heatherington and Bishop 2012), the shorter height of pneumatophores at armoured sites (L. Critchley, unpublished data, Chapter 5) may conceivably reduce wrack retention (see Bishop and Kehaler 2013). Greater flushing of wrack was, interestingly, also seen at the high intertidal than the mid intertidal elevation of the unarmoured sites, suggesting that structural differences in the mangrove forest between elevations rather than differences in inundation may be the more important factor influencing retention. Additionally, wind may also mobilise wrack and reduce its retention at high intertidal elevations.

As with previous studies, we found that shoreline armouring not only influenced accumulations of wrack on intertidal shorelines, but also influenced their composition (Heerhartz et al. 2014). Yet, whereas it is often assumed that the physical structure of seawalls is inhibitory of land-sea connectivity (see Heerhartz et al. 2014; Bishop et al. 2017), we found that in some instances, subsidies could be increased between supratidal and mid-intertidal environments as a result of loss of the high intertidal zone. While on natural shorelines, the small mangrove saplings that typify the high intertidal forest (Osunkoya and Creese 1997) did not add litter to the supratidal, at armoured sites, the large mangrove trees that typify the mid-intertidal canopy, overhung the seawall, adding mangrove litter to the supratidal zone. Similarly, along armoured shorelines, terrestrial litter subsidies to the mid intertidal zone were increased, as compared to natural shorelines, presumably because loss of the high intertidal zone increases the proximity of supratidal and mid intertidal habitats, and removes the high intertidal litter trap.

Changes to the species composition of wrack accumulations in the mid intertidal zone of armoured sites had implications for wrack decomposition. As predicted based on the higher C:N ratio of the *Casuarina* than the mangrove litter, and its greater phenolic content, decomposition of the *Casuarina* litter was much slower than the mangrove litter, with more than the twice the half-life. In general, rates of litter mass loss tend to increase nitrogen content, but decrease with increasing lignin or polyphenol concentration (Enríquez et al. 1993; Hättenschwiler and Vitousek 2000; Melillo et al. 1982; Pérez-Harguindeguy et al. 2000). However, when mangrove and *Casuarina* litter were mixed, there were interactive effects of the two components on mass loss. Although it was expected that the *Casuarina* litter may slow decomposition of mangrove

litter through spillover of inhibitory phenols (see Gartner and Cardon 2004), to the contrary, the presence of *Casuarina* accelerated the rate of mass loss of mangrove litter. Conversely, whereas we expected that leaching of nutrients from the more labile mangrove leaves may accelerate decomposition of the *Casuarina* (see Gartner and Cardon 2004) there was no effect on mass loss of *Casuarina* litter of mixing with mangrove leaves. Even though the mechanism for the interactive effect between litter sources was unclear, the net effect is that where armouring results in mixing of small amounts of *Casuarina* litter in mangrove litter, accelerated decomposition rates occur.

Decomposition rates of wrack may not only differ between armoured and natural sites as a result of litter mixing, but also as a result of differences in the physical (i.e. hydrodynamic forces, sedimentation and/or light availability) and/or biological (i.e. microbial and invertebrate communities) environment in which decomposition occurs. However, contrary to our hypothesis, in the absence of *Casuarina*, decomposition rates of mangrove litter did not differ between armoured and natural sites. Harris et al. (2014) similarly found that along the Hudson River, New York, there was no difference in decomposition rates of common litter sources between sites with and without bulkheads (defined there as vertical walls that protect the shore). Instead, consistent with previous studies that have found that the decomposition rates of a variety of litter sources increase with immersion time (Dick and Osunkoya 2000; Marinucci 1982; Nicastro and Bishop 2002; Robertson 1988; Twilley et al. 1986), we found that at one of our three study sites decomposition of mangrove leaves was significantly faster at the mid than the high intertidal elevation. At the other two sites, however, no significant effect of elevation was seen. Thus, although inundation can accelerate leaching of water-soluble components of litter, it appears that other environmental differences that exist between elevations may, in some instances, offset this effect. The approximately 8-week half-life of mangrove leaf wrack seen in this study matched other studies of *Avicennia* decomposition (Gladstone-Gallagher et al. 2014; Goulter and Allaway 1979; Mackey and Smail 1996).

In this study, surveys and experiments were not temporally replicated. Nevertheless, a study addressing how differences in wrack deposits between armoured and unarmoured sites vary through time found that the direction of difference between these two shoreline types was temporally persistent, although the magnitude of difference varied (Heerhartz et al. 2014). Wrack deposition on shorelines is generally greatest following storm events that mobilise litter sources and deposit them on shorelines and/or during annual periods of leaf shedding by dominant primary producers (e.g. Heerhartz et al. 2014; Orr et al. 2005; Strain et al. 2018). During periods of peak wrack deposition, differences between armoured and unarmoured shorelines are

expected to be greatest, with differences diminishing at times of year with scant wrack supply (Heerhartz et al. 2014). Although differences in the species composition of wrack deposits between armoured and unarmoured sites may display greater temporal variation (Heerhartz et al. 2014), our observations suggest that mangrove litter is the dominant source of organic matter at our study sites throughout the year, with *Casuarina* foliage the dominant terrestrial source (L. Critchley per. obs.). Although our study was limited to 8 locations, spanning 2 estuaries, the similarity of our results with those of studies done elsewhere, in other habitat types (e.g. Harris et al. 2014; Heerhartz et al. 2014; Sobocinski et al. 2010), suggests that there are generalities in the mechanisms by which coastal armouring structures, such as seawalls and bulkheads, influence wrack dynamics. These studies have universally adopted a mensurative approach, comparing wrack deposits and dynamics between armoured and unarmoured shorelines. Although before-after-control-impact designs are required to causally attribute ecological impacts to disturbances (e.g. Underwood 1994), many coastal structures were established decades ago, with no ‘before’ data collected. The concordance of results between sites, within and among studies (e.g. Heerhartz et al. 2014; Strain et al. 2018), suggests that differences between shoreline types are indeed likely to reflect an effect of coastal armouring.

Overall, our results suggest that armouring of estuarine shorelines by seawalls diminishes the size of wrack deposits, alters their species composition, and increases their turnover rate. Although not quantified here, such impacts are likely to have broader ramifications for the ecological communities and functions that wrack underpins. The biomass (Bishop and Kelaher 2008; Bozek and Burdick 2005; Chapman and Roberts 2004) and species composition (Bishop and Kelaher 2008, 2013) of wrack are each major determinants of the invertebrate communities that wrack supports, and influence whether wrack is remineralised, or buried forming blue carbon stores (Franzitta et al. 2015; Hill et al. 2015; Lavery et al. 2013). Studies contrasting the invertebrate communities of armoured and unarmoured shorelines suggest that where wrack deposits are reduced, abundances of invertebrates are also less (Dethier et al. 2016, Heerhartz et al. 2016). Reductions in invertebrate numbers may, in turn negatively impact predator communities (e.g. shorebirds, fishes) that depend on these as a prey resource (Dugan et al. 2003; Spiller et al. 2010), although this has not been explicitly tested.

As a key mechanism for the smaller wrack deposits on armoured shorelines was the more rapid rate at which they were washed away, and wrack retention increases with habitat structure (Bishop and Kelaher 2013, Orr et al. 2005), eco-engineering strategies that add structure to armoured sites at which it has been lost may assist in mitigating impacts of seawalls to food webs dependent on wrack (Strain et al. 2018). This may involve replanting of degraded

vegetation or alternatively, where this is not possible, adding artificial structural elements that mimic the wrack-trapping properties of natural vegetation. Nevertheless, as structural elements may not only trap wrack but also anthropogenic litter in urbanised environments (Aguilera et al. 2016), these should be carefully designed so that they do not simply add a waste trap. Additionally, management strategies that address coastal erosion and shoreline stabilisation by prioritising rehabilitation of coastal vegetation (i.e. living shorelines approaches, Bilkovic et al. 2016) over construction of seawalls and other artificial structures, may assist in conserving wrack dynamics of urban shorelines.

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5. Epifaunal communities in armoured and unarmoured mangrove forests

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Abstract

Along with other sedimentary environments, urban mangrove forests are increasingly being modified by coastal armouring. Where coastal armouring results in changes in the width and habitat structure of mangrove forests, effects on invertebrate communities may also be seen. Here we compared the habitat structure and invertebrate communities of three pairs of adjacent mangrove sites along the Parramatta River, Sydney, Australia, with and without armouring by seawalls. We also compared invertebrate communities colonising wrack deposits on these armoured and unarmoured shorelines. Differences between armoured and unarmoured sites in mangrove forest width, tree density and circumference varied among locations, but overall the armoured sites had less total area of intertidal mangrove trunk available for colonisation by species than the unarmoured sites. At a mid-intertidal elevation, pneumatophore density was generally greater and their height less at armoured than unarmoured sites, but at low intertidal elevations consistent patterns of difference between armoured and unarmoured sites were not seen. Overall, the abundance and richness of invertebrates on sediments/pneumatophores and on mangrove trunks displayed spatially inconsistent patterns of difference between armoured and unarmoured sites. Nevertheless, individual taxa, such as an anemone that inhabits mangrove pneumatophores displayed patterns of difference between armoured and unarmoured sites that followed patterns of difference in pneumatophore density. Colonisation of wrack by invertebrates was generally less at armoured than unarmoured sites, largely due to reduced abundances of Dipteran larvae. Overall, wrack at armoured sites was characterised by a greater abundance of terrestrial taxa, perhaps because loss of the high intertidal zone by mid intertidal seawall placement increases proximity of terrestrial to intertidal environments. Overall the large spatial variation in patterns of difference in invertebrate communities between armoured and unarmoured sites suggests that factors other than armouring are more important in determining differences in the densities and richness of invertebrates. Nevertheless, effects of armouring on invertebrates may still result where there is a change in the overall area of habitat for colonisation.

Introduction

Mangroves are highly important coastal ecosystems that are experiencing global decline (Duke et al. 2007). Mangrove forests stabilise shorelines, buffer wave energy, trap pollutants and are important nursery habitats for juvenile fishes (Ewel et al. 1998; Lee et al. 2014). Additionally, the considerable quantities of leaf litter and debris produced by mangrove forests can be an important organic matter subsidy to adjacent ecosystems (Tsuchiya et al. 2015). The location of mangroves at the interface between marine, terrestrial, and freshwater environments makes mangroves highly susceptible to the effects of anthropogenic modification. In addition to directly modifying mangrove forests through clearing, urbanisation can indirectly modify the structure and function of mangrove forests through alteration of hydrological and sediment regimes (Lee et al. 2006). Globally 1-2% of mangrove forests are lost every year, with an even larger percentage degraded through effects of pollution and upstream land use (Duke et al. 2007).

Macrofaunal invertebrates underpin many of the important functions and services provided by mangrove forests (Lee 2008). The processing by molluscs, and especially decapods, of large amounts of organic matter alters the physical and chemical nature of this resource, influencing whether it is decomposed, consumed, or stored (Robertson 1986; Lee 1998; Proffitt and Devlin 2005). As trophic links between mangrove detritus and higher-order consumers such as fishes and birds, macrofaunal invertebrates are critical to the outwelling of nutrients and carbon from mangrove forests (Sheaves and Moloney 2000). Burrowing macrofauna oxygenate sediments, altering biogeochemical processes that are sensitive to redox status, and making sediments habitable by oxygen-dependent taxa (Fenchel 1996; Williamson et al. 1999; Kristensen and Alongi 2006).

Within mangrove forests, macrofaunal abundances vary spatially according to abiotic factors as well as biotic factors that influence habitat and resource availability (Morrisey et al. 2010). For instance, the abundance and diversity of invertebrates varies with height on the shore, according to variation in immersion time and proximity to adjacent terrestrial and marine habitats (Kaly 1988), and can also display marked within-site variation according to sediment properties, and patchiness in resources such as wrack and benthic biofilms growing on the sediment surface (Chapman and Tolhurst 2004, 2007; Tolhurst and Chapman 2007). Sessile and mobile species that depend on hard substrate for attachment and/or grazing vary spatially according to the density of key structural elements such as pneumatophores and mangrove trunks (Bishop et al. 2012), and habitat forming oysters that attach to trunks and pneumatophores (Minchinton and Ross 1999; Bishop et al. 2012). Consequently, processes that modify both the profile and habitat structure of mangrove forests are likely to have a large influence on macrofaunal communities, and the ecosystem functions they underpin.

Among one of the greatest vectors of change to coastlines is coastal armouring (Bugnot et al. in review). Along some coastlines, seawalls built to protect reclaimed land, protect shorelines from erosion and/or separate housing developments from the marine environment now armour in excess of 50% of the shoreline (Bacchiocchi and Airolidi 2003; Bulleri and Chapman 2010; Dugan et al. 2011; Lee and Li 2013). In modifying shoreline profile and width, and key structural aspects of shorelines such as vegetation density and accumulation of wrack (Heerhartz et al. 2016, Morley et al. 2012), seawalls can have large impacts on the macrofauna of sedimentary shorelines (Dethier et al. 2016; Heerhartz et al. 2016; Heery et al. 2017). Previous research suggests that seawalls built to separate housing developments from mangrove forests can result in reduced forest widths, and alter the density of pneumatophores (Heatherington and Bishop, 2012). However, the consequences of such changes on mangrove macrobenthos remains unexplored.

Here we compare the structure of urban mangrove forests and their epifaunal invertebrate communities between paired sites armoured and unarmoured by seawalls. We hypothesise that greater densities of pneumatophores at armoured than unarmoured sites will result in greater densities of macrofauna at the armoured sites. However, we expect that a reduced shoreline width at armoured as compared to unarmoured shorelines will, overall, result in reduced habitat for macrofauna, that is not compensated for by enhanced macrofaunal densities per unit area or by the presence of a novel hard substrate - the seawall. Additionally, we expect that at armoured sites, the lowered position of the terrestrial-marine interface will facilitate greater colonisation of mid intertidal mangrove habitat by terrestrial fauna, resulting in a greater diversity of colonists at armoured than unarmoured sites.

Methods

Study Sites

The study was conducted in three urban mangrove forests situated along the Parramatta River, the major tributary of Sydney Harbour, Australia. Over 45% of the length of the 146-kilometre (km) shoreline of the Parramatta River has been armoured by seawalls (AECOM 2010), with adjacent land-use including residential, industrial, as well as parkland. Locations were dominated by the mangrove, *Avicennia marina*, and were characterised by adjacent stretches of shoreline, less than 1 km apart, with and without seawalls constructed in the mid-intertidal zone. The locations, situated in Yaralla Bay (33° 50' 12.3" S, 151° 6' 7.5" E), were approximately 20 km from the mouth of Sydney Harbour and experience semi-diurnal tides of 1.5 to 2 meters (m).

Survey

To assess how the structure of mangrove forests and their associated epifaunal communities differ between areas with and without seawalls, a survey of the three mangrove forests was done between October and December 2016 (Australasian Summer). Within the paired sites at each location, sampling was stratified by intertidal elevation (low-, mid-, and high-intertidal). The low-intertidal elevation was defined as the area between the seaward-most pneumatophores, and the seaward-most mangrove trunks. The mid-intertidal elevation was between the seaward-most mangrove trunks and either the landward-most mangrove trunks, or at sites with seawalls, where the intertidal zone was truncated, to 1 m below the seawall. The high-intertidal elevation extended either from 1 m below the base of the seawall to the high-tide line of growth on the seawall at armoured sites, or from the landward extent of mangrove trunks to the landward extent of pneumatophores on the unarmoured section. The width of each zone was measured to the nearest 1 m.

To estimate the surface area of habitat that mangrove trees provide in the intertidal zone of armoured and unarmoured sites of each mangrove forest, within each mangrove densities and sizes were evaluated within a 5 x 5 m quadrat haphazardly placed within the mid-intertidal elevation. Within each quadrat, the number of trees was counted, and the circumference of each at breast-height (1.4 m from the base of the tree) was measured to the nearest centimetre (cm). Where the mangrove tree branched below breast-height, the circumference of each branch was measured, and tallied, separately. To estimate the density of biota utilising mangrove trunks as habitat, within the mid-intertidal elevation, epifauna were surveyed on seven replicate trees, from within the same 5 x 5 m quadrat used to estimate mangrove densities and size, within each armoured and unarmoured site. Within a 0.3 x 0.3 m quadrat, with 100 evenly spaced intersection points, that was positioned just below the high-water mark on each tree, mobile epifauna were enumerated by species, and sessile taxa, such as barnacles and algae were recorded as percentage cover.

Pneumatophore density, and the density of sediment- and pneumatophore- dwelling epifauna were evaluated within seven randomly placed 0.5 x 0.5 m quadrats placed within each intertidal elevation of the unarmoured sites, and the low- and mid-elevations of the armoured sites (this habitat was missing from the high elevation). Within each quadrat, the height of ten randomly selected pneumatophores was measured to the nearest cm. Epifauna were enumerated by morphospecies, with abundances summed across mud and pneumatophore habitats as many taxa migrate freely between these (Hughes et al. 2014). Additionally, at the armoured sites, epifauna on the seawall were enumerated by taxon within seven replicate 0.5 x 0.5 m quadrats, randomly placed just below the high-water mark. In addition to recording the density, by morphospecies,

of mobile epifauna within each quadrat, the percent cover of filamentous or leafy algae, and barnacles was recorded under each of 100 evenly spaced points.

To assess any difference between armoured and unarmoured sites in the intertidal area of mangrove trunks available for colonisation by invertebrates, their total intertidal surface area was estimated within a 1 m wide transect running the width of the mangrove forest. The average tree circumference (m) was multiplied by 0.30 m (the average vertical extent of growth on mangrove trunks situated within the intertidal zone) to obtain the available area for growth per tree (m²). This was then multiplied by the tree density to obtain area available for growth per m². The area available for growth per m² was then multiplied by mid-intertidal forest width (m) to estimate the area available for growth in a 1 m stretch of the forest. Additionally, the total abundance of epifauna, across the shoreline, was estimated for each armoured and unarmoured site. For each intertidal elevation, the density of epifauna per 1 m² was multiplied by shoreline width, to get an estimated total abundance for a 1m wide transect. Estimates for each elevation were then summed to give the total number of invertebrates per 1 m width transect, extending from the low to the high intertidal zone, per site.

Wrack colonisation

To assess how colonisation of wrack by invertebrates is modified by seawalls, wrack from a common source was deployed at: 1) the mid-intertidal elevation of armoured sites, just below the base of the seawall, where wrack accumulates (AM), 2) the high tide mark, where wrack naturally accumulates, at the unarmoured site (UH) and, 3) to assess to what extent any difference is a function of tidal elevation alone or also the presence of the seawall, at a mid-intertidal elevation on unarmoured, natural, sites (UM), equivalent to the tidal elevation of wrack accumulation on armoured sites. Living mangrove foliage, predominantly green with some slightly yellow/brown leaves and stems and smaller branches, was collected from the mangrove forest at the site of deployment and frozen at -30°C for two days to kill and defaunate it. Live material was utilised over dead material to hold starting stage of decay constant.

Approximately 3 litres (L) of this experimental 'wrack' was deployed in 20 x 20 x 7.5 cm cages, constructed of 13 millimetre (mm) diameter wire mesh. This mesh size was smaller than the diameter of the pieces of foliage, ensuring it was retained, yet larger than the diameter of most epifauna, allowing their colonisation. For each of the three positions per location, there were seven cages, each situated at least 2 m apart, to give a total of 21 cages per location, and 63 cages across the three locations. Prior to deployment of wrack, all of the natural wrack and epifauna were cleared from a 0.5 x 0.5 m area beneath and surrounding the placement of each cage.

Caged wrack was left in the field for 9 weeks, to match the approximate 8-week half-life for mangrove leaves at these study sites (Goulter and Allaway 1979) and because colonisation of substrates by mobile fauna in mangrove forests is rapid, typically occurring in less than 2 weeks (Bishop et al. 2009). At the end of the 9 weeks, wrack and associated invertebrates were removed from within the cages, bagged, and frozen at -30°C until time permitted laboratory analysis. Upon defrosting, wrack was washed over a 500 µm mesh to remove sediments, and the sample was stained overnight at 4° C in a rose bengal solution. Invertebrates were separated from the wrack using a magna lamp and then enumerated to morphospecies using a stereomicroscope. In order to assess whether the greater proximity of terrestrial to mid intertidal habitats at the armoured (lacking high intertidal mangrove forest) than the unarmoured sites lead to a greater number of terrestrial colonists, adult stage organisms of terrestrial origin were summed. Insecta, Arachnida, and Isopoda (in this instance woodlouse) were considered as terrestrial in origin. Although adult stage diptera are terrestrial, their larvae require wet habitats and so dipteran larvae were excluded from this analysis.

Statistical Analysis

For the survey, differences in forest widths, tree densities, habitat availability and total epifauna (i.e. across the entire shoreline width) between the three pairs of armoured and unarmoured sites were assessed using paired t-tests. Differences in all other habitat metrics and epifaunal communities between armoured and unarmoured sites were assessed using multivariate and univariate PERMANOVAs. Multivariate analyses used Bray Curtis dissimilarity matrices calculated using untransformed data, while univariate analyses used Euclidean distance matrices. Three-way analyses, with the factors location (3 levels, random), elevation (2 levels, fixed: Mid, Low), and armouring (2 levels, fixed: armoured, unarmoured) were run on each of pneumatophore height and density, as well as the community structure of epifauna on sediments/pneumatophores, their abundance and richness, as well as taxa identified by SIMPER (similarity percentage analysis; Clarke 1993) as key discriminators of multivariate differences between sediment/pneumatophore communities of armoured and unarmoured sites. Additionally, a two-way PERMANOVA with factors location and elevation (high, mid, low) assessed how the abundance and richness of sediment/pneumatophore invertebrates in the high intertidal elevation of unarmoured sites (that was absent from the armoured sites), compared to those of the other elevations of unarmoured sites. Two-way PERMANOVAs with the factors location and armouring were run on the mid-intertidal tree circumferences, the percent cover of algae and barnacles on tree trunks, as well as the high intertidal epifaunal communities, abundances and richnesses on seawalls at armoured sites vs sediments/pneumatophores at unarmoured sites. Extremely low abundances of mobile invertebrates on mangrove trunks prevented analyses on

these. Where significant main effects of or interactions involving armouring were identified, *a posteriori* PERMANOVAs assessed sources of difference.

To assess relationships between the abundances of key discriminating taxa and each of pneumatophore density and height, Pearson's correlations were run on means calculated for each elevation of each site.

Multivariate and univariate PERMANOVAs assessed differences in the colonisation of wrack by invertebrates between armoured and unarmoured sites. The analyses had 2 factors, location (3 levels, random) and treatment (3 levels, fixed: AM, UM, UH), with multivariate PERMANOVAs run on invertebrate community data and univariate PERMANOVAs run on total invertebrate abundance and richness, the total abundance of terrestrial and of marine taxa, numerically dominant taxa, and taxa identified by SIMPER as key contributors to differences between armoured and unarmoured sites. Treatment of data, and *a posteriori* tests were as described above.

PERMANOVA and SIMPER analyses were performed using PRIMER 7, with PERMANOVA (Clarke and Gorley, 2015; Anderson et al. 2008). Pearson's correlations and paired t-tests were run using PAST (Hammer et al. 2001).

Results

Habitat structure

Neither tree circumference (PERMANOVA sig. Location x Armour interaction; pseudo- $F_{2, 92} = 3.60$, $p(\text{mc}) = 0.034$) nor density (paired t-test: $t_2 = 0.13$; $p = 0.910$) showed a consistent pattern of difference between armoured and unarmoured sites, among the three locations sampled.

Whereas at two locations tree circumference was larger at the armoured than the unarmoured site (PERMANOVA *a posteriori* test: L2: $t_{24} = 1.61$, $p(\text{mc}) = 0.126$; L3: $t_{30} = 2.06$, $p(\text{mc}) = 0.049$), at the third the reverse pattern was seen (L1, $t_{38} = 1.44$, $p(\text{mc}) = 0.160$). Tree density was greater at the armoured than unarmoured site at one location, was less at the armoured than the unarmoured site at another, and did not differ between armoured and unarmoured sites at the third (Table 1).

Table 4; Mangrove forest characteristics at a mid-intertidal elevation of three locations along the Parramatta River. In each location, mangrove forest width, tree density, and tree circumference were measured at paired sites with and without armouring by a seawall. These characteristics were used to estimate the total intertidal area of mangrove trunk for organismal attachment.

Location	Armouring	Width (m)	Tree Density (no. per 25m ²)	Tree Circumference (cm)	Area for Attachment (per m ²)
1	Armoured	6	30	38.9 ± 3.1	0.14
	Unarmoured	47	10	47.1 ± 3.0	0.06
2	Armoured	12	13	48.2 ± 3.1	0.08
	Unarmoured	28	13	34.2 ± 8.2	0.05
3	Armoured	33	8	33.1 ± 6.2	0.03
	Unarmoured	24	24	21.4 ± 2.6	0.06

Across the locations, mangrove forest widths did not significantly differ between sites with and without armouring ($t_2 = 1.11$, $p = 0.383$; Table 1), but two of the three forests were wider at sites without armouring. Overall there was a non-significant trend towards a greater area of mangrove trunk available for invertebrate attachment on shorelines with than without armouring ($t_2 = 2.15$, $p = 0.082$; Fig. 1).

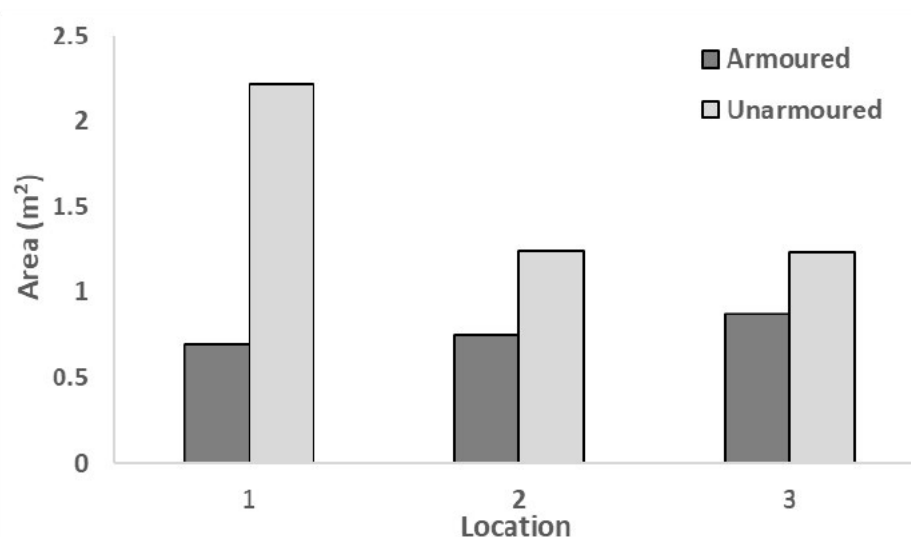


Figure 4; Area (in m²) available for epifaunal attachment in a 1-m wide transect extending the width of the mid intertidal zones of armoured and unarmoured mangrove forests. Calculated by multiplying the average tree circumference by tree density and mid-intertidal shoreline width. It is assumed that epifauna can live in a 30 cm vertical zone above the sediment.

Differences in pneumatophore heights and densities between armoured and unarmoured sites varied among locations and according to intertidal elevation (PERMANOVA, sig. Location x Elevation x Armour interaction: heights; pseudo- $F_{2, 982} = 39.62$, $p(\text{mc}) < 0.001$; densities; pseudo- $F_{2, 72} = 5.30$, $p(\text{mc}) = 0.008$). At the mid-intertidal elevation, where pneumatophore heights ranged from 4-13 cm, and densities from 80-340 per 0.25 m² quadrat, significantly shorter pneumatophores, of greater density, were found at armoured than unarmoured sites at two of the three locations ($p(\text{mc}) < 0.001$, PERMANOVA *a posteriori* tests), with no significant

difference between sites at the third ($p_{(mc)} > 0.05$, PERMANOVA *a posteriori* tests; Fig. 2a, b). By contrast, at the low-intertidal elevation, where pneumatophore heights ranged 3-7 cm and densities from 140 to 260 per 0.25 m² quadrat, pneumatophore heights were taller at armoured than unarmoured sites at two of three locations, with the reverse pattern found at the third ($p_{(mc)} < 0.05$, PERMANOVA *a posteriori* tests; Fig 2c), but there was no significant difference in density between armoured and unarmoured sites ($p_{(mc)} > 0.05$, PERMANOVA *a posteriori* pairwise tests; Fig 2d).

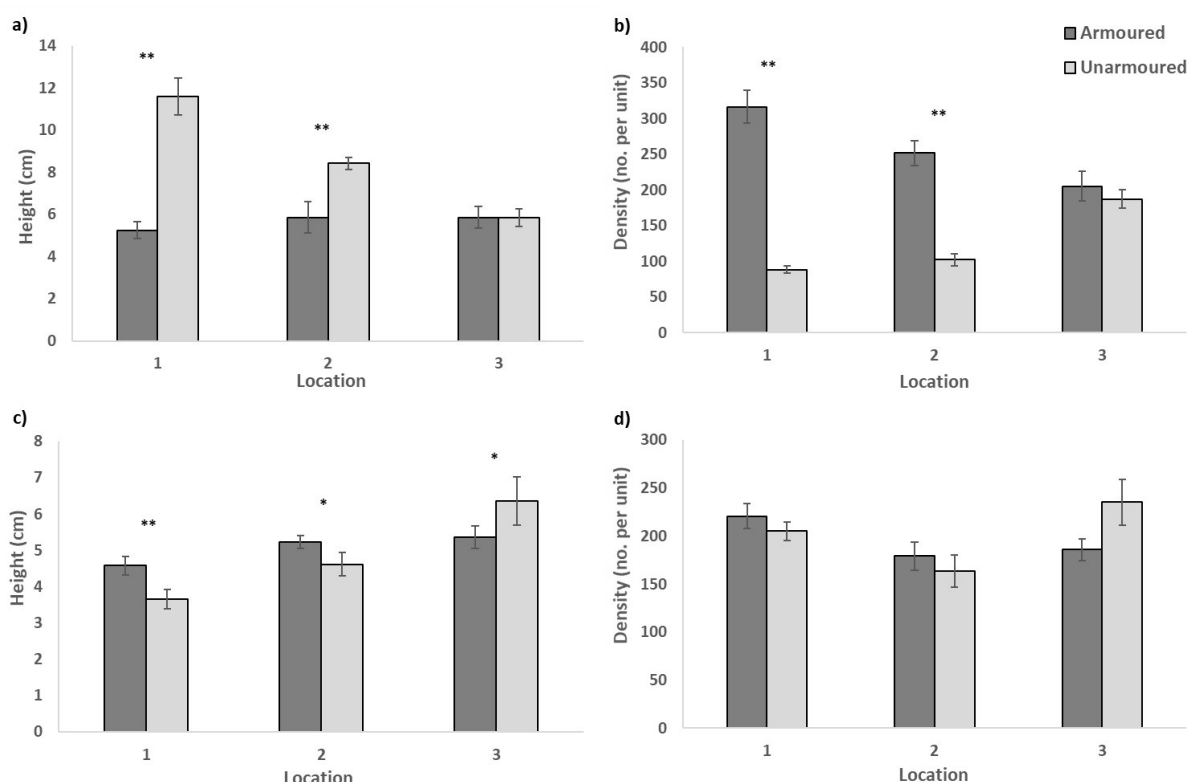


Figure 5; Mean (\pm SE) pneumatophore height and density at mid (a, b) and low (c, d) elevations of sites with (armoured) and without (unarmoured) seawalls, at each of three locations in Yaralla Bay, Sydney, Australia. Significant differences between sites with and without armouring (PERMANOVA *a posteriori* pairwise tests) are marked (*: $p < 0.05$; **: $p < 0.001$). $n = 7$.

Community structure

Epifaunal survey

Overall, across all locations and intertidal heights, 6 taxa of epifauna were identified from armoured and 11 from unarmoured sites, with 5 taxa were common to both. Communities were dominated by one Anthozoa species, which comprised 39.7 % of all individuals, and six species of Gastropoda, which comprised 43.1 % of all individuals, with one species of *Ophicardelus ornatus* contributing 27.4 % to total abundance.

At the unarmoured sites, invertebrate communities on mud and pneumatophores displayed a significant effect of elevation that varied among locations (pseudo- $F_{4, 54} = 4.31$, $p_{(mc)} < 0.001$) with significantly higher abundances at the low intertidal than both the high ($t_{12} = 3.30$, $p_{(mc)} =$

0.003) and mid ($t_{12} = 2.12$, $p(\text{mc}) = 0.044$) intertidal at location 2, and higher richness at the low intertidal than the high intertidal ($t_{12} = 2.49$, $p(\text{mc}) = 0.019$) at location 1. Additionally, when these communities were compared between armoured and unarmoured sites at mid and low intertidal elevations, a significant interaction between location, intertidal elevation, and armouring was found (pseudo- $F_{2, 72} = 2.42$, $p(\text{mc}) = 0.023$) with significantly higher abundances and richnesses at the mid intertidal of the armoured than unarmoured site of location 2 (Abundance: $t_{12} = 3.96$, $p(\text{mc}) < 0.001$; Richness: $t_{12} = 2.73$, $p(\text{mc}) = 0.015$). Despite this, neither the abundance nor the richness of invertebrate communities of mud and pneumatophores varied among high, mid or low intertidal elevations at any of the unarmoured sites (Abundance: pseudo- $F_{4, 54} = 1.67$, $p(\text{mc}) = 0.121$; Richness: pseudo- $F_{4, 54} = 1.47$, $p(\text{mc}) = 0.207$), but the abundance did significantly vary between locations (pseudo- $F_{2, 54} = 3.64$, $p(\text{mc}) = 0.012$).

Likewise, analyses of epifaunal abundance and richness at mid and low intertidal elevations of armoured and unarmoured sites did not display a significant interaction between location, intertidal elevation, and armouring (Abundance: pseudo- $F_{2, 72} = 2.16$, $p(\text{mc}) = 0.091$; Richness: pseudo- $F_{2, 72} = 1.59$, $p(\text{mc}) = 0.196$; Fig. 3), or significant two-way interactions between any of the factors (location, intertidal elevation, or armouring) (PERMANOVA; $p(\text{mc}) > 0.05$).

However, abundance varied with the main effect of intertidal elevation (pseudo- $F_{4, 54} = 12.77$, $p(\text{mc}) = 0.017$) with significantly higher abundances at the low intertidal than the mid intertidal ($t_{12} = 3.57$, $p(\text{mc}) = 0.018$), and richness varied according to armouring (pseudo- $F_{1, 72} = 18.97$, $p(\text{mc}) = 0.018$) with significantly higher abundances with armouring than without ($t_{12} = 4.36$, $p(\text{mc}) = 0.016$).

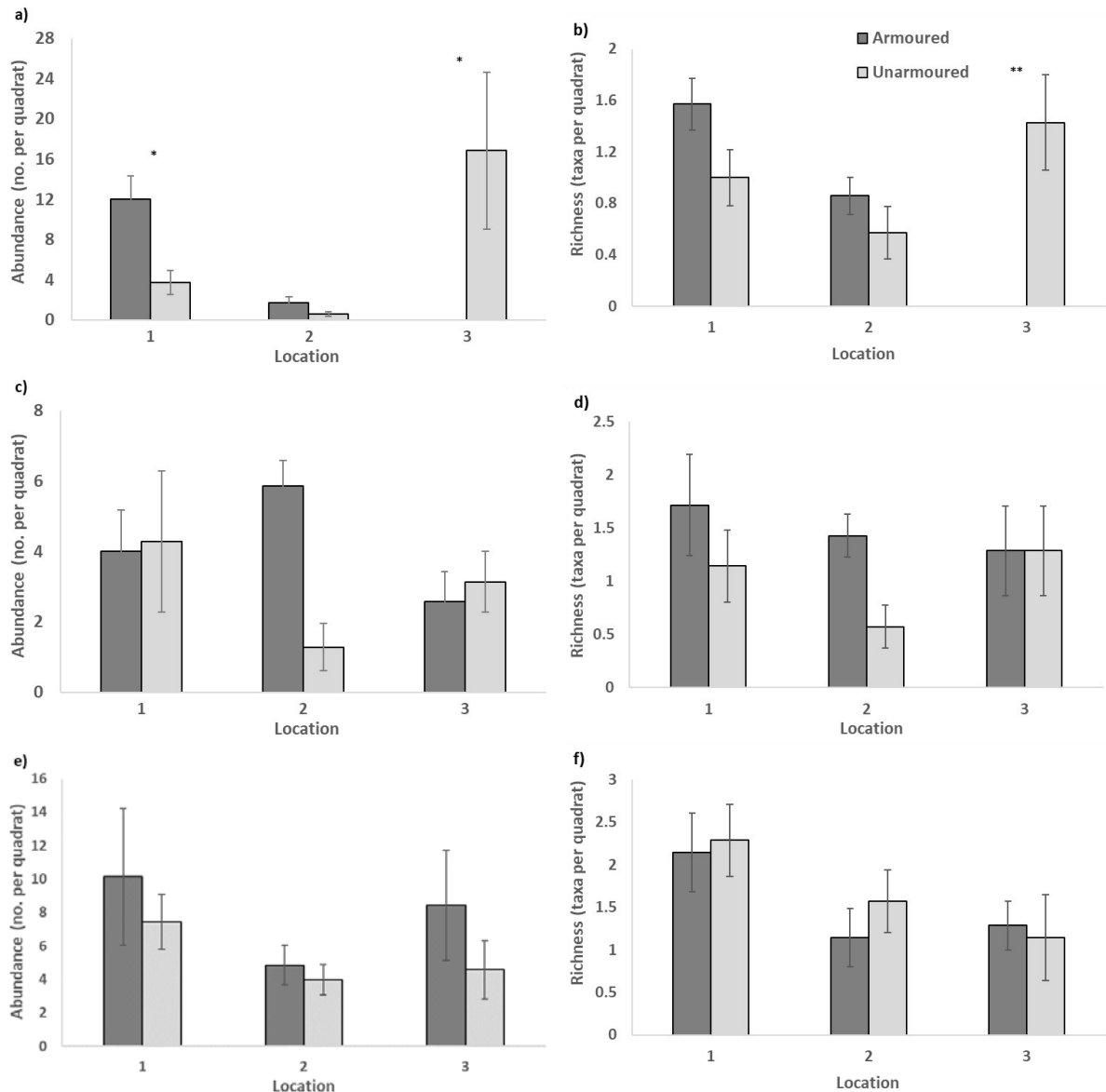


Figure 3; Mean (\pm SE) epifaunal abundance and richness on sediments and pneumatophores at (c, d) mid-intertidal and (e, f) low-intertidal elevations, of armoured and unarmoured sites, at each of 3 locations. At the high intertidal elevation (a,b) contrasts were between epifauna on seawalls at armoured sites and on sediments/mud at unarmoured sites with significant differences between sites with and without a seawall (PERMANOVA *a posteriori* pairwise tests) are marked (*: $p < 0.05$; **: $p < 0.001$) $n = 7$.

SIMPER analysis indicated that an *Actiniaria* sp. and *Ophicardelus ornatus* contributed the most to the dissimilarity in invertebrate communities among elevations on the unarmoured shorelines, with each species displaying a significant location by elevation interaction (*Actiniaria*: pseudo- $F_{4,54} = 4.07$, $p(\text{mc}) = 0.002$; *Ophicardelus*: pseudo- $F_{4,54} = 6.49$, $p(\text{mc}) < 0.001$). *Actiniaria* contributed 38.2% of the dissimilarity between the high and the low intertidal and 47.1% of the dissimilarity between the mid and low intertidal. Abundances of *Actiniaria* generally decreased with intertidal elevation and were significantly greater at the low than the high intertidal elevation of all locations ($p(\text{mc}) > 0.05$, PERMANOVA *a posteriori* tests), at the low than the mid intertidal elevation of two of the three locations ($p(\text{mc}) > 0.05$, PERMANOVA *a posteriori* tests), and at the mid than the high intertidal elevation of one location ($t_{12} = 3.50$, $p(\text{mc}) = 0.003$), with all other pairwise comparisons non-significant. *Ophicardelus ornatus* contributed 39.1% of the

dissimilarity between the high and mid elevations on unarmoured shorelines, with significantly higher abundances at the high intertidal than the mid or low intertidal elevations of two of the three locations ($p_{(mc)} > 0.05$, PERMANOVA *a posteriori* tests).

Actiniaria and the shore-crab *Heloecius cordiformis* contributing most (59.7% and 13.1%, respectively in SIMPER tests) to dissimilarity in the epifaunal communities of sediments/pneumatophores between armoured and unarmoured sites at the mid and low intertidal elevations. The abundance of *Actiniaria* displayed a significant interaction between location, elevation and armouring (pseudo- $F_{2, 72} = 3.85$, $p_{(mc)} = 0.028$), with significantly greater abundances at armoured than unarmoured sites at the mid intertidal elevation of two of the three locations, but no significant differences between armoured and unarmoured sites at the mid intertidal elevation of the third location, or at any of the locations for the low-intertidal elevation ($p_{(mc)} > 0.05$, PERMANOVA *a posteriori* tests; Fig. 4a, c). *Heloecius cordiformis*, by contrast did not significantly differ among armoured and unarmoured sites, at any of the locations or elevations on the shore (pseudo- $F_{2, 72} = 0.78$, $p_{(mc)} = 0.497$; Fig. 4b, d), however a significant interaction between location and height (pseudo- $F_{2, 72} = 5.73$, $p_{(mc)} = 0.003$) showed higher abundances at the low intertidal than the mid intertidal of one location ($t_{24} = 2.90$, $p_{(mc)} = 0.004$) but no significant difference in abundances between the mid and low intertidal at the other two locations (Fig. 4b,d).

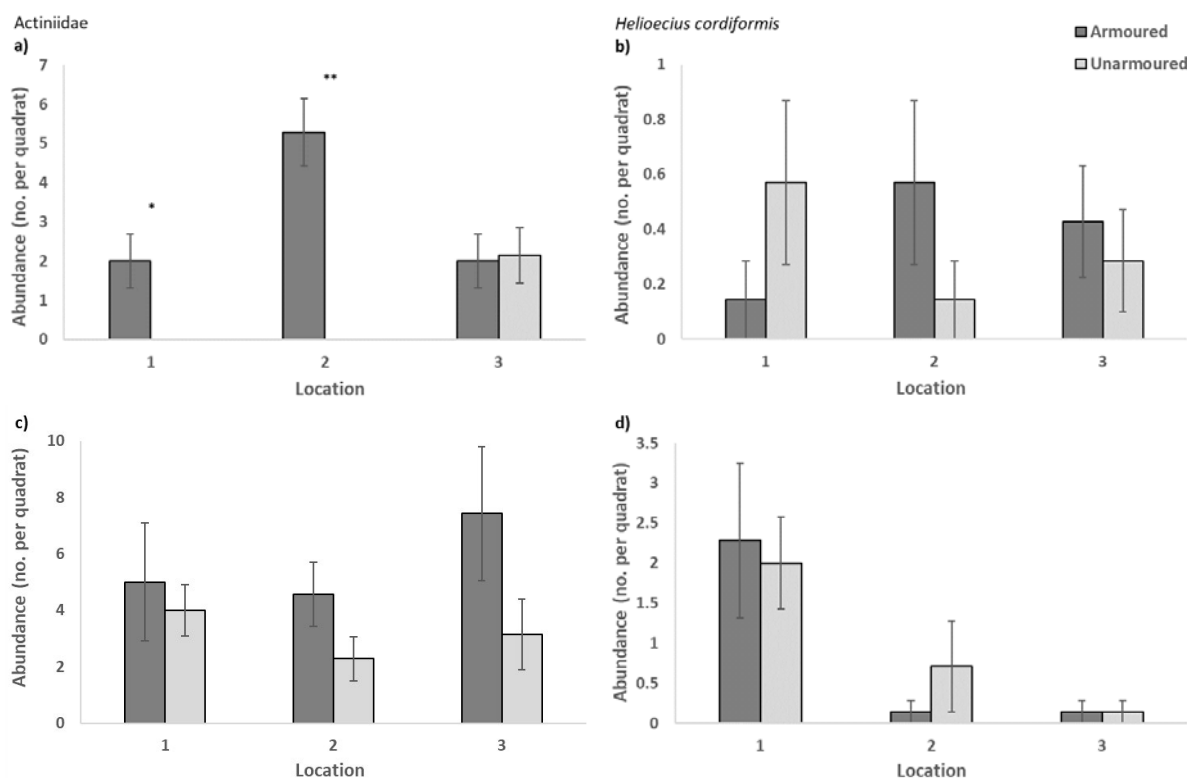


Figure 4; Mean (\pm SE) of *Actiniaria* and *Heloecius cordiformis* abundances at the (a,b) mid and (c,d) low intertidal of armoured and unarmoured sites. Significant differences between sites with and without armouring (PERMANOVA *a posteriori* pairwise tests) are marked (**: $p < 0.001$) $n = 7$.

When the structure of epifaunal communities was compared between the high intertidal habitats of the armoured (i.e. the seawall itself) and the unarmoured (i.e. mud, pneumatophores) sites a significant interaction between location and armouring was seen for total abundance (pseudo- $F_{2, 36} = 12.04$, $p(\text{mc}) < 0.001$), richness (pseudo- $F_{2, 36} = 12.55$, $p(\text{mc}) < 0.001$), as well as community structure (pseudo- $F_{2, 72} = 14.58$, $p(\text{mc}) < 0.001$). PERMANOVA *a posteriori* tests found significant differences in abundances of invertebrates between unarmoured and armoured habitats at two of the three locations, with greater abundances at the armoured site of one location ($t_{12} = 2.71$, $p(\text{mc}) = 0.006$) and the reverse pattern of lower abundance at the armoured site for the other ($t_{12} = 3.31$, $p(\text{mc}) = 0.001$) (Fig. 3a). Richness was greater at the unarmoured than armoured site at one of the three locations ($t_{12} = 4.66$, $p(\text{mc}) < 0.001$), with no significant difference with respect to armouring at the other two (Fig. 3b).

SIMPER analysis revealed that at the high intertidal elevation, the gastropod *Ophicardelus ornatus* contributed most (48.9%) to the dissimilarity between armoured and unarmoured sites, with higher abundances seen at sites with than without armouring at two locations (PERMANOVA *a posteriori* test; L1: $t_{12} = 6.97$, $p(\text{mc}) < 0.001$; L2: $t_{12} = 2.02$, $p(\text{mc}) = 0.067$) but at the third location, the opposite pattern was seen ($t_{12} = 2.76$, $p(\text{mc}) = 0.007$) (Fig. 5).

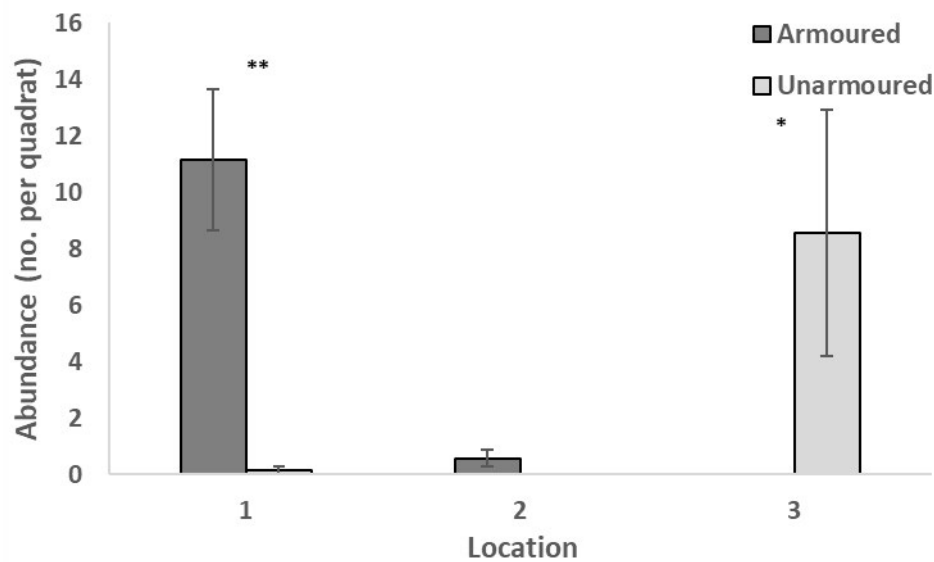


Figure 5; Mean (\pm SE) abundance of *Ophicardelus ornatus* in the high intertidal of armoured and unarmoured sites. Significant differences between sites with and without armouring (PERMANOVA *a posteriori* pairwise tests) are marked (*: $p < 0.05$; **: $p < 0.001$) $n = 7$.

Across the mid and low intertidal elevations of all sites, the abundances of *Actiniaria* displayed a strong positive, but non-significant, correlation with pneumatophore density (*Actiniaria*: $r = 0.78$, $n = 6$, $p = 0.068$) and a strong negative, also non-significant, correlation with height ($r = -$

0.79, $n = 6$, $p = 0.064$), with pneumatophore height and density negatively correlated ($r = -0.84$, $n = 6$, $p = 0.036$). The abundance of *Ophicardelus ornatus*, by contrast displayed no relationship to pneumatophore density ($r = -0.58$, $n = 6$, $p = 0.230$) and was, instead, positively correlated with pneumatophore height ($r = 0.89$, $n = 6$, $p = 0.018$).

Estimates of the total epifaunal abundance in a 1 m wide transect, spanning the entire width of the mangrove forest indicated that there was no significant difference in total abundance between armoured and unarmoured shorelines ($t_2 = 0.78$, $p = 0.515$; Fig. 6).

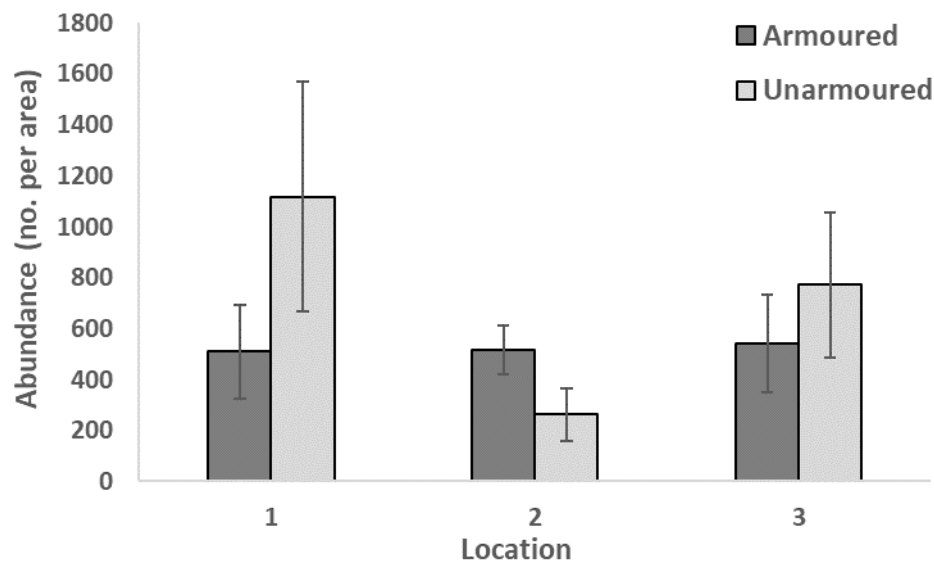


Figure 6; Estimates of total epifaunal abundance in a 1 m wide transect, extending from the low to the high intertidal mangrove forest, of armoured and unarmoured sites.

Benthic cover on seawalls significantly differed between locations (pseudo- $F_{18, 20} = 20.71$, $p(\text{mc}) < 0.001$), with cover of turfing algae ranging from (mean \pm SE) 0.0 ± 0.0 to $46.3 \pm 14.7\%$ and barnacles from 0.0 ± 0.0 to $1.6 \pm 0.3\%$ at the scale of locations. Benthic cover on trees showed a significant interaction between location and armouring (pseudo- $F_{2, 44} = 22.09$, $p(\text{mc}) < 0.001$), with significantly higher abundances of algae at armoured than unarmoured sites at two of the locations (L1: $t_{18} = 3.83$, $p(\text{mc}) = 0.002$; L2: $t_{17} = 8.55$, $p(\text{mc}) < 0.001$; Fig. 7a) and of barnacles at the armoured than unarmoured site at one location ($t_{18} = 3.64$, $p(\text{mc}) = 0.002$) with no significant differences in these taxa between armoured and unarmoured sites at the other locations (Fig. 7b).

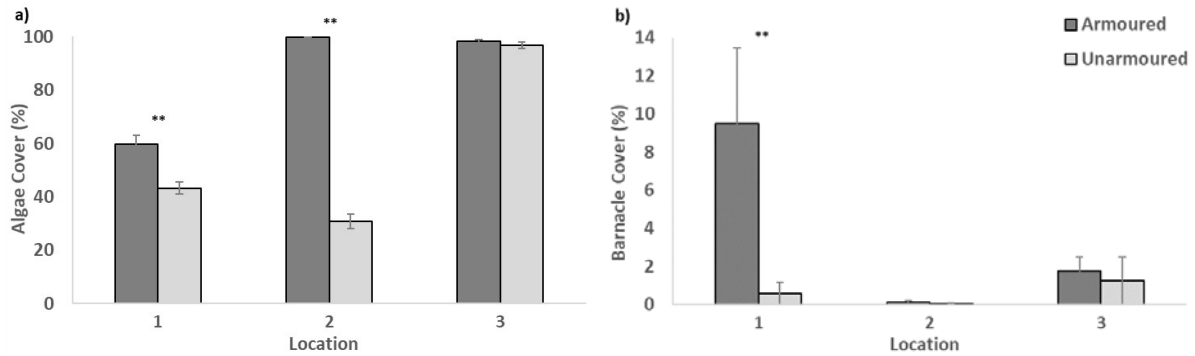


Figure 7; Mean (\pm SE) cover of (a) barnacles and (b) algae on trees within the mid intertidal of armoured and unarmoured sites. Significant differences between sites with and without armouring (PERMANOVA a posteriori pairwise tests) are marked (**: $p < 0.001$) $n = 7$.

Wrack

Dipteran larvae accounted for 64.7% of the total abundance of invertebrates colonising wrack, with their abundance varying spatially according to the interacting effect of treatment and location (pseudo- $F_{4, 36} = 4.39$, $p < 0.001$). At all three locations, a smaller number of dipterans colonised wrack placed at the mid-intertidal elevation of the armoured site than either the mid- (L1: $t_8 = 2.37$, $p(\text{mc}) = 0.039$; L2: $t_8 = 5.37$, $p(\text{mc}) < 0.001$; L3: $t_8 = 2.40$, $p(\text{mc}) = 0.012$) or high-intertidal (L1: $t_8 = 3.60$, $p(\text{mc}) = 0.005$; L2: $t_8 = 4.39$, $p(\text{mc}) = 0.003$; L3: $t_8 = 2.51$, $p(\text{mc}) = 0.009$) elevations of the unarmoured site, although the magnitude of this effect differed. By contrast, there was no significant difference in dipteran abundance between mid- and high-intertidal elevations of the unarmoured sites (L1: $t_8 = 1.23$, $p(\text{mc}) = 0.251$; L2: $t_8 = 2.06$, $p(\text{mc}) = 0.074$; L3: $t_8 = 0.83$, $p(\text{mc}) = 0.425$) (Fig. 8).

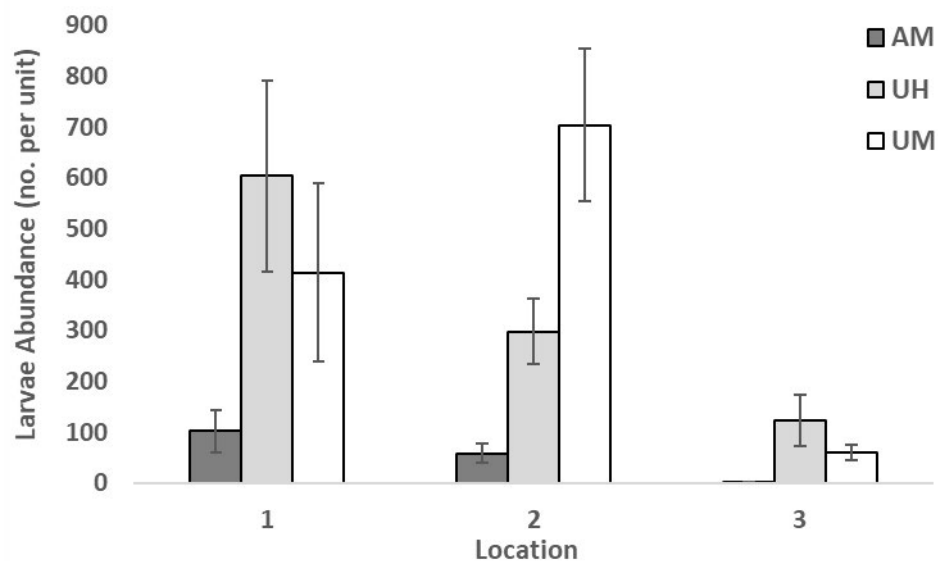


Figure 8; Mean (\pm SE) abundance of dipteran larvae in wrack deployed at the mid-intertidal elevation of armoured sites (AM), or at a mid- (UM) or high intertidal elevation (UH) of unarmoured sites, at each of three mangrove forests. $n = 7$.

The total abundance of all other invertebrates (i.e. excluding dipteran larvae) similarly varied according to the interacting effects of location and treatment (pseudo- $F_{4,36} = 5.38$, $p(\text{mc}) < 0.001$; Fig. 9a). The abundance of these invertebrates differed between the mid-intertidal elevation of the armoured site and the high-intertidal of the unarmoured site at two locations, however in opposite directions, with one location having a greater invertebrate abundance in the high-intertidal elevation of the unarmoured site (L1: $t_8 = 2.31$, $p(\text{mc}) = 0.029$), while another had greater invertebrate abundance at the mid-intertidal elevation of the armoured site (L3: $t_8 = 2.74$, $p(\text{mc}) = 0.010$). Additionally, at one of the three locations, significantly more of these invertebrates were found at the mid-intertidal elevation of the armoured than the unarmoured site ($t_8 = 3.69$, $p(\text{mc}) = 0.001$). All other comparisons were not significant (Fig. 9a).

The total richness of invertebrates showed a significant interaction between location and treatment (pseudo- $F_{4,36} = 4.64$, $p(\text{mc}) < 0.001$; Fig. 9b). At one of the three locations (L2), significantly fewer species were found at the mid-intertidal of the armoured site than either the mid-intertidal ($t_8 = 3.59$, $p(\text{mc}) = 0.001$) or high-intertidal ($t_8 = 3.59$, $p(\text{mc}) = 0.001$) elevation of the unarmoured site, but all other comparisons were not significant (Fig. 9b).

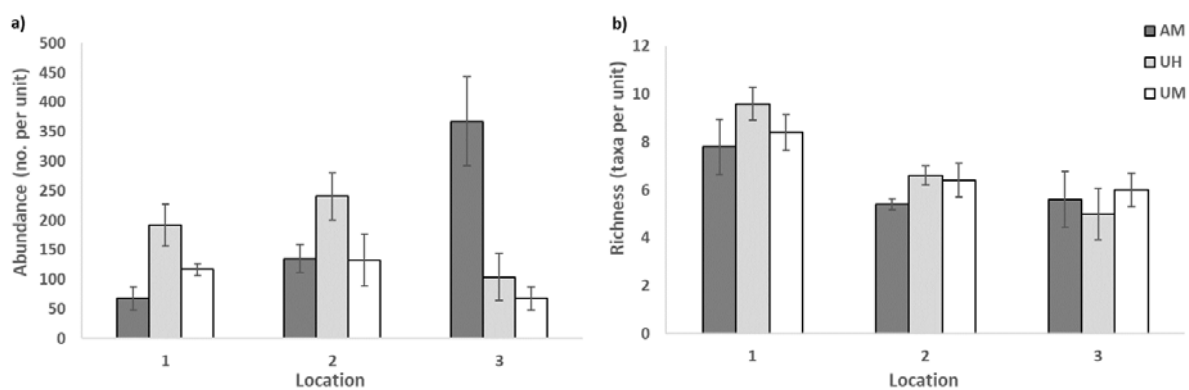


Figure 9; Mean (\pm SE) (a) total abundance excluding dipterans and (b) richness of invertebrates colonising wrack deployed at the mid-intertidal elevation of armoured sites (AM), or at a mid- (UM) or high intertidal elevation (UH) of unarmoured sites, at each of three mangrove forests. $n = 7$.

SIMPER analysis showed that the Talitrid amphipod *Orchestia* sp., the Decapod crustacean *Paragrapsus laevis*, the terrestrial isopod *Armadillidium vulgare*, and the bivalve *Soletellina alba* contributed most to dissimilarity among treatments. While PERMANOVAs showed a significant interaction between location and treatment for all of these species (*Orchestia* sp.: pseudo- $F_{4,36} = 3.11$, $p(\text{mc}) = 0.002$; *Paragrapsus laevis*: pseudo- $F_{4,36} = 2.65$, $p(\text{mc}) = 0.020$; *Armadillidium vulgare*: pseudo- $F_{4,36} = 4.71$, $p(\text{mc}) < 0.001$; *Soletellina alba*: pseudo- $F_{4,36} = 7.48$, $p(\text{mc}) < 0.001$), the specific differences between locations and treatments varied with species (Fig. 10).

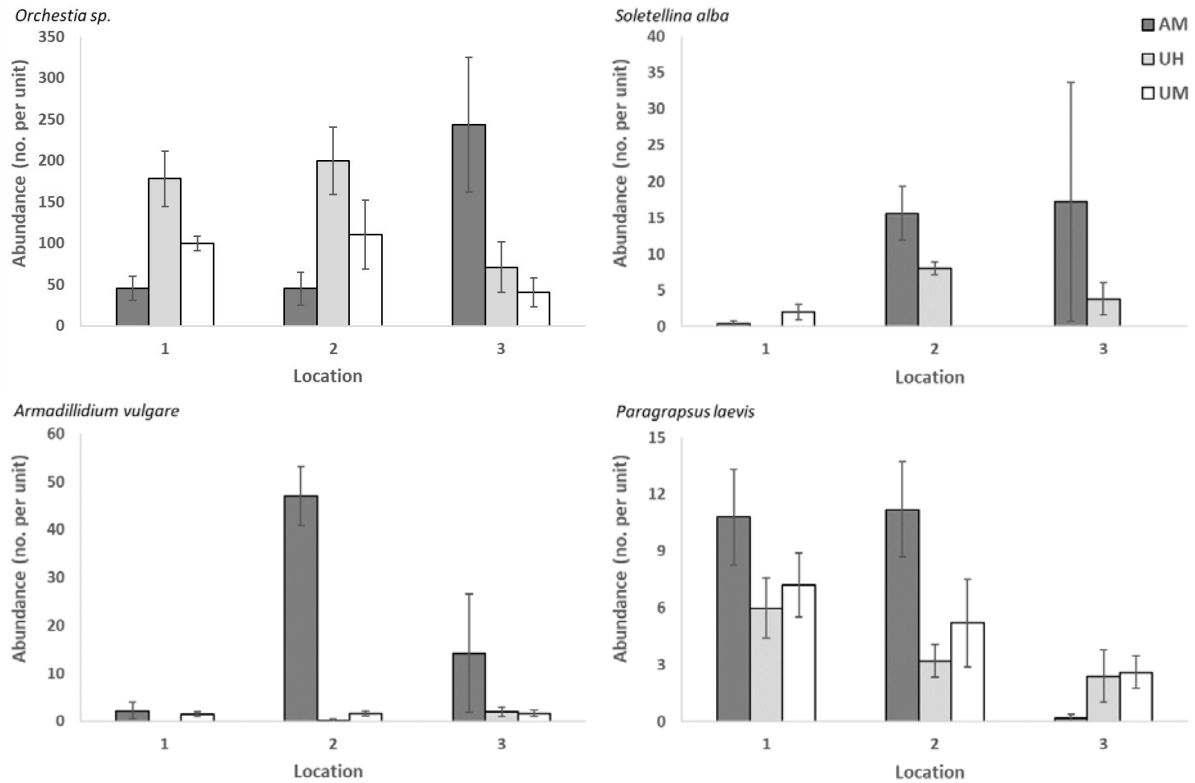


Figure 10; Mean (\pm SE) abundances of *Orchestia sp.*, *Soletellina alba*, *Armadillidium vulgare*, and *Paragrapsus laevis* colonising wrack deployed at the mid-intertidal elevation of armoured sites (AM), or at a mid- (UM) or high intertidal elevation (UH) of unarmoured sites, at each of three mangrove forests. $n = 7$.

The abundance of terrestrial fauna colonising the wrack showed a significant interaction between location and treatment (pseudo- $F_{4, 36} = 3.92$, $p(\text{mc}) < 0.001$). At one of the three locations (L2), the mid-intertidal elevation of the armoured site had significantly higher abundances of terrestrial fauna than either the high-intertidal ($t_8 = 8.99$, $p(\text{mc}) < 0.001$) or mid-intertidal ($t_8 = 6.83$, $p(\text{mc}) < 0.001$) elevation of the unarmoured sites, with all other pairwise comparisons non-significant (Fig. 11a). Terrestrial species richness did not show a significant interaction between, or significant main effects, location and treatment (Lo x Tr: pseudo- $F_{4, 36} = 2.17$, $p(\text{mc}) = 0.079$; Lo: pseudo- $F_{2, 36} = 0.79$, $p(\text{mc}) = 0.473$; Tr: pseudo- $F_{2, 36} = 3.02$, $p(\text{mc}) = 0.132$; Fig. 11b).

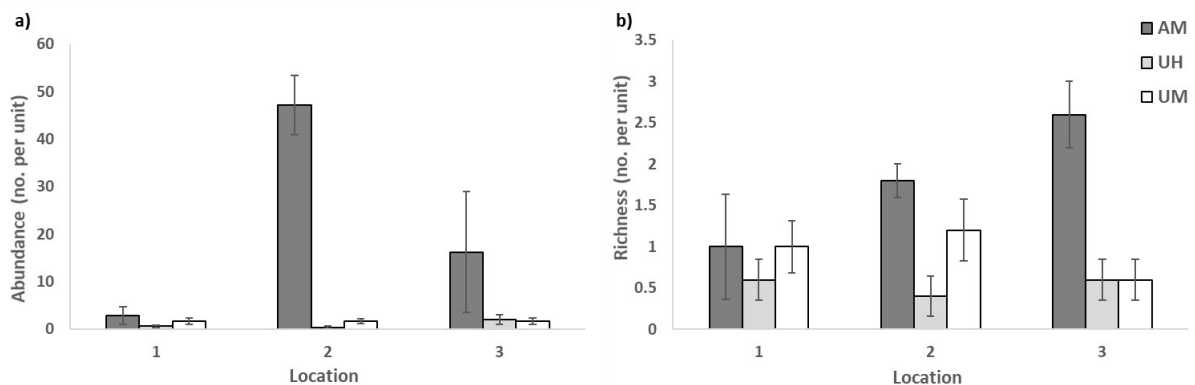


Figure 11; Mean (\pm SE) of terrestrial species (a) abundances and (b) richnesses colonising wrack deployed at the mid-intertidal elevation of armoured sites (AM), or at a mid- (UM) or high intertidal elevation (UH) of unarmoured sites, at each of three mangrove forests. $n = 7$.

Discussion

In eliminating high intertidal habitat and modifying shoreline profiles, seawalls can produce structural changes in habitats (Griggs 2005; Dugan et al. 2008; Shipman 2010; Heatherington and Bishop 2012; Heerhartz et al. 2014; Pontee 2013) that may flow on to influence invertebrate communities (Dethier et al. 2016; Heerhartz et al. 2016). Here, as in a previous study (Heatherington and Bishop 2012), we found that armoured mangrove forests were generally characterised by a truncated shoreline, and an enhanced density of mangrove pneumatophores, of shorter height, as compared to unarmoured sites, with inconsistent patterns of difference between armoured and unarmoured sites in tree size and density. Despite the differing density (and height) of pneumatophores between armoured and unarmoured shorelines, we found that at the patch scale, there was no consistent pattern of difference in the total abundance and richness of their invertebrate communities. Nevertheless, our calculations indicate an overall reduction in habitat available to invertebrates on armoured as opposed to unarmoured shorelines. Additionally, our experimental deployments of wrack suggest that when background habitat heterogeneity among sites is eliminated, stronger differences in the faunal communities of armoured and unarmoured shorelines may be seen.

Like previous studies that have censused faunal communities on other types of sedimentary shoreline (e.g. Dethier et al. 2016; Heerhartz et al. 2016; Sobockinski et al. 2010), our surveys of mangrove forests found spatially variable patterns of difference between armoured and unarmoured sites in the density and richness per unit area of epifauna. Instead, epifaunal communities displayed large differences in abundance and richness among locations. In highly urbanised environments subject to multiple stressors (Kenworthy et al. 2016), local-scale factors other than armouring, for example contaminant concentrations (Rumisha et al. 2012), exposure to boat wake (Bishop 2004), and adjacent land use (Lindgarth and Hoskin 2001) may play a more important role in shaping communities. Additionally, any difference among locations in the height, intertidal elevation, and date of construction of seawalls may also contribute to contrasting patterns of differences (see Heery et al. 2017).

In previous studies, the only taxa to show a consistent response to armouring across locations were those that burrow on the high shore and are hence displaced by coastal armouring structures constructed below the high-water mark (Dethier et al. 2016; Dugan et al. 2003; Sobockinski et al. 2010;). By contrast, in the present study, an anemone that attaches to pneumatophores and is more abundant on the lower and mid intertidal than the high intertidal shore was among the taxa to display the strongest spatial pattern with respect to armouring. The differing abundance of this taxon between armoured and unarmoured sites appears to have been driven by its positive

relationship with pneumatophore density, which as in a previous study (Heatherington and Bishop 2012), was greater at armoured than unarmoured sites. Differences in pneumatophore density between armoured and unarmoured sites may be attributable to differences in shoreline profile and hence tidal inundation. In influencing the redox potential of the soil, the duration of flooding can influence pneumatophore density (Dahdouh-Guebas et al. 2007; Toma et al. 1991) because a longer inundation period leads to a lower redox potential of the sediment (Toma et al. 1991). In addition to influencing the availability of hard substrate for attachment, a higher pneumatophore density at armoured sites may influence patterns of animal movement and their susceptibility to predation (Bishop et al. 2007; Primavera 1997).

Although, on unarmoured shorelines, the gastropod *Ophicardelus ornatus*, was present at greater density at high than mid or low intertidal elevations, its density was not consistently negatively affected by displacement of high intertidal mud and pneumatophore habitats by seawalls. Instead, we found that this species was capable of occupying seawalls as an alternate substrate and, in some instances, displayed greater densities on this than natural substrates of the high intertidal. Nevertheless, because the intertidal habitat provided by a vertical seawall is much less than that granted by the more horizontally orientated profile of an unarmoured shoreline, the total number of animals on an armoured shoreline would be expected to be reduced.

In addition to reducing the habitat area available to intertidal organisms, the other implication of a lowered interface between the terrestrial and aquatic zone at armoured sites is a reduced distance between terrestrial and mid-low intertidal habitats. Whereas previous studies have found a reduced contribution of terrestrial taxa to biodiversity at armoured sites (Sobocinski et al. 2010), to the contrary, we found a greater contribution of terrestrial species to biodiversity in the mid intertidal of armoured than unarmoured sites. This suggests that in our study, the seawall was not acting as a barrier to species colonisation as is frequently posited (Bishop et al. 2017), but rather enhanced connectivity between the mid intertidal and terrestrial environments. Further, this enhanced connectivity, with the greater contribution of terrestrial species to biodiversity at some locations, can be expected to alter biotic interactions that may only be recognised over longer time-frames (Wisz et al. 2013). Nevertheless, some individual taxa, that likely colonised from the terrestrial zone, displayed reduced abundances on armoured as compared to unarmoured shorelines.

Whereas previous studies sampling natural wrack accumulations on armoured and unarmoured shorelines have not detected any difference in the density of dipterans between these (Sobocinski et al. 2010), here we found that in standardised deployments of wrack, armoured sites had significantly less larvae than unarmoured sites. The mechanism for this difference is unclear.

Differences in wrack decomposition and retention are unlikely to account for this difference as litter was stabilised with cages, and in another study (chapter 4) we found that decomposition rates did not differ between armoured and unarmoured sites when litter composition was held constant. Previous studies have attributed greater densities of insects at armoured than unarmoured sites to overhanging riparian vegetation (Heerhartz et al. 2014) that likely contributes to both input of insects (Toft et al. 2013) and to cooler and damper conditions on the shore (Rice 2006).

Overall, our results suggest that habitat loss rather than modification will be the greater contributor to changes in the faunal communities of armoured mangrove forests. Densities and richness per unit area of fauna generally displayed idiosyncratic patterns of difference with respect to armouring across the three study sites. By contrast, our calculations indicate at all three locations a reduced availability of hard substrate for attachment due to a combination of shoreline truncation and, at some sites, also a reduction in mangrove density and tree circumference. The ecological implications of such changes will vary among functional groups. Whereas marine predators (e.g. fishes, swimmer crabs) that forage on invertebrates in the intertidal zone may be relatively unaffected by armouring because it does not appreciably influence faunal density at mid and low intertidal zones, predators that focus foraging at a high intertidal elevation may be more affected. Additionally, ecosystem services that are affected more by the total number of organisms present at a site scale than their local density may be negatively affected by reductions in habitat.

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6. Discussion

Much of the previous research on ecological impacts of seawalls has been concerned with the extent to which they provide equivalent habitat to their closest natural analogue, rocky shores (Bulleri 2005; Bulleri et al. 2005; Lee and Li 2013). By contrast, there has been relatively little work assessing impacts of seawalls on sedimentary ecosystems, and the research that has been done has primarily focused on open ocean beaches (Dugan et al. 2003; Lucrezi et al. 2010).

While in the Northern Hemisphere there has been some work examining impacts of armouring on estuarine shorelines that are unvegetated or dominated by marsh (e.g. Heerhartz et al. 2014, 2016; Dethier et al. 2016), few studies exist for estuarine sedimentary shorelines of the Southern Hemisphere, or for those that support mangrove forests (but see Heatherington and Bishop 2012). This thesis addressed these gaps by assessing differences in the structure and ecological function of unvegetated and mangrove shorelines with and without seawalls, in temperate east Australian estuaries, albeit limited to two estuaries and only a minor temporal component. This thesis had a particular focus on invertebrate communities, that underpin estuarine fisheries productivity, nutrient cycling and other important ecosystem services (Barbier et al. 2011; Prather et al. 2013) and on wrack dynamics, which influence the provision of food and habitat to invertebrates (Moore et al. 2004).

It was hypothesised that there would be differences in invertebrate communities between sedimentary shorelines with and without a seawall, and this was seen at sandy, muddy, and mangrove dominated shorelines. However, the patterns exhibited were varied; for example, in some instances, sites with a seawall had a greater abundance and richness of invertebrates than sites without a seawall, while in other instances the reverse pattern was seen. The size, composition and dynamics of wrack deposits, by contrast, displayed more consistent patterns of difference between mangrove forests with and without a seawall. Wrack deposits were generally smaller, with a greater component of terrestrial litter and a higher turnover rate at armoured sites. These patterns of difference in wrack between armoured and unarmoured sites were consistent with differences in the morphology and habitat structure of mangrove forests with and without seawalls.

The context dependency of results, their application to management, as well as future research directions are elaborated upon in the sections that follow.

Impacts of seawalls on detrital dynamics

Among the mechanisms by which shoreline armouring is posited to influence invertebrate communities is by changing the size, composition and dynamics of wrack deposits (Dethier et al. 2016). Wrack, dead macrophytic material that generally accumulates at the high water mark of intertidal shoreline, provides food and habitat to invertebrate communities, that in turn fuel higher taxonomic levels such as fish and shorebirds (Dugan et al. 2003; Munsch et al. 2015a,b; Rolet et al. 2015). In chapter 4, I found clear differences in wrack deposits between armoured and unarmoured mangrove forests. Deposits were generally smaller on armoured than unarmoured shorelines, and contained a greater proportion of terrestrial litter. Experiments examining differences in the retention and decomposition of wrack between armoured and unarmoured shorelines revealed that both the more rapid flushing of wrack on armoured shorelines and a more rapid decomposition rate likely contributed to smaller deposits.

Structural differences in the mangrove habitats of armoured and unarmoured mangrove forests appear to have underpinned these patterns of difference. Pneumatophores, which may influence trapping and retention of wrack (Bishop et al. 2013), were denser but shorter in armoured mangrove forests (chapter 5), so potentially less effective at trapping and retaining wrack. Additionally, armoured mangrove forests were, due to placement of seawalls in the mid-intertidal zone, of truncated width (chapters 4, 5). This meant that wrack accumulated lower on the shore, and was inundated more frequently by tides that can transport material away. The truncated profile also allowed mangrove tree branches to over-hang the seawall and drop leaves into the supratidal environment, resulting in a greater proportion of mangrove leaf litter in the supratidal environment of armoured than unarmoured mangrove forests. There was also a pattern of greater inputs of terrestrial litter into mid-intertidal wrack deposits of armoured than unarmoured sites, likely due to the increased proximity of the mid intertidal zone to the terrestrial environment where placement of seawalls results in loss of the high intertidal zone.

While, within mangrove forests, litterfall from mangrove trees is generally the dominant source of wrack (Alongi 2014; Kristensen et al. 2017), there are portions of litter from benthic and epiphytic algal growth, seagrass from adjacent meadows or phytoplankton that wash up tidally, or input from terrestrial sources that are imported from surface runoff (Kristensen et al. 2017). Intertidally placed seawalls provide a substrate on which algae can grow, and sloughing of this may introduce wrack to the adjacent environment (Heery et al, 2017). Conversely, if armouring negatively impacts the area of other hard substrates, such as mangrove trees, on which algae can grow, detrital substrates may be negatively impacted. In chapter 5, I found that, predominantly, at armoured sites there was a reduction in the availability of hard substrate for organismal attachment. Nevertheless, cover of algae on mangrove trunks and seawalls was low, perhaps

because of the high sediment loads and low light availability in this environment. Hence, it is unlikely that algal subsidies would be modified by armouring by such mechanisms in this environment.

The identity (and hence morphological and chemical traits) of wrack plays an important role in determining the community it supports (de Oliveira et al. 2012; Rodil et al. 2008), by influencing its palatability and fate (Lastra et al. 2015; Rodil et al. 2015). The differing composition of wrack deposits at armoured as compared to unarmoured sites led to differences in its decomposition rate, with the presence of *Casuarina* accelerating mangrove leaf decomposition (chapter 4). The consequences of this more rapid decomposition for invertebrate communities was not directly assessed but an enhanced turnover rate may reduce the period over which wrack is available as food and habitat. The addition of *Casuarina* to mangrove litter may also influence invertebrate communities by influencing the heterogeneity of habitat for organisms that reside within deposits. However, this was also not addressed in this thesis.

As mangrove wrack plays an important role in structuring benthic communities and trophic structure not only of mangroves but also of adjacent habitats, understanding how the introduction of seawalls influences its accumulation and fate is critical to understanding wide-scale ecosystem impacts, and developing management strategies to counter these.

Impacts of seawalls on invertebrate communities

Across the various sedimentary shoreline types examined in this thesis, the direction of differences in the invertebrate communities between armoured and unarmoured sites varied and, at times, were at odds with the prevailing literature. Many studies have found decreased invertebrate diversity at sedimentary sites with armouring (Dethier et al. 2016; Harris et al. 2014; Heerhartz et al. 2016; Lowe and Peterson 2014; Morley et al. 2012; Seitz et al. 2006), often attributing this to reduced wrack accumulations at armoured sites. While I found that the invertebrates of unvegetated muddy shorelines displayed a similarly negative relationship with respect to seawalls, wrack deposits were, at the time of sampling, small and did not differ with respect to armouring (chapter 3). By contrast on unvegetated sandy shorelines I found the reverse pattern of greater invertebrate abundances and richnesses at armoured sites (chapter 3), and in mangrove forests, where I did find smaller wrack deposits at armoured than unarmoured sites (chapter 4), patterns in invertebrates were largely idiosyncratic with respect to armouring (chapter 5). Results indicating no differences between armoured and unarmoured sedimentary shorelines or higher abundances of invertebrates are not unique, but may reflect variability in

environmental conditions at sites (Strayer et al. 2012) or species-specific responses (e.g. barnacles (Munsch et al. 2015a); polychaetes/bivalves (Rolet et al. 2015)).

Most of the other studies examining effects of armouring on invertebrate communities are from sandy beach type habitats (Dethier et al. 2016; Harris et al. 2014; Heerhartz et al. 2016; but see Lowe and Peterson 2014 as an example of salt-marsh community). There are numerous differences between sandy beach and mangrove habitats that may account for the differences in results, for example differences in 1) wrack characteristics, including quality and quantity, 2) environmental conditions, such as ambient moisture content and temperature, ultraviolet radiation, and sediment quality, and 3) invertebrate community structure, e.g. mangrove forests may have species that are already adapted to hard-substrate where sandy-beach type habitats may not. It is also possible that methodological differences contributed to the divergent results our study. For example, whereas our study examined differences between armoured and unarmoured sites with respect to intertidal height, other studies pooled across these or considered only a single tidal zone, i.e. supralittoral (Sobocinski et al. 2010), littoral (Harris et al. 2014; Morley et al. 2012; Rolet et al. 2015), sublittoral (Seitz et al. 2006; Munsch et al. 2015b). However, studies that, like this thesis, stratified sampling of invertebrate abundance across multiple intertidal elevations (Heerhartz et al. 2016; Dethier et al. 2016) found no significant difference between intertidal heights for total abundances, while my study of benthic invertebrates on sandy and muddy shorelines found significant differences between intertidal heights, and that effects of armouring were limited to the mid-intertidal zone. Other factors that must be taken into account when evaluating our results are the time of year sampling occurred, the limited spatial extent of sampling, and the type of armouring structures themselves. My studies were conducted during the Australasian summer, and did not span a multiyear timeframe, limiting my ability to identify seasonal or long-term trends.

Although differences in invertebrate communities between armoured and unarmoured stretches of mangrove forests were largely idiosyncratic with respect to locations, some common patterns emerged. First, there were generally greater densities and richnesses per unit area of terrestrial species at sites with than without armouring. Second, several taxa, such as an anemone that attaches to pneumatophores, displayed greater densities at armoured sites. The pattern of higher terrestrial species abundance and richness at sites with a seawall is likely as a direct result of a decreased distance these species have to travel to reach the intertidal habitat. The greater abundances of anemones at sites with seawalls, which followed the pattern of greater density, suggests that modification of the availability of hard substrate acts as a mechanism of change invertebrate communities on sedimentary shorelines. In another study of sedimentary shorelines,

those with a seawall, as opposed to without, had higher abundances of species adapted to hard substrate (Munsch et al. 2015b).

Context-dependency of ecological impacts

Sedimentary shores are morphologically dynamic environments, that are situated in a variety of geomorphic and hydrodynamic settings. This thesis found that effects of coastal armouring on sedimentary ecosystems varied spatially at the scale of sites within estuaries. In chapter 3, whether invertebrate abundances were lesser or greater at armoured than unarmoured sites varied according to tidal elevation and whether shorelines were comprised of sandy or muddy sediments. In chapter 4, there was variation in the magnitude of differences in wrack accumulation between armoured and unarmoured sites, across shorelines differing in seawall placement and shoreline width. In chapter 5, differences in invertebrate communities between armoured and unarmoured sites were spatially inconsistent among sites, suggesting other local-scale factors may mediate or indeed outweigh any armouring effect.

The sandy and muddy sites of Brisbane Waters differed not only in their sediment properties, but also in their wave exposure and the faunal assemblages that they supported (chapter 3). Each of these factors may, potentially, influence effects of seawalls on their communities (Heery et al. 2017). Dugan et al. (2017) proposed a framework for considering impacts of coastal armouring, in which ecological effects of armouring intensify with the energy of the environment in which they are placed, with wave energy both a function of the environment and also the intertidal height at which a seawall is placed. The differing pattern, with respect to seawalls, exhibited by infauna of sandy and muddy shorelines, is as predicted by this framework. Interestingly, however, patterns of difference at the more exposed, sandy, locations were in the direction of increased abundance at armoured sites. Hence, future frameworks should consider not only how the magnitude but also the direction of impacts may be expected to vary across exposure gradients.

Sedimentary shores encompass a wide range of habitat types, i.e. sandy beaches, muddy tidal-flats, saltmarshes, mangrove forests. My sampling of the invertebrate communities of unvegetated shorelines (chapter 3) and of mangrove forests (chapter 5) revealed differing patterns, with respect to armouring, between these. Whereas on unvegetated shorelines, consistent patterns of difference in faunal abundance with respect to armouring were seen among locations of similar type, in urban mangrove forests, patterns were largely idiosyncratic. Mangrove forests are generally considered lower energy environments than unvegetated

estuarine shorelines (Dugan et al. 2017), such that the weaker patterns in mangrove forests are consistent with the Dugan et al. (2017) model.

In chapter 4, I found that although the direction of difference in the size and composition of wrack deposits between armoured and unarmoured sites was consistent among locations, the magnitude of the difference differed. Among the sites sampled, there was variability in shoreline width and placement of the seawalls. There was also variation in the adjacent vegetation community. Each of these factors likely contributed to spatial variation in the magnitude of effects. Previous studies have highlighted the role that adjacent land use change, which often accompanies armouring, can play in contributing to changes in wrack deposits at sites with coastal armouring (Higgins et al. 2005). Impacts of coastal defences on ecological process are generally acknowledged to increase as structures are placed lower on the shore (Dugan et al. 2017).

Overall the spatially variable results indicate the need to consider environmental and biological setting when considering impacts of seawalls.

Managing urbanisation of sedimentary shorelines

There is growing recognition that designing infrastructure to align with ecological principles (termed ecological engineering) is vital to mitigating negative impacts (Bergen et al. 2001; Mitsch 2012; Dafforn et al. 2015; Dyson et al. 2015; Lai et al. 2015, Lewis 2015). Despite this growing recognition, marine ecological engineering is still in its infancy (Elliott et al. 2016) and has most commonly involved adding microhabitats to seawalls to mimic those of rocky shorelines (Martins et al. 2016; Chapman et al. 2017). Hybrid structures, whereby seawalls are combined with plantings of saltmarsh, mangroves or other biogenic habitats, may partially mitigate impacts of hard engineering on sedimentary shorelines (Bilkovic and Mitchell 2013; Gittman et al. 2016). Additionally, living shorelines approaches, whereby shorelines are stabilised using living habitat-forming species may remove the need for hard engineering (Davis et al. 2006)

When implementing ecological engineering principles in sedimentary, as in other environments, it is useful to design with specific ecological goals in mind. This will determine the type of approaches that should be used, i.e. shoreline stability via plantings (Chung 2006), mitigating eutrophication effects from surface runoff via constructed wetlands (Vymazal 2007), conserving habitat area via creating living shorelines (Bilkovic et al. 2016), coastal protection via managing ecological engineering species (Borsje et al. 2011). The finding by this thesis that wrack retention is reduced at armoured as compared to unarmoured sites (chapter 4) suggests that

wrack retaining structures may be part of an ecoengineering approach that conserves ecosystem function in spatially subsidised sedimentary habitats. Previous research has found that breakwaters along urban shorelines are traps for anthropogenic trash, as well as wood (Aguilera et al. 2016). This trapping feature of breakwaters may be harnessed in the design of structures that retain wrack to support a trophic web. In urban environments, however, this will need to be accompanied with anthropogenic litter management so that the structures are not simply anthropogenic litter traps.

Knowledge of when and where impacts of coastal armouring on sedimentary ecosystems is greatest might help to identify areas in which the investigation of alternate, soft engineering approaches should be pursued. These approaches may include beach nourishment, which maintains beach width (Cooke et al. 2012), or living shoreline approaches that use natural habitat forming species for coastal protection. Additionally, the need for coastal armouring may be lessened through the enforcement of construction setbacks (Clark 1991; Fish et al. 2008; Jonah et al. 2016; Maloney and O'Donnell 1977).

Future directions

This thesis used a mensurative approach to investigate impacts of coastal armouring on sedimentary ecosystems, comparing benthic community structure and ecological processes between armoured and unarmoured sites. This approach was utilised because the construction of the majority of seawalls in Sydney Harbour significantly pre-dated the commencement of study. Such spatial contrasts can be informative of impacts in the absence of before data, and dominate the coastal armouring literature (e.g. Davis et al. 2002; Dethier et al. 2016; Heerhartz et al., 2014, 2016; Morley et al. 2012; Sobocinski et al. 2010). The general concordance of my results with those of similar studies done elsewhere in other habitats (e.g. armouring reduces shoreline widths and modifies intertidal wrack accumulation, Dethier et al. 2016; Heerhartz et al. 2014; Sobocinski et al. 2010: high spatial variability in invertebrate communities and decreases in detectable differences at lower intertidal elevations, Davis et al. 2002; Dethier et al. 2016), and the general consistency of impacts with hypotheses is suggestive that differences between armoured and unarmoured sites is indeed due to seawalls. Nevertheless, in order to establish causation between a putative disturbance and an ecological impact, Before-After-Control-Impact studies are required (Underwood 1991). Seawalls and other coastal armouring structures are generally constructed in environments most at risk of erosion and inundation, or in which there is important infrastructure to protect, so it is possible that there are pre-existing differences between armoured and unarmoured locations, that are unrelated to the presence of seawalls. Identifying sites at which construction of seawalls is planned, but yet to begin, and determining a

before impact baseline, and post-construction effects, at these and control sites would be desirable.

The focus of this study was on site-scale impacts of coastal armouring, but there is growing recognition that in impacting ecological connectivity, this infrastructure may produce ecological impacts over much larger spatial scales (Bishop et al. 2017). In chapters 4 and 5, I showed that armoured mangrove forests are typically narrower than unarmoured sites. If the reduced habitat for mangrove trees results in reduced litter production, the question arises, what happens in adjacent habitats that rely on subsidies from the lost habitat? Is there a reduction in biodiversity? It is almost certain that there will be effects from marine urbanisation at a distance from the actual sites of structure placement. Modelling, coupled with sampling of these adjacent habitats may address questions about the scale of impacts of coastal armouring,

Throughout this thesis, I found significant site-scale variability in the magnitude, and some instances the direction of differences in community structure and wrack dynamics between armoured and unarmoured sites. Variation in environmental factors such as wave exposure and sediment characteristics, variation in the local species pool that can colonise and interact, as well as variation in the design of seawalls, the height of their placement on the shore and the number of years since construction could all potential influence the magnitude and direction of impacts (chapter 2, Heery et al. 2017). As the number of studies on impacts of seawalls and revetments from around the world continues to grow, meta-analyses may be used to address the relative importance of these factors, similar to Dugan et al. (2017) which examined hydrological conditions. This will be contingent upon studies providing relevant detail on environmental conditions, the community structure and seawall characteristics at their study sites. Targeted contrasts between factors of interest may also be made by sampling interspersed locations representative of the differing conditions.

Overall, the range of environmental conditions under which my studies were conducted was relatively limited. The surveys and experiments were confined to two heavily urbanised estuaries in temperate eastern Australia. Nevertheless, seawalls and other coastal armouring structures are increasingly being used to support regionally important infrastructure in smaller population centres too (Bishop et al. 2017). If these less degraded estuaries are of higher biodiversity than the heavily urbanised estuaries in which the majority of research on ecological impacts of armouring has been conducted, patterns of impact may differ. On the one hand, communities whose composition has not already been filtered by other stressors may be more sensitive to disturbance (Lawes et al. 2017). Alternatively, the biodiversity-ecosystem function literature suggests that more diverse communities may display greater resistance and resilience to perturbation (Oliver et al. 2015) and biotic invasions (Jeschke 2014).

The relatively short time frame of the studies comprising this thesis also plays a role in how the results can be evaluated. Assessments of differences between armoured and unarmoured sites were generally based on single sampling times. Although it is expected that effects may persist through time, the magnitude of differences may vary seasonally according to variation in community composition and in litter inputs. Long-term studies are needed to understand how processes are affected by the presence of coastal armouring, and are important to understanding the impacts of marine urbanisation.

The pressure from a rapidly increasing human population and the associated development of the coastal zone necessitates appropriate management strategies if we are to maintain ecosystem function and diversity goals. Research avenues that will assist in this endeavour include 1) the evaluation of the environmental conditions under which impacts are greatest, and in which construction of new seawalls should, if possible, be avoided, 2) the identification of design elements of coastal structures that may mitigate impacts of these on ecosystem dynamics and 3) the development of a framework for assessing and modelling the cumulative impacts of multiple coastal armouring structures that are increasing in number in the coastal zone. While design elements for coastal armouring are being developed to mimic natural rocky shorelines with some success (Strain et al. 2018), the research into design for dynamic sedimentary shorelines is limited, partially by a lack of quantitative knowledge of sedimentary shoreline ecosystem processes. This limitation is not insurmountable, however, integrating ecological and engineering disciplines to a deeper understanding is essential (Mitsch 2014), as is developing methods to promote social acceptance. Implementation of alternate approaches to shoreline stabilisation and protection (i.e. living shoreline, or hybrid approaches, Dethier et al. 2017) that incorporate ecological species, such as saltmarsh or bivalve reefs, that perform this role may be part of best management practice. Developing an understanding of the cumulative and larger-scale impacts of coastal armouring will require quantitative understanding of the various trophic compartments of coastal ecosystems as well as the transfers between them. If an ecological network model can be produced for sedimentary habitats, seawalls can then be added to models to assess their impacts and used by coastal managers for marine spatial planning.

Conclusions

This thesis addressed ecological impacts holistically, not just focusing on biological community response, but considering environmental conditions that may be affected by coastal armouring. By taking a whole system view, the possible mechanisms by which impacts arose could be evaluated. Throughout this thesis it was seen that armoured shores were morphologically distinct from natural shorelines, not only in width, but also in structural elements.

In mangrove forests with a seawall, shoreline width, and consequently the availability of habitat was less than in forests without a seawall. Further, there were differences in pneumatophore height and density and the size and composition of wrack subsidies. The greater contribution of terrestrial litter sources to wrack at armoured sites increased the decomposition rate of mangrove wrack while the more stunted pneumatophores, coupled with the lowering of the terrestrial-marine interface, likely contributed to the reduced retention of wrack at the temporal scale of tidal cycles. In combination, the increased rate of wrack decomposition and reduced wrack retention at sites with seawalls increased the rate of detrital turnover and likely were contributing factors to the smaller wrack deposits. Contrasts of invertebrate community structure between mangrove forests with and without a seawall suggested that the reduced distance between terrestrial and marine habitats at sites with seawalls altered the composition of the community with higher terrestrial species abundances and richnesses.

The unvegetated shores showed differences in sedimentary characteristics that aligned with location rather than state of armouring. However, among shorelines of similar sediment grain size, the structure of invertebrate communities varied consistently with respect to armouring and was correlated with sediment variables such as organic and mud content.

Overall, the results presented in this thesis suggest that coastal armouring modifies invertebrate communities through changing habitat structure and environmental conditions. Understanding the specific ecological conditions under which coastal armouring will contribute to reductions in invertebrate diversity, or contribute to the propagation of invasive or opportunistic species, is needed to evaluate whether the implementation of coastal armouring is appropriate, or another method of shoreline protection is preferable. This thesis contributes to a growing set of literature that clarifies the importance and likely impacts of coastal armouring in habitats that are under increasing anthropogenic pressure, coastal sedimentary habitats. The information provided by this thesis will assist environmental managers in evaluating the potential ecological consequences of constructing seawalls and in developing mitigation strategies that align engineering with ecological principles.

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Review

Identifying the consequences of ocean sprawl for sedimentary habitats



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ABSTRACT

Extensive development and construction in marine and coastal systems is driving a phenomenon known as "ocean sprawl". Ocean sprawl removes or transforms marine habitats through the addition of artificial structures and some of the most significant impacts are occurring in sedimentary environments. Marine sediments have substantial social, ecological, and economic value, as they are rich in biodiversity, crucial to fisheries productivity, and major sites of nutrient transformation. Yet the impact of ocean sprawl on sedimentary environments has largely been ignored. Here we review current knowledge of the impacts to sedimentary ecosystems arising from artificial structures.

Artificial structures alter the composition and abundance of a wide variety of sediment-dependent taxa, including microbes, invertebrates, and benthic-feeding fishes. The effects vary by structure design and configuration, as well as the physical, chemical, and biological characteristics of the environment in which structures are placed. The mechanisms driving effects from artificial structures include placement loss, habitat degradation, modification of sound and light conditions, hydrodynamic changes, organic enrichment and material fluxes, contamination, and altered biotic interactions. Most studies have inferred mechanism based on descriptive work, comparing biological and physical processes at various distances from structures. Further experimental studies are needed to identify the relative importance of multiple mechanisms and to demonstrate causal relationships. Additionally, past studies have focused on impacts at a relatively small scale, and independently of other development that is occurring. There is need to quantify large-scale and cumulative effects on sedimentary ecosystems as artificial structures proliferate. We highlight the importance for comprehensive monitoring using robust survey designs and outline research strategies needed to understand, value, and protect marine sedimentary ecosystems in the face of a rapidly changing environment.

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Mapping global impacts of marine built infrastructure: current trends, future projections and data challenges

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Abstract

Built infrastructure is rapidly replacing natural habitats, resulting in the global loss of biodiversity and ecosystem services. Management strategies to mitigate these impacts require quantitative information about the area of habitat lost (footprint) and degraded (halo effects) at local to global scales. Here, we provide the first global estimate of the current and future extent of the impacts of marine infrastructure or “ocean sprawl” on the seafloor. Marine infrastructure occupies a total area of ~43,000 km² and disturbs over 3M km² of seabed, with most impacts located in nearshore areas. Ocean sprawl is expected to expand by > 19% by 2027 (~8,000 km²), revealing an opportunity to manage offshore development while it remains in the growth phase. With varying resolution, quality and availability of data among regions, the compilation of spatially explicit data to create open source databases is essential to accurately measure cumulative impacts and manage the ecological consequences of ocean sprawl.

Keywords: built infrastructure, ocean sprawl, ecosystem impacts, environmental management, global assessment

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