An examination of the effectiveness of estuarine conservation management tools and their theoretical underpinnings

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General Summary

Estuarine ecosystems provide a wide range of valuable ecosystem services including the provision of food and raw materials, shoreline protection, carbon sequestration and recreational opportunities. These ecosystem services are underpinned by local biodiversity, which determines resistance and resilience in the face of environmental perturbations. However, estuarine biodiversity is under increasing pressure from coastal development and anthropogenic climate change. The protection of estuarine ecosystem services requires conservation measures that ensure the persistence of biodiversity. This thesis examines: 1) the utility of key ecological theories in informing estuarine conservation planning; 2) the applicability of ecosystem-level risk assessments to estuaries; and 3) the applicability of existing estuarine typologies and ecological metrics of community structure to the implementation and monitoring of conservation interventions in estuaries. Using meta-analysis of existing literature, I show qualified support for the application of island biogeographic theory to estuarine habitats. However, field studies reveal that the spatial arrangement of habitat patches in estuarine mosaics affect community structure in ways that extend beyond the covarying effects of habitat patch size and isolation. The proximity of different habitats to one another may facilitate greater abundance in habitat patches through the addition of nutrients or allowing mutualist relationships that would otherwise not exist. These effects are not currently incorporated in estuarine conservation planning. Through a retrospective risk analysis of Chesapeake Bay, USA, I show that the International Union for the Conservation of Nature’s Red List of Ecosystems may in some instances overestimate the risk of collapse in estuarine ecosystems and that criteria based on abiotic and biotic change, rather than ecosystem area, may be more appropriate for such systems. I use existing data to demonstrate that an Australian estuarine typology for estuaries, based on geomorphological and hydrological factors, is effective at describing the habitat mosaics present. Such typologies, may therefore, be of use to estuarine conservation planners in identifying groups of estuaries across ecological processes may be similar. Finally, I test the ability of zeta diversity, a recently developed metric of community structure, to provide a simple and low-cost method of monitoring estuarine seascapes for habitat homogenisation. Overall, these results show that existing conservation tools are effective in the management of estuarine ecosystems but could be made more effective through adaptation.

Statement of Sources Declaration

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

Peter C. Mahoney

May 2018

Contributors

This thesis contains material that has been submitted or prepared for publication as indicated. Please note that the formatting of individual data chapters reflects the requirements of journals to which papers have been, or will be, submitted.

Chapter 1: Introduction

I completed the literature review and writing of this chapter with constructive feedback from my primary supervisor, Associate Professor Melanie Bishop.

Chapter 2: Application of island biogeography theory varies with inhabitant group and environmental setting in estuarine and coastal seascapes

Peter C. Mahoney, Melanie J. Bishop

This chapter is formatted for submission to the journal *Estuarine, Coastal and Shelf Science.*

My contribution to the research paper: concept – 95%, data collection – 100%, analysis – 90%, writing – 80%. Total – 90%.

I received assistance with study design from my supervisor and co-author Associate Professor Melanie Bishop and with statistical analyses from Emeritus Professor Richard Frankham of Macquarie University.

Chapter 3: Epifaunal and infaunal invertebrate communities in estuarine vegetation patches vary according to the identity of adjacent habitat

Peter C. Mahoney, Melanie J. Bishop.

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My contribution to the paper: concept – 80%, data collection – 80%, analysis – 80%, writing – 80%. Total – 80%.

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Chapter 4: Assessing risk of estuarine ecosystem collapse

Peter C. Mahoney, Melanie J. Bishop

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Chapter 5: Are geomorphological typologies for estuaries also useful for classifying their ecosystems?

Peter C. Mahoney, Melanie J. Bishop

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Chapter 6: A test of zeta-diversity as a metric for assessing loss in estuarine habitat mosaics

Peter C. Mahoney, David A. Nipperess

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Chapter 7: Discussion

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"And if ye mingle your affairs with theirs, then (they are) your brothers." (The noble Qur'an.)

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Chapter 1: Introduction

The importance of biodiversity

Biodiversity is the full panoply of living organisms present in an environment, including the functional variability between individuals, species and ecosystems (Mace et al. 2012). Biodiversity underpins ecosystem functions, which are natural ecological processes and ecosystem configurations resulting from interactions between the biological organisms within ecosystems as well as from interactions between those organisms and the abiotic environment (de Groot et al. 2002; Costanza et al. 2014). These functions include the conversion of light or heat energy into chemical form by autotrophs, the production of biomass, the regulation of biogeochemical cycles, carbon sequestration and the provision of habitat (de Groot et al. 2002).

Biodiversity may be viewed as a form of 'ecosystem insurance' (Loreau et al. 2003; Mooney et al. 2009). High biodiversity provides redundancy within functional groups in ecosystems, reducing the risk that the loss of a single species may result in the elimination of a critical ecological function or process (Dunne et al. 2002; Reich et al. 2012). Furthermore, high biodiversity leads to more efficient utilisation of all available resources within ecosystems (Worm et al. 2006; Danovaro et al. 2008; Mooney et al. 2009). The functional redundancy and higher resource-use efficiency resulting from high biodiversity increases the resilience of ecosystems to environmental perturbations (Folke et al. 2004; Tscharntke et al. 2005). Conversely, reductions in biodiversity may result in the loss of interspecies mutualisms, lower resistance to biological invasion and secondary extinctions in species where key mutualist or prey species have vanished (Loreau et al. 2001; Dunne et al. 2002; Zavaleta & Hulvey 2004).

Ecosystem services are those ecological functions of ecosystems that provide goods and/or services of social or financial value to humans. The annual monetary value to humans of ecosystem services as a whole has been estimated at more than twice the total global GDP of human society (Costanza et al. 2014). Biodiversity loss drives non-linear reductions in ecosystem functions and, often exponential, declines in ecosystem services (Danovaro et al. 2008; Mooney et al. 2009). To date, over 60% of ecosystem services have been diminished in scope as a result of anthropogenic activities, predominantly within the last half century (Millennium Ecosystem Assessment 2005; Mooney et al. 2009).

Ecological theories of biodiversity distribution and community structure

Niche theory (Elton 1927) explained the geographic distribution of species and formed the basis of much thinking around the composition of biotic communities. Niche-based models of community structure may be split into environmental filtering and niche differentiation types. Environmental filtering models assume that species are unable to establish or persist in areas where abiotic conditions exceed their physiological tolerances and, therefore, coexisting species should converge in their traits (Hutchinson 1965; Engelbrecht et al. 2007). Alternatively, niche differentiation models predict that competitive exclusion should cause coexisting species to diverge in their traits (Stubbs & Wilson 2004). Environmental filtering models tend to better explain community composition in harsh physical environments, whereas niche differentiation models are more appropriate in benign landscapes (Cornwell et al. 2006; Mayfield & Levine 2010). However, from the late 1960s, several new theories arose that expanded on *niche theory* and enriched the way that community structure was viewed.

Island biogeography theory (MacArthur & Wilson 1967) proposed that community composition on oceanic islands is controlled by two independent factors: distance from a stable mainland source of colonisation, which determines rates of immigration, and island size, which controls rates of species extinctions. Island communities are predicted to achieve dynamic equilibrium when immigration and extinction rates are in balance (MacArthur & Wilson 1963, 1967). However, MacArthur and Wilson's model has been criticised for its underlying assumption that islands were interchangeable and lacked differentiating characteristics (Sauer 1969).

Metapopulation theory (Levins 1969) explored the structure of multiple populations of a species within a patchy landscape that are distinct from each other yet connected to some extent by the dispersal of individuals. Levins' theory shared many core principles with *island biogeography*. Population abundance is determined by the area of the habitat patch occupied and increasing distance between patches imposes escalating time and risk costs on dispersing individuals, reducing colonisation rates (Thomas & Jones 1993; Morris 2003; Bonte et al. 2012). *Metapopulation theory* overcame the criticism levelled at *island biogeography* by incorporating the idea that habitat patches vary in character and quality as well as size and isolation (Hanski & Gilpin 1991; Hanski & Simberloff 1997). Thus, the variable availability of key resources among habitat patches may also affect population abundance and persistence (Székely et al. 2013; Székely & Langenheder 2014). Advances in *metapopulation theory* demonstrated that populations with small or highly variable census sizes are at risk of extirpation from stochastic events such as environmental perturbations, genetic drift and allee effects such as inbreeding depression (Caughley 1994; Frankham et al. 2010, 2017).

In both *island biogeography* and *metapopulation* theories, populations are considered to be autonomous entities that exist for a limited span of time before becoming extirpated as a result of stochastic environmental or demographic factors meaning that habitat patches are not continuously occupied and that both metapopulations and communities are dynamic in their composition (Levins 1969). However, intra-generational migration has been shown to provide a 'rescue effect' to threatened populations (Brown & Kodric-Brown 1977), meaning that colonisation and extinctions rates are not independent of each other as envisaged in *island biogeography theory*.

Landscape ecology theory, arising in the 1980s, incorporated effects of spatial and temporal patterns of habitat patches within the wider landscape or seascape setting on the structure of communities (Risser et al. 1984). *Metacommunity theory* expanded on *metapopulation theory* to incorporate portions of early models based on species traits as well as emerging theories about the effects of complex inter-species interactions (Wilson 1992). New research has identified specific physiological traits as being strongly correlated with extinction risk. Colonisation success tends to be higher in species whose physiological traits or life history strategies provide high dispersal ability (Hanski 1999; Ehrlén & Eriksson 2000). The ability of species to effectively migrate in the face of environmental change is controlled by their generational length and dispersal ability while persistence *in-situ* is positively correlated with fecundity and chromosome numbers in plants but negatively correlated with gestation length, age at maturity and body mass in animals (Murray et al. 2002; O'Grady et al. 2004; Cardillo et al. 2005; Kotiaho et al. 2005; Pandit 2006; Pearson et al. 2014).

Interspecies interactions play a strong role in shaping the distribution of biodiversity and structuring biotic communities. A species may be affected directly through interactions such as competition or predation which alter abundance. However, effects may also result from interactions with other species mediated via intermediate pathways such as trophic linkages, altered environmental conditions or chemical pathways. The effects of such indirect interatcions may be independent of abundance, such as altered behaviours or reproductive success (Menge 1995). Examples of inter-species interactions, both positive and negative, shaping communities are ubiquitous in the literature. The *stress gradient hypothesis* (Bertness & Callaway 1994) predicts that positive interactions between species such as facilitation or mutualism should be frequent in stressful environments but that negative interactions such as competition and predation should be prevalent communities in more benign environments.

Positive interactions provide benefits to species through facilitation and mutualistic relationships. Such interactions may allow species to establish or persist in locations that would otherwise be unsuitable, or may permit greater survival, abundance or fitness than would otherwise be possible (Jones et al. 1997; Stachowicz 2001). For example, ecosystem engineers modify the physical environment and are often keystone species that form an obligate foundation for the biological communities of which they are a part (Jones et al. 1997).

Negative biological interactions such as competition cause harm to one or both species involved. Where coexisting species compete for limiting resource, the result will often be the competitive exclusion of the weaker competitor (Ives & May 1985). However, where stochastic processes give the inferior competitor an atypical advantage, such as where superior competitor displays highly clustered distribution or the inferior competitor is able to disperse more effectively than the superior competitor, an unstable equilibrium state may exist (Hanski & Ranta 1983; Hanski 1987). A similar state may be reached in situations where predation pressure is significantly greater on the superior competitor (Paine 1974). Predation pressure may act as a control on the population size of prey species (Krebs et al. 2001). Changes in this top-down control may result in destabilising changes to community structure that cascade through all trophic levels (Hairston et al. 1960). Predator-prey interactions drive oscillations in the abundance of both predator and prey species, with the population cycle of the prey species generally preceding that of the predator (Krebs et al. 2001).

The sixth mass extinction event

It is now broadly recognised that Earth has entered a sixth mass extinction event, significantly threatening global biodiversity (Pimm et al. 1995; May 2010; Ceballos et al. 2015). Mass extinctions are defined as the loss of ≥ 75% of global species richness within a geologically brief time period (Jablonski 1994). More than 900 extinctions have been recorded since the year 1500, largely amongst birds, reptiles and mammals but across a much broader range of taxa over the last century (Baillie et al. 2004; Mooney et al. 2009; Barnosky et al. 2011). The current global extinction rate is conservatively calculated at between eight and 100 times the background rate of species loss prior to human activities becoming a major influence on the biosphere, estimates of which range from 0.1-2 extinctions per million species per year (Raup 1991; May et al. 1995; Alroy 1996; Baillie et al. 2004; Barnosky et al. 2011; Ceballos et al. 2015). Many more species face possible extinction in the near future. The International Union for the Conservation of Nature (IUCN) currently list 12,709 species as *Endangered* or *Critically Endangered* (IUCN 2016). At a finer scale, the loss of individual populations within species is extremely common and may be as ecologically significant as species extinctions (Hughes et al. 1997; Ceballos & Ehrlich 2009). A recent review by the World Wildlife Fund (2016) reported the extirpation of 58% of local populations across all assessed vertebrate taxa between 1970 and 2012.

Environmental causes of biodiversity loss

Contemporary species extinctions are primarily driven by anthropogenic activities resulting in habitat loss and fragmentation, overexploitation of natural systems, the spread of invasive species and widespread environmental pollution, with many extinctions resulting from novel synergies between these threats (Purvis et al. 2000; Baillie et al. 2004; Brook et al. 2008; Barnosky et al. 2011; Ceballos et al. 2015). Furthermore, extant threats to biodiversity are expected to increase through the direct and indirect effects of anthropogenic climate change (Brook et al. 2008; Bellard et al. 2013).

To date, 83% of Earth's ice-free terrestrial surface is estimated to be directly impacted to some extent by human activity (Sanderson et al. 2002; Bai et al. 2008). Humans have modified approximately $66,500,000km^2$ of land for anthropogenic use, primarily agriculture (Hooke et al. 2012). In estuarine and coastal zones, approximately 35% of global mangrove area was lost to deforestation between 1980 and 2000, seagrass and coastal saltmarsh habitats declined by >65% and oyster reefs by > 85% across the last 250 years, and declines in canopy-forming macroalgae have exceeded 80% in some regions (Valiela et al. 2001; Airoldi et al. 2008; Connell et al. 2008; Waycott et al. 2009; Beck et al. 2011). In the ocean, ongoing oxygen depletion in coastal marine waters has resulted in formerly viable habitat being lost to hypoxic 'dead zones', the combined areas of which now exceed $245,000km^2$, and benthic habitat is increasingly structurally homogeneous due to dredging and bottom trawling activities (Gray et al. 2006; Diaz & Rosenberg 2008).

Numerous modern extinctions are directly attributable to human overexploitation. A wave of such extinctions has tracked human expansion across the globe (Burney & Flannery 2005; Liu et al. 2006). Approximately 8% of extant mammal species and 4% of birds are currently threatened with extinction from overexploitation (Hilton-Taylor 2000). The overharvesting of species may result in cascading effects through entire trophic webs (Pace et al. 1999; Coleman & Williams 2002). Furthermore, anthropogenic overexploitation of global stocks of high trophic level fish and the concomitant decrease in their numbers has subsequently led to unsustainable increases in in extractive pressure on successively lower levels of the marine trophic web (Pauly et al. 1998).

Invasive species are believed to have played a role in more than 50% of recent mammalian, avian and reptilian extinctions globally (Doherty et al. 2016). Invasive species drive reduced population sizes in threatened species, simplify community structures, alter fire regimes and disrupt trophic webs and nutrient cycling (Vander Zanden et al. 1999; Ehrenfeld 2003; Brooks et al. 2004; Gurevitch & Padilla 2004; Estes et al. 2011). Introductions, both deliberate and accidental, of invasive species have tracked human expansion across the globe. The rate of unintentional biological invasion has increased significantly since the 1940s, largely due to expanding global trade which opened new sea, land and air trade routes and greatly increased the volume of goods being transported between bioregions (Ruiz et al. 2000; Aide & Grau 2004; Seebens et al. 2013). Carlton (1999) estimated that, at any given time, >10,000 species are in transit in the ballast water of ships.

Environmental pollution is now ubiquitous in Earth's major biomes (Gibbon et al. 2000; Pereira et al. 2010; Liu et al. 2012; Wilcox et al. 2015). Chemical contaminants and toxins may bioaccumulate within individuals and biomagnify through trophic levels, directly reducing the survival and/or reproductive success of exposed individuals (Reijnders 1986; Espinosa et al. 2007; Kelly et al. 2007; Dietrich et al. 2010). However, the indirect effects of sub-lethal chemical enrichment within waterbodies and the atmosphere also play a strong role in biodiversity loss. Anthropogenic atmospheric enrichment with carbon dioxide is a primary cause of global temperature increase, changes in weather patterns and ocean acidification and is predicted to drive increasing biodiversity loss into the future (Cook et al. 2013; IPCC 2014). The enrichment of aquatic, estuarine and ocean areas with nutrients, particularly nitrogen and phosphorus, has resulted in extensive hypoxic 'dead zones' in those environments worldwide (Diaz & Rosenberg 2008; Gooday et al. 2009; Rabalais et al. 2009, 2010). Furthermore, anthropogenic light and noise pollution have been demonstrated to have a negative impact on a wide range of terrestrial and aquatic taxa (Hölker et al. 2010; Halfwerk et al. 2011; Ortega 2012; Davies et al. 2014).

Climate change is altering a wide range of environmental conditions such as temperature and precipitation regimes in the atmosphere as well as sea level, and pCO_2 levels and salinity in the ocean. Where environmental conditions exceed biological tolerances, organisms must adapt to the new conditions, migrate to more suitable regions, or face extinction (Sala et al. 2000; Thomas et al. 2004; Garcia et al. 2014). Additionally, altered environmental cues are modifying the timing of reproductive and migratory behaviours in many species, sometimes leading to phenological mismatches between peak demand for and availability of food resources that threatens species persistence (Parmesan 2006; Both et al. 2010). Previous mass extinction events in the late Ordovician, Devonian, Permian, Triassic and Cretaceous Periods were similarly linked to fluctuations, albeit of natural origin, within the atmospheric and oceanic compartments of the planetary carbon cycle (Veron 2008).

Conservation as an emerging field

Realisation of the emerging biodiversity crisis was a key driver of the new ecological theories explaining the distribution of biodiversity and the structuring of biotic communities that began to emerge in the late 1960s (Brown & Lomolino 2000; Resasco et al. 2017). These new theories subsequently formed the structural basis for the emerging discipline of conservation biology (Brussard 1985; Soulé 1985; Schama 1995). Further development of those theories has driven changes in the scale and nature of conservation management (Link 2002; Nicholson et al. 2009).

Concerned with slowing, halting or even reversing the decline of biodiversity through protection or restoration, conservation biology has been described as a 'crisis discipline' in which decisions must be made based on the best information available, often in spite of uncertainties arising from incomplete understanding of the ecological systems being managed, to avoid undesirable ecological outcomes (Soulé 1985; Krebs 2008; Green et al.

2015). Accordingly, many conservation interventions were undertaken based on early ecological theories, whose application often lacked empirical evidentiary support (Laurance 2008). For example, *island biogeography theory* was widely applied in fragmented landscapes with habitat patches as a metaphor for oceanic islands, despite multiple flaws in the logic behind such application (Resasco et al. 2017).

Early conservation efforts focused on the identification of species at high risk of extinction and the amelioration of stressors directly affecting those species (Rodrigues et al. 2006). Extinction risk is commonly assessed using metrics such as total extent of occurrence, area of occupancy within that range, overall abundance, mean generational length and degree of connectivity between populations (IUCN Species Survival Commission 2012). The abundance and genetic diversity of individual populations is monitored in many locations using methods such as visual surveys, camera traps or tagging of individuals (Mills 2012). Conservation reserves were created in many regions to safeguard habitat critical to endangered species (Margules & Pressey 2000). Numerous habitat restoration projects were undertaken with the aim of returning an ecosystem to a former, 'natural' state to protect endangered residents (Aronson et al. 1993). However, judgements as to the natural state of ecosystems are highly subjective and are subject to the *shifting baseline syndrome* (Pauly 1995), where the standard of 'natural' is eroded over time and restoration to former states may not be feasible, or even desirable, in light of projected changes in Earth’s climate (Choi 2007). Harvest quotas and controls on harvest seasons were imposed to curb the overexploitation of many species (Woodward & Griffin 2003; Cinner & Aswani 2007). However, as populations generally do not exhibit steady abundance through time, optimal exploitation levels are variable and have often been overestimated (Caddy & Gulland 1983; Ludwig et al. 1993). Globally, eradication programs have been a crucial tool in the management of invasive species (Gosling & Baker 1989; van Dooren 2011; Genovesi 2005).

These programs have met with success in the removal of terrestrial vertebrates but have been far less effective against plants, invertebrates and marine species which often display rapid adaptation to novel environments and develop resistance to control measures (Allendorf & Lundquist 2003; Bax et al. 2003; Stockwell & Ashley 2004; Genovesi 2005; Regan et al. 2006). Interventions focused on reducing environmental contamination have traditionally focused on establishing legislative guidelines as to acceptable pollution loadings, usually based around defined ecotoxicological levels such as the concentration of a pollutant at which 50% mortality occurs (LC50) and below which no ecological effects are observed (NOEC) in the target species, respectively (De Lange et al. 2010). However, this approach was not predictive of broader ecosystem structure and functioning.

In the 1990s, species sensitivity distribution models (SSDs) became widely used in risk assessment. These models extrapolated from single-species laboratory assays to predict thresholds for toxins that were considered protective of whole communities (Del Signore et al. 2016). A criticism of SSDs was that laboratory assays did not necessarily capture species' responses in the natural environment or the interactions of multiple stressors. This led to the development of field-based species sensitivity models (f-SSDs) which use multivariate data on species abundance and the concentration of chemicals present derived from field surveys to develop guidelines for pollution loadings in the environment (Leung et al. 2005; Hewitt et al. 2009).

The biological interactions between species (often dependent on population densities) that affect species richness, abundance and spatial distribution introduce an additional layer of complexity not considered in species-based approaches to conservation (Hanski 1999; Hubbell et al. 1990; Lebrija-Trejos et al. 2010). Over time, advances in ecological theory coupled with the shortcomings of species-based approaches and inability of species-scale risk assessment to capture important ecological processes and inter-species interactions underpinning many ecosystem functions and services, led researchers to suggest that ecosystems presented a more appropriate scale for conservation assessment and actions (Noss 1996; Link 2002; Nicholson et al. 2009; Keith et al. 2013). By incorporating multiple species and ecological processes, ecosystem-scale approaches to conservation offer more efficient use of limited resources and funding, often a key factor in the low rate of implementation of conservation assessments published in the scientific literature (Balmford 2003; Brooks et al. 2006; Ferraro & Pattanayak 2006; McCarthy et al. 2012; Keith et al. 2013). Furthermore, it has been argued that incorporating ecosystem services into conservation planning may highlight the direct benefits of conservation interventions to humans and result in higher rates of project implementation (Knight et al. 2006).

At this broader scale, risk assessment focuses on the collapse of key ecosystem functions rather than species extinctions to facilitate the prioritisation of intervention targets (Margules & Pressey 2000; Miller et al. 2006; Keith et al. 2013). Key assessment criteria in assessing risk of ecosystem collapse include declining or restricted distribution, degradation of the abiotic environment and the disruption of key biotic processes and interactions (Nicholson et al. 2009). At the level of communities or ecosystems, a key tactic in ameliorating the stress of habitat loss and/or overexploitation has been the creation of networks of reserves that are connected through the dispersal of propagules, larvae or mature organisms and that contain all major habitat types utilised by resident species, replicated across multiple sites to provide redundancy against environmental disturbances (Green et al. 2014). Habitat rehabilitation programs have become popular recent decades (see review by Benayas et al. 2009). Unlike habitat restoration, rehabilitation focuses on repairing or reintroducing degraded or lost ecosystem functions, without reference to an idealised state or endpoint (Aronson et al. 1993), assuming that an increase in biodiversity and ecosystem functioning will follow (the *field of dreams hypothesis*; see Palmer et al. 1997). While this approach has not always been successful a review of 89 rehabilitation projects found an average increase of 44% in local biodiversity present and 25% in ecosystem functioning (Larson et al. 2001; Dodds et al. 2008; Benayas et al. 2009).

In the prevention of overexploitation, there has been a general move towards ecosystem-based management. This has been particularly noticeable in the administration of fisheries and forests (Pikitch et al. 2004; Kuuluvainen 2009). Ecosystem-based management approaches attempt to increase understanding of ecosystem functioning in order to maintain the utility of ecosystems to humans while minimising the risk of ecosystem collapse avoid degradation of ecosystems and, where knowledge is insufficient, to implement precautionary management policies (Pikitch et al. 2004). In many countries, there have been moves to to limit the extraction of biomass from ecosystems to replaceable levels that do not impact on non-harvested species or disrupt trophic interactions, the disruption of which may cascade through entire ecosystems (Pace et al. 1999; Pikitch et al. 2004).

The eradication of invasive species may actually increase the invasibility of ecosystems through leaving ecological niches untenanted (González et al. 2017). Consequently, management strategies for the control of many invasive taxa are now focused on keeping population densities below the thresholds at which major ecological or economic damage occurs and management of key invasion vectors (Regan et al. 2006; Yokomizo et al. 2009; Britton et al. 2011). Ships are commonly treated with biocidal anti-fouling paints to prevent the spread of species attached to the hulls of vessels and the discharge of ballast water is subject to increasing legislation in many countries mandating treatment by filtration, oxidisation of water by the introduction of ozone, exposure to ultraviolet light or the addition of chemical biocides to prevent the introduction of non-indigenous species (Hulme 2009; Tsolaki & Diamadopoulos 2009).

Estuaries and their ecosystems

Estuaries are broadly defined as semi-enclosed coastal water bodies with a free connection to the open sea, within which water is measurably diluted with fresh water derived from land drainage (Pritchard 1967). In much of the literature, coastal lagoons are considered a type of estuary (e.g. Whitfield 1992; Roy et al. 2001; Razinkovas et al. 2008; Mikhailov & Goran 2012) as they are semi-enclosed areas of coastal marine water separated from the ocean either partially or fully by the formation of a barrier but still experiencing connection to the ocean either permanently or intermittently (Kjerfve 1994). However, lagoons lack a significant freshwater input, except in areas of high rainfall, and may become hypersaline rather than experiencing dilution with freshwater (Roy et al. 2001; Pérez-Ruzafa et al. 2011). For the purpose of this thesis, use of the term 'estuaries' is inclusive of coastal lagoons.

The unique environmental characteristics of estuaries, as ecotones where terrestrial, freshwater and marine environments merge, give rise to distinctive ecosystems that provide a wide range of vital ecosystem functions (Gray 1997; Elliott et al. 2007a; Barbier et al. 2011). Estuaries are formed from mosaics of differing habitat types, such as mangrove forests, shellfish reefs, saltmarsh, seagrass meadows, macroalgal beds and rocky reef, as well as unvegetated sand and mud flats (Gain et al. 2017). Estuarine ecosystems supply a range of important goods (e.g. fish and shellfish, timber from mangroves) and services (e.g. safe harbour for ships, coastal erosion buffering, recreational opportunities). Biogenic habitats, such as saltmarsh, mangroves, seagrass and reef-forming bivalves, provide habitat for numerous associated species by providing food, shelter, and substrate for attachment (Jones et al. 1997; Worm et al. 2006; Hewitt et al. 2008). Such habitats promote biodiversity by increasing local beta diversity and enhancing environmental stability (Hastings et al. 2007).

Most definitions of the term 'estuary' do not consider the habitats or ecosystems present. Recently, a few researchers have sought to incorporate the presence of ecosystems into the definition of an estuary. While retaining the requirement for some degree of enclosure as well as, at least intermittent, marine and freshwater inputs, Whitfield and Elliott (2011) expand on previous scientific definitions by including the presence of 'a characteristic biota'. Basset et al. (2013) argue that Transitional Waters, defined by the European Union Water Framework Directive as partly saline in character as a result of proximity to coastal water but which is substantially influenced by freshwater flows, are synonymous with ecosystems, implying that the resident biotic communities are integral to the categorisation. Such modified definitions may be of greater use to estuarine managers focused on conservation than previous definitions.

Estuaries have historically been centres of human settlement due to the access to freshwater and sheltered ports that they provide. The number of humans living on coastlines is expected to pass six billion by the year 2025 (Kennish 2002). As a result, environmental modification and degradation from anthropogenic activity has driven a global decline in estuarine and coastal marine environmental conditions and ecosystem function (Hughes et al. 2005; Lotze et al. 2006; Worm et al. 2006; Halpern et al. 2008). Many estuaries have undergone habitat homogenisation due to trawling, dredging and shoreline development, with key biogenic habitats being degraded or lost and replaced by macroalgal turf or bare substrates (Hauxwell et al. 2001; Thrush et al. 2006, 2008; Barbier et al. 2011). Globally, more than 65% of all estuarine wetlands and seagrasses and 35% of mangroves are severely degraded or lost, with the loss of essential nursery habitats and refuge from predation for numerous associated species (Jackson 2008; Barbier et al. 2011). Overharvesting of finfish and shellfish has resulted in the severe depletion of stocks worldwide, with 74% of large pelagic finfish and 91% of oysters being lost, exposing estuarine ecosystems to trophic cascades and loss of ecological functioning (Jackson 2008). Invasive species, introduced accidentally via ballast water from shipping and deliberately for mariculture, have become a global problem, damaging local ecosystems by altering habitats and trophic webs as well as spreading exotic pathogens (Kennish 2002). Point and non-point source pollution has exposed many estuaries to nutrient enrichment, resulting in eutrophication and periods of anoxic water, as well as discharges of oil-based contaminants that have degraded estuarine habitats and chemical toxins that produce lethal or sub-lethal effects in estuarine organisms (Kennish 2002; Jackson 2008; Barbier et al. 2011). Furthermore, the effects of these stressors in estuarine ecosystems are often synergistic, with their combined effects being greater than their additive properties (Jackson et al. 2001). For example, the effects of eutrophication in Chesapeake were greatly exacerbated by overharvesting of the filter feeding eastern oyster (*Crassostrea virginica*), resulting in algal blooms that drove seasonal hypoxia and the loss of local seagrass meadows (Orth & Moore 1984; zu Ermgassen et al. 2013). The high value of estuarine ecosystems and the wide range of stressors with which they are faced present unique conservation challenges.

Challenges in the management of estuarine ecosystems

Estuaries are extremely numerous worldwide, with more than 900 in Australia alone and almost as many in the USA (Kennish 2002; Chapter 5). This level of abundance at global, and even regional, scales necessitates a method for effectively assessing risk of ecosystem collapse to allow decision makers to prioritise management interventions. The IUCN Red List of Ecosystems assessment criteria, at first glance, provide an ideal tool for informing estuarine conservation decisions. However, several knowledge gaps currently exist that may impede the Red List of Ecosystems assessment criteria from functioning effectively in estuarine environs. The IUCN assessment criteria, that were initially developed for terrestrial vegetation ecosystems, are largely untested in aquatic ecosystems or in ecosystems formed from a mosaic of differing habitat types (Chapter 4). At regional scales, decisions about how to apply and prioritise management interventions across different estuaries would be assisted by a typology for estuarine ecosystems. Estuaries vary considerably in geomorphic, hydrological and physiochemical factors as well as in the biotic communities that they support (Kennish 2002). Existing typological schemes for estuaries (e.g. the Australian Ternary Classification of Coastal Systems, the New Zealand Estuary Environment Classification, the South African Conceptual Estuary Classification) are based on hydrological or geomorphological features rather than local ecology. The applicability of such typologies to estuarine ecosystems has not been tested (Chapter 5). At local scales, the carrying capacity of estuaries as well as the resilience of estuarine ecosystem function to environmental change and the subsequent impacts on ecosystem services is inadequately quantified (Elliott et al. 2007b). How the spatial configuration of habitat mosaics influences estuarine ecology is, at present, poorly understood. Variable spatial structure may be a response to environmental change and, therefore, an essential component of population and community persistence (Kerr et al. 2010). Ecological theories of population and community functioning, such as *island biogeography theory* (MacArthur & Wilson 1967), have obvious applications in understanding patterns of spatial variability. However, little research to date has tested these theories in habitat-mosaic aquatic landscapes (O’Neill 2005).

This thesis

This thesis investigates the value of current ecological theories and management practices in the conservation of estuarine ecosystems. I test the utility of ecological theories underpinning many current conservation practices at the level of habitat patches within estuaries and at the broader scale of estuarine seascapes. I subsequently examine whether existing ecosystem risk assessment criteria, often based on such ecological theories, are effective when applied to whole estuarine ecosystems and whether currently used typological classification systems for estuaries accurately reflect their resident ecosystems. Finally, I test a potential tool for the ongoing, cost-effective monitoring of habitat heterogeneity in estuarine ecosystems. Subsequent to this Introduction, my thesis is presented in five data chapters plus a Discussion. A summary of the key questions investigated in each of those chapters is presented below.

Chapter two

Island biogeography theory (MacArthur & Wilson 1967) is applied to patchy landscapes, with patches of physically complex habitat being used as metaphors for oceanic islands (Diamond et al. 1976; Haila 2002). However, empirical proof of the applicability of this theoretical model to such situations is equivocal (Resasco et al. 2017). Nevertheless, predictions of community structure based in such usage have informed a range of conservation decisions in the terrestrial and marine environments (Simberloff & Abele 1982; Margules et al. 1982; Nicholson et al. 2009). Here I use a meta-analytical approach to assess the applicability of MacArthur and Wilson's (1967) theory to patches of physically complex habitat within estuarine seascapes. Specifically, I test the predictions that species richness in habitat patches is positively correlated with patch size but negatively correlated with patch isolation.

Chapter three

Estuaries comprise a mosaic of physically complex habitats set in a sedimentary landscape matrix (Gain et al. 2017). Patches of these complex habitats are frequently interspersed, and their spatial arrangement may act as a control on the structure of resident communities (Arroyo-Rodríguez et al. 2013). I assess the differences in invertebrate communities between subtidal *Zostera capricorni* seagrass beds with and without adjacent intertidal *Avicennia* *marina* mangrove forests and between *A. marina* forests with and without adjacent subtidal *Z. capricorni* beds. Additionally, I compare colonisation by invertebrates of artificial seagrass units, of standardised morphology, adjacent to intertidal mangrove forests or unvegetated shorelines.

Chapter four

The large number of estuaries globally necessitates risk assessment to prioritise conservation efforts (Brooks et al. 2006). However, schemes for assessing the risk of collapse are largely conceived for use in terrestrial ecosystems, often defined by a characteristic vegetation type (Nicholson et al. 2009; Keith et al. 2013), and their application to estuarine environments, characterised by mosaics of habitat types, is largely untested. Here I examine the causes and symptoms of estuarine ecosystem collapse in relation to assessment criteria common across risk assessment schemes, with a particular focus on the International Union for the Conservation of Nature Red List of Ecosystems criteria, to assess the efficacy of ecosystem risk assessment schemes in estuaries. A risk assessment of Chesapeake Bay in the United States, *circa* 1980, is presented as a case study.

Chapter five

Classification schemes for estuaries have been instituted in many countries for a range of purposes. However, these are primarily based on hydrologic and/or geomorphic conditions rather than ecology. Typologies capable of identifying ecologically comparable estuaries, susceptible to similar threatening processes, may assist in identifying groups of estuaries across which common conservation strategies, once developed, may be implemented. This chapter assesses the extent to which a national Australian typology (Dalrymple et al. 1992), classifying estuaries and coastal waterways into geomorphic classes according to wave, tidal and fluvial forcings, also captures differences in the mosaic of habitat types present.

Chapter Six

Structurally complex habitat in estuaries is predominantly biogenic in nature and varies spatially and/or temporally (Gain et al. 2017). Worldwide, estuarine ecosystems are threatened by habitat loss, with individual habitats expanding or contracting in a zero-sum manner, often resulting in complex habitats being replaced by sedimentary matrix (Airoldi et al. 2008; Waycott et al. 2009; Chapter 4). Here I assess the utility of zeta-diversity (Hui & McGeoch 2014), a recently developed metric that robustly describes biodiversity patterns based on overlapping species in incidence records, to monitor changes in the composition of estuarine habitat mosaics accurately.

Chapter seven

This chapter presents a synthesis of the findings in this thesis and a summary of their implications for estuarine conservation. I make specific recommendations for conservation management practices and suggest new lines of investigation arising from my research.

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Chapter 2: Application of island biogeography theory varies with inhabitant group and environmental setting in estuarine and coastal seascapes

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Abstract

The theory of island biogeography explains the structure of communities on oceanic islands as a function of the independent factors of size and isolation. These factors control rates of extinction and immigration, with community equilibrium being achieved at the point where the two processes are in balance. The principles of island biogeography have subsequently been applied to isolated patches of habitat set within a surrounding hostile matrix. Estuaries and inshore marine environments consist of mosaics of complex, generally biogenic, habitats set within a sedimentary matrix. These habitat patches have been considered as metaphors for oceanic islands in the planning of conservation interventions. However, this application of island biogeography theory is controversial. In a meta-analysis of existing literature, we assessed whether the taxonomic richness of communities associated with complex estuarine and marine habitats increased with patch size and decreased with patch isolation. Community richness showed a positive association with patch size. However, the magnitude of this effect varied between benthic and nektonic taxa and among differing habitat types. Patch isolation did not significantly affect community richness. While we show qualified support for the application of island biogeography theory in estuarine and inshore marine settings, other aspects of patch quality, often conflated with patch size, may offer a stronger theoretical basis for conservation planning. This study highlights a lack of empirical evidence as to the effects of patch isolation in estuarine environments.

Key words: estuarine habitat, island biogeography, landscape ecology, patch size, connectivity, meta-analysis

1. Introduction

The theory of island biogeography posits that the species richness of islands can be predicted based on their area and isolation from a source of colonisation (MacArthur and Wilson 1963, 1967). According to the theory, extinction rates decrease with island area, and colonisation rates increase with proximity to the mainland, with the intersection point between the two curves predicting the equilibrium species richness (MacArthur and Wilson 1963, 1967). MacArthur and Wilson predicted that this point of equilibrium would vary with geographic setting and with the taxonomic group being considered, in accordance with the species-area and species-isolation equations for specific taxa developed by Preston (1962a, b). Early mensurative studies of avian species on Pacific Ocean islands supported this theory (Diamond 1969, 1972; Hunt and Hunt 1974). However, the earliest manipulated experimental test of island biogeographic theory, using the species richness of arboreal arthropods, showed a positive correlation between island size and species richness, but found no correlation, either negative or positive between island isolation and the richness of associated arthropod communities (Simberloff and Wilson 1969, 1970; Wilson and Simberloff 1969).

Although initially developed with oceanic islands in mind, the theory was soon applied to a variety of other isolated environments at regional scales. Alpine areas isolated by surrounding lowlands, patches of alpine vegetation surrounded by bare rock, closed lakes and pockets of savannah set within dense rainforest were all treated as analogues to oceanic islands (Diamond et al. 1976; Weins 1995; Haila 2002). At a smaller grain, conservation biologists began to view fragmented patches of habitat set within a matrix inhibitory of dispersal as analogous to oceanic islands (Diamond et al. 1976). Predictions from island biogeography theory have been used to design reserve networks (May 1975; Simberloff and Abele 1982; Margules et al. 1982) and ecological restoration projects (Huxel and Hastings 1999; Grimbacher and Catterall 2007). For example, based on the predictions of the theory, Diamond (1975) suggested that a single large reserve would be preferable in terms of biodiversity conservation to several smaller reserves whose total area was equal to the larger area.

However, the application of island biographic theory to conservation is controversial as it fails to incorporate several key drivers of community structure (Sauer 1969). Empirical studies have demonstrated that the establishment and persistence of species is often dependent on their unique physiological traits and their interactions with other species and with the abiotic environment (Cardillo et al. 2005; Pearson et al. 2014). Intra-generational migration has been shown to provide a ‘rescue effect’ to threatened populations (Frankham 2015), meaning that colonisation and extinctions rates are not independent of each other as envisaged in island biogeography theory. In many situations, the matrix surrounding habitat patches is not totally inhospitable as per MacArthur and Wilson’s original model and environmental gradients at these boundaries create ‘edge effects’ that alter community structure at the periphery of habitat patches (Cook et al. 2002). These issues raise doubts about the utility of island biogeography theory for conservation planning.

Globally, estuarine and coastal ecosystems are among the most threatened ecosystems from the combined effects of coastal development and climate change (Lotze et al. 2006), but also among the most important in terms of fisheries productivity and carbon sequestration

(Costanza et al. 1997; Choi and Wang 2004). Consequently, their constituent habitats are increasingly the targets of conservation and rehabilitation measures (e.g. Paling et al. 2009; Schulte et al. 2009). Estuarine and coastal biogenic habitats, including seagrass meadows, salt marshes, macroalgal beds, shellfish reefs and mangrove forests (Hewitt et al. 2008), typically exist as a mosaic of high-biodiversity patches set within a lower biodiversity sedimentary matrix of mud or sand (Boström and Bonsdorff 1997). Consequently, these biogenic habitats may be viewed as ‘islands’. Indeed, the first experimental tests of island biogeography theory came from the manipulation of mangrove islands on the Florida coast (Simberloff and Wilson 1969, 1970).

Here we conduct a synthesis of published research to assess the applicability of island biogeography theory to estuarine and coastal habitats. Specifically, we test the predictions that: the taxonomic richness of fauna within these biogenic habitat patches will 1) increase with patch area; 2) decrease with distance from the nearest neighbouring patch that may serve as a source of colonisation; and 3) that the strength of these effects will vary between taxonomic groups and environments.

2. Methods

2.1. Data collection

We used the online databases *Web of Science, Scopus,* and *Google Scholar* to search the literature for studies published prior to 2018 that examined the effect of estuarine and coastal biogenic habitat area and/or isolation on the taxonomic richness of inhabitant fauna. To identify papers investigating how the species richness of seagrass patches varies with area, we used the search terms "seagrass" AND "patch size" OR "area" AND "species richness". To identify papers investigating how the species richness of seagrass patches varies with isolation, we used the search terms "seagrass" AND "isolation" OR "distance" AND "species richness". We subsequently reran our search for the habitat types: "mangrove", "algae", "coral", "seaweed", "kelp", "saltmarsh", "oyster", "mussel", "shellfish"; and "reef". We included results from mensurative studies and manipulative experiments that compared taxonomic richness of any aquatic marine faunal group or groups from at least two different patch areas or inter-patch distances in like forms of physically complex habitat. To be included, papers needed to provide: 1) *p*-values from univariate analyses; 2) sample sizes and an appropriate measure of effect size; or 3) sufficient details to allow those details to be calculated. To avoid the complicating factor of edge effects, studies where taxonomic richness was measured only at the edges of habitat patches were excluded from our results and, where richness was recorded from both patch edges and interiors, only results from interior measurements were used.

Collected data were coded by: 1) the broad taxonomic category amongst which taxonomic richness was measured (benthos or nekton); 2) the tidal zone in which the habitat occurred (inter- or subtidal); and 3) whether that study was observational, describing naturally occurring variation in communities, or was experimentally controlled using either or artificial modified natural habitats.

2.2. Statistical analyses

We used two methods to test our predictions. First, Fisher’s (1932) method of combining probabilities (as described by Sokal and Rohlf 1981) tested for a significant effect (at $\alpha = 0.05$) on richness, across all studies, of each of patch area and isolation. Second, where effect sizes were provided by studies, or could be calculated from data supplied by the authors, we used meta-analysis to determine the magnitude of the effect of patch area and isolation on taxonomic richness across all studies combined. Additionally, for the *p*-values and effect sizes of studies examining patch area, we conducted separate sub-analyses of studies featuring benthic versus nektonic taxa, intertidal versus subtidal zones, observational versus experimental studies, and natural versus artificial habitat patches. It was not feasible to conduct these sub-analyses for patch isolation due to the low number of studies available.

In several cases, multiple *p*-values or effect sizes were obtained from a single geographic location. This occurred where papers provided separate analyses of richness in benthos and nekton, separate simultaneous experiments using natural and artificial habitats or, in one case, where authors repeated the same experiment in the same location with a five-year separation. To prevent individual locations from being over-represented in our data we combined the *p*-values from such analyses using Fisher's combined probability method (Fisher 1932) or calculated weighted means for effect sizes for analyses of the overall effect of patch area and isolation.

Prior to using Fisher's combined probability method, all reported *p*-values were converted to one-tailed values. Where studies included only the threshold level of significance (e.g. $p < 0.05$), that value (i.e. 0.05) was included in our dataset as such values are highly conservative and unlikely to increase the rate of Type 1 error. However, one study reported that $p > 0.05$ and this was excluded from our dataset as it would have greatly increased the potential for Type 1 error. Analyses combining *p*-values used only one-tailed *p*-values.

As the majority of the effect sizes reported by studies were measures of association (i.e. relationships between patch size and richness) we adopted Pearson's correlation coefficient (r) as a measure of effect size in our meta-analyses. Where r was not reported, but test statistics, such as t, F or R^2, for other tests of relationship were provided, Pearson's r was calculated following methods described by Rosenthal (1991). Where Spearman's rank-order correlation coefficient (ρ) was reported, this was converted to Pearson's r using the table from

Gilpin (1993). In the case of multi-factor ANOVAs or multiple regression analyses, we calculated the proportion of the total variance (R^2) attributable to patch area or isolation before converting to *r*.

Prior to meta-analysis, raw Pearson's *r* values were transformed into standard scores using Fisher's *Z* transformation (Rosenthal 1991). We then utilised the random effects model of Hedges and Vevea (1998) to calculate mean effect sizes ($\bar{r}$) for the influence of patch area and isolation on species richness as well as 95% confidence intervals for the population mean. Unlike traditional fixed-effects models, random effects models account for between-studies variance (heterogeneity) resulting from differing statistical populations as well as sampling variance within studies and are highly conservative in their calculation of both mean effect sizes and confidence intervals (Gurevitch et al. 2018). Finally, calculated means and confidence intervals were back-transformed to Pearson’s *r*. Mean effect sizes were considered to be significant if the 95% confidence intervals did not include zero. Mean effect sizes between sub-analyses were considered to be significantly different where 95% confidence intervals did not overlap.

We assessed potential publication bias in our analyses using Spearman's rank-order correlation to test for an association between standardised effect sizes and the variance of each study (Begg and Mazumdar 1994). Significant deviations of ρ from zero suggest that the true mean effect size may be lower or higher (depending on the sign of the correlation coefficient) than the calculated mean effect size and indicate the possibility of publication bias (Koricheva et al. 2013). Spearman's correlation tests were carried out using IBM SPSS Statistics Version 24.0.0.2 software.

3. Results

Our literature search yielded 24 published studies containing 32 statistical analyses of variation in taxonomic richness across at least two differing patch areas and three studies containing four analyses of variation in taxonomic richness across multiple levels of patch isolation (Table 1). Among the analyses of patch area, 21 of the 32 reported two-tailed *p*-values were significant (at $\alpha = 0.05$), 18 reported positive Pearson's *r* values and eight reported negative effect sizes. Two effect sizes (one positive and one negative) could not be used for meta-analysis as corresponding sample sizes were not reported. Observational studies (18) were more than twice as common as experiments using artificial habitat mimics or manipulated natural habitats (7). Within analyses of the influence of patch isolation on faunal richness, three analyses focused on subtidal seagrass and one examined intertidal rocky headlands. Only one reported two-tailed *p*-value, from a seagrass study, was significant at $\alpha = 0.05$. Three effect sizes from seagrass habitats were all negative while one from the rocky intertidal was positive (Table 2).

Across all habitat types, environments and faunal groups, combined one-tailed probability values showed significant effects in the predicted directions of both patch area and patch isolation on the taxonomic richness of associated fauna. Sub-analyses utilising Fisher's method of combining probabilities similarly showed that, for each category, relationships between patch size and inhabitant richness were significant (Table 3).

Meta-analyses of effect sizes found that relationships were more variable. The mean effect of patch area on inhabitant species richness was consistently positive but varied in magnitude across sub-analyses. Between faunal groups, community richness varied significantly with patch area in benthic taxa but not in nekton. Observational studies also showed a significant effect of patch area where experimental studies did not. Studies using coral habitats showed a significant effect of patch area, but this effect was not significantly different to zero in seagrass, bivalve or algal habitats (Fig.1; Table 4). The effect of patch isolation on inhabitant richness was in the predicted direction but was not significantly different from zero in our meta-analysis ($\bar{r}$ = -0.387; 95% CI: -0.810 to 0.036). Tests for potential publication bias were all non-significant except for analyses of the effect of patch area in algal habitats and of patch isolation (Table 5).

Table 1. A summary of studies synthesised to test the effect of patch area on the richness of associated faunal communities. Columns show: the habitat type in which patch area was measured; the broad taxonomic group (Benthos or Nekton) amongst which richness was measured; the highest taxonomic level at which richness was measured; the tidal zone (Intertidal or Subtidal) in which the habitat was located; the type of study (Observational or Experimental using natural, artificial or modified natural habitats); minimum and maximum patch areas included in the study; sample size, *p*-value and effect size (Pearson's *r*) from the study. Matching superscript numbers indicate pairs of *p*-values or effect sizes combined into a single number when both appear in the same analysis. Values missing from the table indicate that the information was not reported in the published study.

Author(s) & date	**Habitat type**	**Taxon group**	**Max. ID level**	**Tidal zone**	**Study type**	**Min. (m^2)**	**Max. (m^2)**	***n***	***p* (2-tail)**	***Effect (r)***
Ault and Johnson 1998	Coral	N	Species	S	On			39	< 0.050	
Borthagaray et al. 2009	Rock	B	Species	I	On			19	0.088	0.949
Bowden et al. 2001	Seagrass	B	Species	S	On			48	0.005	0.902
Galst and Anderson 2008	Seagrass	N	Species	S	On	2	382	19	0.020	0.600
Gladfelter et al. 1980	Coral	N	Species	S	On			25	< 0.001	0.776
	Coral	N	Species	S	On			15	< 0.010	0.737
Grober-Dunsmore et al. 2007	Coral	N	Species	S	On			22	< 0.001	0.656
Hanke et al. 2017	Bivalve	B	Family	I	On			22	0.004 [1]	-0.357 [1]

Author(s) & date	Habitat type	Taxon group	Max. ID level	Tidal zone	Study type	Min. (m^2)	Max. (m^2)	*n*	*p* (2-tail)	*Effect (r)*
	Bivalve	N	Species	I	On			22	0.730 [1]	-0.071 [1]
	Bivalve	B	Family	I	Ea	10	100	27	0.010 [2]	0.725 [2]
	Bivalve	N	Species	I	Ea	10	100	27	0.430 [2]	-0.180 [2]
	Bivalve	B	Family	I	Ea	10	100	27	0.050 [3]	0.593 [3]
	Bivalve	N	Species	I	Ea	10	100	27	0.680 [3]	-0.231 [3]
Hattori and Shibuno 2010	Coral	N	Species	S	On	0.5	45.4	84	< .0001 [4]	0.825 [4]
Hattori and Shibuno 2015	Coral	N	Species	S	On	0.07	45.4	81	< 0.001 [4]	0.775 [4]
Jelbart et al. 2006	Seagrass	N	Species	S	On	2,290	211,200	27	0.804 [5]	-0.100 [5]
Jelbart et al. 2007	Seagrass	N	Species	S	On	2,300	6,630	96	< 0.050 [5]	-0.872 [5]
Johnson et al.2011	Coral	N	Species	S	On	0.01	170	185	< 0.0001	0.849
Källén et al. 2012	Seagrass	B	Species	I	On	520	5176		< 0.0005	
Mateo Ramırez and García Raso 2012	Seagrass	N	Species	S	On	0.62	10.34		0.370	-0.022
Matias et al. 2010	Algae	B	Species	I	Ea	0.01	0.03	54	0.074	0.419
Matias et al. 2015	Algae	B	Species	I	Em	0.09	0.72	36	< 0.001	0.964
Mills and Berkenbusch 2009	Seagrass	B	Species	I	On	< 200	> 1000	19	0.00001	0.933
	Seagrass	B	Species	I	On	< 200	> 1000	19	0.091	0.389
Nohrén and Odelgård 2010	Algae	B	Family	S	Em	0.25	2	80	0.732	0.128
Norling and Kautsky 2007	Bivalve	B	Species	I	Em			10	< 0.001	

Author(s) & date	**Habitat type**	**Taxon group**	**Max. ID level**	**Tidal zone**	**Study type**	**Min. (m^2)**	**Max. (m^2)**	***n***	***p* (2-tail)**	***Effect (r)***
Norling and Kautsky 2008	Bivalve	B	Species	S	On	0.0025	> 1	12	0.028 [6]	
	Bivalve	B	Family	S	On	0.0025	> 1	12	0.020 [6]	
Pierri-Daunt and Tanaka 2014	Seagrass	B	Family	S	Ea	0.1	2.25		0.555	0.422
Schroeder and Parrish 2006	Coral	N	Species	S	On	12	186	32	< 0.0001	0.595
Stier et al. 2014	Coral	N	Species	S	Em			18	0.950	-0.027
Tsuchiya and Nishihira 1985	Bivalve	B	Species	I	On	0.0004	0.05	24	< 0.001	

Table 2. A summary of studies synthesised to test the effect of patch isolation on the richness of associated faunal communities. Matching superscript numbers indicate pairs of *p*-values or effect sizes combined into a single number when both appear in the same analysis. Columns show: the habitat type in which patch area was measured; the broad taxonomic group (Benthos or Nekton) amongst which richness was measured; the highest taxonomic level at which richness was measured; the tidal zone (Intertidal or Subtidal) in which the habitat was located; the type of study (Observational or Experimental using natural or artificial habitats); minimum and maximum inter-patch distances included in the study; sample size, *p*-value and effect size (Pearson's *r*) from the study. Matching superscript numbers indicate pairs of *p*-values or effect sizes combined into a single number when both appear in the same analysis. Values missing from the table indicate that the information was not reported in the published study.

Author(s) & date	**Habitat type**	**Taxon group**	**Max. ID level**	**Tidal zone**	**Study type**	**Min. dist (m)**	**Max. dist (m)**	***n***	***p* (2-tail)**	***Effect (r)***
Arponen and Boström 2012	Seagrass	B	Genus	S	Ea	0	3	17	0.982 ^{1}	-0.053 ^{1}
	Seagrass	B	Genus	S	Ea	0	3	16	0.666 ^{1}	0.246 ^{1}
Borthagaray et al. 2009	Rock	B	Species	I	On	0	240,000	19	0.005	-0.608
Gustafsson and Salo 2012	Seagrass	B	Species	S	Ea	0	20	24	0.83	-0.509

Table 3. Combined probabilities of tests for a positive relationship between patch area and taxonomic richness across all studies and sub-sets of studies, and for a negative relationship between patch isolation and richness. (*k* = the number of individual *p*-values combined.)

Analysis of	**Basis for grouping *p*-values**	χ^2	***k***	**Combined *p* (one-tail)**
Patch area	All reported *p*-values	277	26	< 0.001
	Benthic taxa	155	15	< 0.001
	Nektonic taxa	131	14	< 0.001
	Intertidal zone	118	11	< 0.001
	Subtidal zone	159	15	< 0.001
	Observational study	221	18	< 0.001
	Experimental study	57	8	< 0.001
	Natural habitat	256	22	< 0.001
	Artificial habitat	21	4	0.006
	Coral habitat	119	8	< 0.001
	Seagrass habitat	72	8	< 0.001
	Bivalve habitat	56	6	< 0.001
	Algal habitat	25	3	< 0.001
Patch isolation	All *p*-values	15	3	0.022

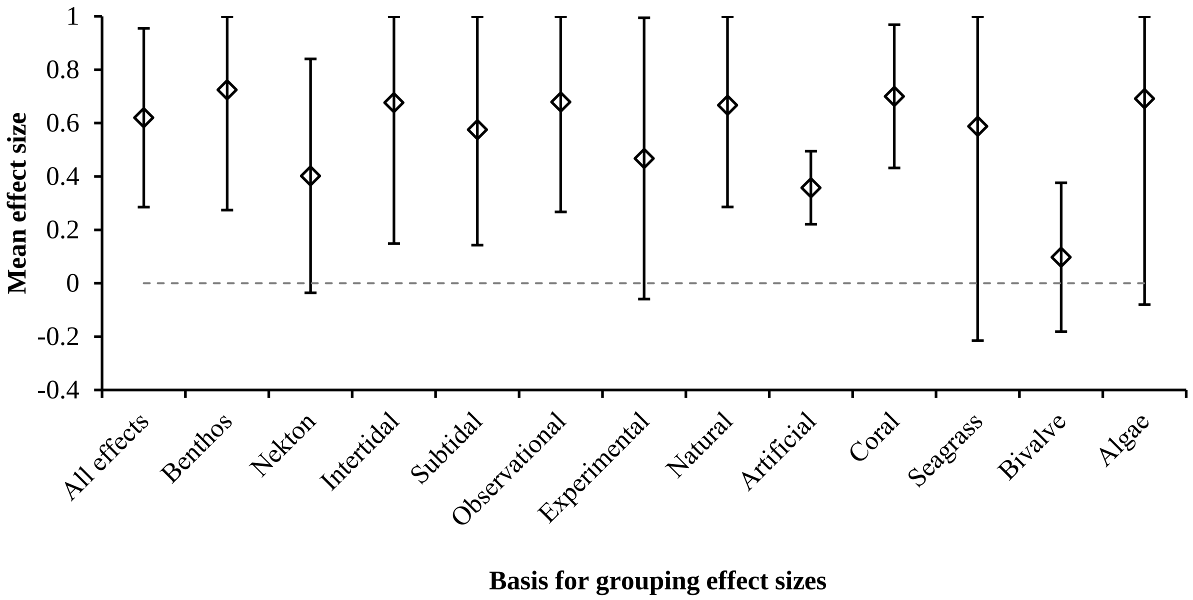

Figure 1: Mean effect size (± 95% confidence interval) of patch area on the taxonomic richness of physically complex estuarine and inshore marine habitats, across all studies and across subsets of these. Dashed line indicates effect size of zero. Errors bars that intersect with dashed zero line indicate no significant difference from zero in effect size for that grouping of studies.

Table 4. Results of random effects meta-analyses for the effect of patch area on taxonomic richness across all studies and sub-sets of studies, and for the effect of patch isolation on taxonomic richness across all studies. Shown are calculated mean effect sizes ($\bar{r}$), standard errors and 95% confidence intervals for the true effect size. (k = the number of analyses from published studies included in individual analyses.)

Analysis of	**Basis for grouping**	k	$\bar{r}$	**SE**	**95% CI**
Patch area	All reported effect sizes	19	0.620	0.171	0.285 to 0.955
	Benthic taxa	10	0.724	0.230	0.274 to 1.000
	Nektonic taxa	12	0.402	0.224	-0.036 to 0.840
	Intertidal zone	8	0.677	0.269	0.149 to 1.000
	Subtidal zone	11	0.575	0.221	0.143 to 1.000
	Observational study	13	0.679	0.210	0.267 to 1.000
	Experimental study	6	0.468	0.269	-0.059 to 0.995
	Natural habitat	16	0.667	0.194	0.286 to 1.000
	Artificial habitat	3	0.358	0.070	0.221 to 0.495
	Coral habitat	7	0.700	0.137	0.432 to 0.969
	Seagrass habitat	5	0.588	0.410	-0.215 to 1.000
	Bivalve habitat	3	0.010	0.142	-0.181 to 0.376
	Algal habitat	3	0.692	0.394	-0.080 to 1.000
Patch isolation	All reported effect sizes	3	-0.387	0.216	-0.810 to 0.036

Table 5. Results of tests for publication bias. Significant Spearman's ρ values indicate potential differences between the calculated mean effect size ($\bar{r}$) and the true effect size.

Analysis of	**Basis for grouping**	**df**	ρ	p
Patch area	All reported effect sizes	17	-0.004	0.989
	Benthic taxa	8	0.197	0.586
	Nektonic taxa	10	-0.095	0.770
	Intertidal zone	6	-0.012	0.977
	Subtidal zone	9	-0.273	0.417
	Observational study	11	0.020	0.950
	Experimental study	4	-0.348	0.499
	Natural habitat	14	-0.079	0.772
	Artificial habitat	1	-0.866	0.333
	Coral habitat	5	-0.643	0.119
	Seagrass habitat	3	0.224	0.718
	Bivalve habitat	1	-0.866	0.333
	Algal habitat	1	1.000	< 0.001
Patch isolation	All reported effect sizes	1	1.000	< 0.001

4. Discussion

Overall, we found that the inhabitant richness of communities in patches of physically complex estuarine and inshore marine habitats generally increased with patch area. Furthermore, sub-analyses revealed that the magnitude of the effect of patch area varied according to the identity of inhabitants (nekton vs. benthos), study type (observational vs. experimental), and among habitat types. However, while we show a significant *p*-value for our prediction that richness in such habitat patches decreases with patch isolation, we do not demonstrate a significant effect size of this factor. This finding is consistent with the early experimental investigation of island biogeography theory by Simberloff and Wilson (1969, 1970), although that study was focused on terrestrial fauna. Hence, we can offer only qualified evidence for the effectiveness of island biogeography theory in conservation planning for estuarine and coastal locations.

Our results show support for the well-established species-area relationship, in which island biogeography theory is rooted. Numerous mathematical equations have been proposed as predicting this relationship, with simpler explanations such as the power model generally offering the most predictive power (Triantis et al. 2011). These differing models generally describe the species-area relationship as a convex-upwards curve (Dengler 2009). However, researchers have suggested that this broad general relationship may be influenced by the grain-size, spatial extent and number of samples used in studies (Palmer and White 1994). Therefore, study methodology may strongly affect estimates of species richness (Dengler 2009).

The greater effect of patch area on benthic taxa than nektonic taxa may reflect differences in patch-fidelity between these two groups. Whereas the adult life-history stages of many benthic species display limited mobility or are even sedentary, nekton display greater mobility and may migrate between habitat patches across tidal cycles, seasons or stages in their ontogenetic development (Rabalais et al. 2001). Hence, of greater relevance to nekton may be total availability of habitat, over larger spatial scales, than the area of a patch, at local scale.

While the effect of patch area on taxonomic richness was positive in observational studies, in experimental investigations it did not differ significantly from zero. This finding is unexpected as observational studies often show lower mean effect sizes than controlled experiments in meta-analyses due to the great statistical noise in uncontrolled settings (Koricheva et al. 2013). The differing relationships shown here between these two types of study may reflect differences in the range of patch areas they consider. Whereas habitat patches sampled in observational studies ranged from $0.1m^2$ to $211,200m^2$, experimental studies utilised smaller patches (maximum $80m^2$ in manipulated natural settings and $100m^2$ in artificial habitat mimics), most likely due to the logistical difficulties inherent in creating and deploying large areas of artificial habitat units or experimentally manipulating the environment. Alternatively, the short time periods employed in experimental studies, generally only weeks to months, may not have allowed experimental studies to accurately replicate the local natural environment. This result may also reflect the greater number of observational studies (13) than experimental studies (6) that have been conducted. A fourth possibility is that the greater effect size in observational studies is an artefact of an unmeasured factor that directly influences both patch size and taxonomic richness. As most studies measured community richness at the species level, differences in the taxonomic levels considered are not likely to be a driver of this difference.

Coral was the only habitat type to show a significant mean effect size. This result is surprising as all studies in coral habitats focused entirely on nektonic taxa where studies in other habitat types were predominantly of benthos. However, all coral studies except one were observational while other habitats featured a mix of observational and experimental investigations. Hence, the effect of study type may be conflated here with habitat type. It is also notable that studies in coral are more numerous than those in other habitat types.

While our results show qualified support for the effect of patch area and, at least, no evidence against the effect of patch isolation as proposed in MacArthur and Wilsons' theory of island biogeography, more recent ecological theories offer alternative or expanded conceptual explanations for the structure of communities in patchy landscapes which may be more informative for conservation managers. Metapopulation theory (Levins 1969) acknowledges that habitat patches may vary in quality as well as area. Landscape ecology theory, arising in the 1980s, incorporated effects of spatial and temporal patterns in the wider landscape on the structure of communities (Risser et al. 1984). Conservation managers should, therefore, consider the qualities of habitat patches beyond overall size when planning reserve systems and incorporate connectivity to other habitat types within the seascape as well as connectivity to analogous habitat patches in planning decisions.

Evidence for the variable quality of habitat patches is borne out in the estuarine and inshore marine realms by numerous experiments investigating habitat attributes other than patch area. Studies of reef structures and canopy forming algal habitats have shown that patch volume has a greater effect on community structure than patch area (Wernberg and Goldberg 2008; Hattori and Shibuno 2015). Additionally, patch characteristics affecting the average size of interstitial spaces are important in structuring local communities (Gratwicke and Speight 2005) and modify local environmental characteristics such as current flow and wave force (Fonseca and Cahalan 1992). Macrofaunal abundance and richness vary with blade density in seagrass beds, regardless of predation level and community richness is positively correlated with surface rugosity in reefs-dwelling taxa (Luckhurst and Luckhurst 1978; Bell and Westoby 1986; Markert et al. 2010). Several studies have demonstrated an effect of patch shape on associated faunal assemblages (Bologna and Heck 2000; Jelbart et al. 2006). This is likely the result of shape-dependent changes in perimeter:area ratios which determine the relative influence of edge effects.

A strong point of meta-analyses is their ability to highlight gaps in the literature (Koricheva et al. 2013). We were surprised by the low number of studies examining the effects of patch area and isolation on the richness of communities in estuarine and inshore marine environments. In particular, studies looking at the area of seagrass, shellfish and algal habitats were few and none looked at mangroves, a key habitat type in many estuarine ecosystems. Among published studies examining effects of patch isolation on the richness of associated communities, none looked specifically at nektonic species. All focused, instead, on benthic taxa. However, even benthic studies were scarce, and the effects of inter-patch distance may be particularly relevant to benthic taxa given their wide range of dispersal and mobility capabilities (Vance 1973; Rabalais et al. 2001).

Island biogeographic theory continues to underpin much conservation management in the marine realm. Debate continues over the Single Large Or Several Small problem in the design of marine reserves (Moussaoui and Auger 2015). Patch area is still a key concern in restoration of saltmarsh and seagrass habitats (Chapman et al. 2017; Gittman et al. 2018) and in 2016 the International Union for the Conservation of Nature published draft guidelines for the protection of habitat connectivity as a key conservation strategy (Worboys et al. 2016). However, patch area and isolation may be less important considerations than other metrics of habitat quality, such as patch volume, density or rugosity, or the overall distribution of habitats within the local seascape and effective conservation management into the future will require the incorporation of these factors into planning and monitoring activities.

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Chapter 3: Epifaunal and infaunal invertebrate communities in estuarine vegetation patches vary according to the identity of adjacent habitat

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Abstract

Context

The spatial configuration of different types of habitat patch may affect the community structure present within a landscape by controlling beta diversity and colonisation rates. Estuaries comprise multiple habitat types that are frequently interspersed at the patch-scale.

Objectives

Using benthic invertebrate communities as a model, we assessed how the community composition of seagrass and mangrove habitat varies according to the proximity of these two habitat types to one another.

Methods

We examined differences in invertebrate communities between subtidal *Zostera mulleri* seagrass beds with and without adjacent intertidal *Avicennia marina* mangrove forests and between *A. marina* forests with and without adjacent subtidal *Z. mulleri* beds. Additionally, we compared colonisation by invertebrates of artificial seagrass units, of standardised morphology, adjacent to mangrove forests or unvegetated shorelines.

Results

Mangrove invertebrate communities were unaffected by the proximity of forests to seagrass beds. By contrast, invertebrate abundances were generally greater in natural seagrass beds adjacent to shorelines with than without mangroves. Specifically, the abundance of deposit feeding gastropods was greater in seagrass near to than distant from mangrove forests while a key filter- feeding bivalve species showed the opposite pattern.

Conclusions

These results suggest that the spatial configuration of habitat types in patchy landscapes does influence invertebrate communities but that the precise effects are taxon-specific and dependent on specific local factors. The influence of mangrove promixity on seagrass, but not *vice versa*, may reflect directional flows of resources for which mangrove is the donor and seagrass the recipient, for example organic matter.

Key words: Seascape • Seagrass • Mangrove • Connectivity • Benthic invertebrates • Landscape ecology • Habitat proximity • Biogenic habitat

Introduction

Understanding those factors that shape species distributions and abundances is a principal goal of ecology. Abiotic conditions are broadly acknowledged to be the primary control on species distributions across landscapes and seascapes (Sousa 1984), with metapopulation dynamics of individual species and biotic interactions within habitats important secondary controls (Noss 1995). Within landscapes and seascapes, low connectivity among habitat patches generally leads to a low diversity of patch inhabitants as only good dispersers are able to colonise (Hanski 1999) and successful colonists are able to establish dominance and exclude other species (Sale 1978). High connectivity results in the migration of individuals between habitat patches (Uezu et al. 2005), generally increasing local species richness and potentially providing a genetic rescue effect to small populations, allowing weaker competitors to persist where they would otherwise become locally extinct (Brown and Kodric-Brown 1977; Hanski and Ranta 1983).

Habitat types do not exist in isolation from their surroundings and ecological connectivity may operate both within and across habitat types (Turner 1989). Habitat patches may be connected through the dispersal of propagules, the migration of mature organisms, or the movement of resources such as organic matter (Sheaves 2009). The spatial arrangement of patches of different habitats in a landscape or seascape affects the availability of resources and the abundance, movement and colonisation rates of associated species (Pittman et al. 2007; Umetsu and Pardini 2007).

Estuaries contain mosaics of habitat patches of varying types, which may include seagrass, mangrove, saltmarsh, oyster reef, rocky reef and unvegetated sediments (Gain et al. 2017). Many species display tidal, diurnal, seasonal and/or ontogenetic migrations among habitats to access resources or to avoid predators and/or other stressors (Sheaves 2009). Hence, although these habitats support distinct biotic communities (e.g. Alfaro 2006), they often display considerable overlap in the identity of the species they support (Sheaves 2009). Studies investigating how the spatial arrangement of estuarine habitat patches influences assemblages of nekton have demonstrated that abundances of several species of fish and crustacean are greater in seagrass beds that are proximate as opposed to distant from saltmarsh (e.g. Irlandi and Crawford 1997; Saintilan et al. 2007) or mangrove (e.g. Skilleter et al. 2005; Jelbart et al. 2007; Saintilan et al. 2007), and that densities of fish and crustacean species in intertidal oyster reefs are greater when these are near seagrass beds (Gain et al. 2017). By contrast few studies have examined the effect of seascape pattern on epi- and in-faunal invertebrates, many of which have sessile and/or sedentary adults (but see Eggleston et al. 1999; Grabowski et al. 2005; Lefcheck et al. 2016 for studies including invertebrate fauna and Barros et al. 2001; González-Ortiz et al. 2016 for studies of infaunal communities).

In general, densities and diversities of epifauna and infauna are greater in biogenic than bare habitat (Heck et al. 1989; Boström and Bonsdorff 1997). The structural complexity of biogenic habitat provides refuge and substrate to many organisms and may enhance food resources (Airoldi et al. 2008). Whereas nekton may migrate across bare substrate, from one biogenic habitat patch to another, the low mobility of some epifaunal and infaunal invertebrates and/or the higher energetic costs and predation risks of small-bodied organisms migrating across bare substrate may result in fewer and/or shorter migrations (Kristensen et al. 2013). Instead, movement of epifauna and infauna between habitat patches may be passive, driven by waves and currents, and occur primarily at the larval stage (Levin 1984). Hence, the mechanisms structuring epi- and infaunal invertebrate assemblages may differ from those controlling the distribution of nekton.

Here we assess whether the structure of epifaunal and infaunal invertebrate communities varies spatially among established patches of the seagrass *Zostera mulleri* according to the proximity of *Avicennia marina* mangrove forest and among established mangrove forests according to seagrass proximity. If these invertebrate groups respond similarly to habitat configuration as nekton, we predict that the abundance and richness of invertebrates in each type of vegetation will be greater in habitat patches that are adjacent to the other type of vegetation than to unvegetated sediment. We also assess how, in standardised habitat units, habitat context influences colonisation processes. We test two *a priori* predictions: 1) that the addition of physically complex habitat to unvegtetated subtidal sediment will alter invertebrate community structure at that location; and 2) that colonisation of artificial seagrass units will vary spatially according to habitat context, reflecting the proximity of source populations from which species can colonise.

Methods

Study sites

The mensurative survey investigating how invertebrate communities of seagrass and of mangroves vary according to the identity of adjacent habitat was conducted in Brisbane Waters (33° 30’25.83” S, 151° 20’47.55” E), an estuary 42 km north of Sydney, New South Wales, Australia. The colonisation experiment, assessing how habitat context influences colonisation of artificial seagrass units (ASUs), was carried out at two sites: Towra Point (34° 1’25.33” S, 151° 10’57.52” E) and Kurnell (34° 0’31.30” S, 151° 11’21.02” E), in Botany Bay, Sydney, Australia. Both estuaries have a semi-diurnal tide of approximately 1.5 m range. All study sites were situated within 6.5 km of the estuarine mouth.

Mensurative survey

Invertebrates were sampled from shallow subtidal *Z. mulleri* seagrass beds (n = 4 sites per treatment) adjacent to intertidal shorelines with (hereafter ‘mangrove’) or without (hereafter ‘unvegetated’) intertidal *A. marina* mangrove forests and from intertidal *A. marina* mangrove forests (n= 3 sites per treatment) adjacent to shallow subtidal sediments with (hereafter ‘seagrass’) or without (hereafter ‘unvegetated’) shallow subtidal *Z. mulleri* beds. At sites with adjacent intertidal mangrove and shallow subtidal seagrass habitats, 15-25 m of unvegetated sediment separated the two. Sites were spatially interspersed with respect to treatment, and separated by at least 800 m. All mangrove forests and seagrass beds were ≥ 100 m long, measured parallel to the shoreline, and a minimum of 10m wide, measured perpendicular to the shoreline.

Invertebrates were sampled from each of the four habitat types in March 2014 with 100 mm deep benthic cores of 100 mm diameter. Seven cores were collected per replicate site. Sampling within *Z. mulleri* seagrass beds was at a tidal elevation just below the lowest astronomical tide (LAT). Sampling within *A. marina* mangroves was at ~ 0.6 m above LAT. Cores were collected from at least 1 m from the boundaries of habitats to avoid edge effects and were spaced 10 m apart along a transect aligned parallel to the shoreline. Each sample was separately sieved over a 500 µm mesh and the retained fraction was fixed in a 7 % formalin solution. Macroinvertebrates were identified under a dissecting microscope to morphospecies (*sensu* Oliver and Beattie 1996), enumerated and then preserved in a 70 % solution of ethanol.

Colonisation experiment

In early January 2016, ten ASUs were deployed on unvegetated subtidal sediment, just below LAT, at each of two sites that contained adjacent stretches of shoreline with and without *A. marina* mangroves. Within each site, five ASUs, each separated by ~ 20 m, were positioned along the stretch of shoreline with mangroves (hereafter 'mangrove') and five along the stretch of shoreline without mangroves (hereafter 'unvegetated'), with approximately 200 m between the two habitat treatments. The ASUs were each within 10-17 m of natural seagrass beds that may serve as sources of organisms and 12-15 m from intertidal mangroves or unvegetated sandflat of equivalent intertidal elevation.

The ASUs were 100 cm × 50 cm in area, aligned with their longer axis parallel to the shoreline. They included both an above ground component, mimicking seagrass shoots (Bell et al. 1985; Pête et al. 2015), and a below-ground component, mimicking seagrass roots (artificial rhizome; Nicastro and Bishop 2013). The shoot mat consisted of strips of 5 mm wide emerald green polypropylene curling ribbon (Koch and Co.) affixed to a 100 cm × 50 cm piece of 1.5 mm diameter plastic trellis (Whites Outdoor Supa-net) with a mesh size of 20 mm × 20 mm. The ribbon was cut to lengths of 510 mm which, when doubled over and affixed to the mesh, gave two leaves of 250 mm height. These were arranged in clusters of six leaves (ie. three doubled over ribbons) and affixed haphazardly at a density of 320 clusters per m^2 (Fig. 1). This closely approximated the natural shoot length and density of natural *Z. mulleri* beds in the area (Nicastro and Bishop 2013). The artificial rhizome consisted of a 6.16 m length of 3 mm polyethylene rope (Grunt Utility Cord) to which 100 mm lengths of polypropylene string (Grunt Baling Twine) were affixed at 40 mm intervals (as per Nicastro and Bishop 2013). The length and width of the rope and the distance between pieces of string were chosen to match the natural branching pattern of seagrass at nearby sites (Nicastro and Bishop 2013). Each end of the artificial rhizome rope was secured to the sediment surface using a 3 mm × 150 mm metal lawn-peg, inserted in diagonally opposite corners of the ASU plot and inserted in the sediment until fully covered to a depth of 50 mm. The rhizome mimic was evenly snaked across the plot and pushed into the sediment to a depth of 30-50 mm, the natural depth of *Z. mulleri* below-ground biomass (Hansen et al. 2000). The sediment was then smoothed over the top of the root system and the shoot mat anchored directly above using twelve additional metal lawn pegs.

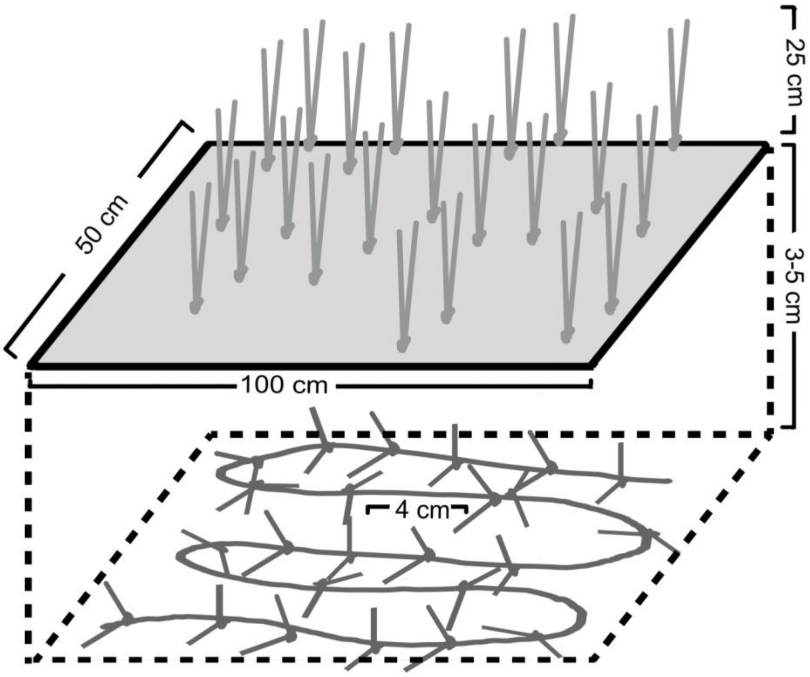

Figure 1. Design of Artificial Seagrass Units used in field experiment. Units consisted of a rhizome mimic that was buried 30-50 mm in the sediment and an above-ground shoot mimic anchored to the sediment directly above the rhizome mimic. Note that figure is not to scale.

Invertebrate communities associated with ASUs were sampled at low tide in late May 2016, four months after ASU deployment. Water depth at the time of sampling was approximately 40 cm. Mobile epifauna were sampled by quickly placing a 50 × 50 × 60 cm (length, width, height) impermeable plastic enclosure in the centre of each ASU to prevent species migration, and then dragging a 12 cm × 8 cm hand-held sweep net of 500 µm mesh size across the base of the ASU in five sweeps to cover the entire 50 cm × 50 cm sampling enclosure before repeating this process at successively greater height above the sediment until the entire water column was searched. Artificial seagrass shoots, ASU bases and the sediment surface were then searched by hand to locate any additional mobile epifauna within the sampling enclosure. Infauna were sampled by peeling back the mesh anchoring the artificial shoots and taking a 100 mm diameter core of 100 mm depth from beneath the centre of the ASU.

To compare the communities colonising the ASUs to those of potential source habitats, additional samples were collected from intertidal habitats (unvegetated or mangrove) adjacent to ASUs and from natural seagrass beds and unvegetated subtidal sediments adjacent to ASUs. Intertidal sampling occurred at an elevation of LAT + 0.6 m. Samples were taken three hours after low tide, to keep the time of day as similar as possible between sub- and intertidal areas. At the time of sampling, intertidal areas were covered by ~ 5 cm of water. Methods of sampling were as outlined above: within each habitat, five 50 cm × 50 cm plots were established from which sweep net samples were taken, and a single sediment core was collected from the centre of each. Samples from natural seagrass beds were collected from 1 m inside the nearest point of the closest seagrass bed (distances ranged from 11-18 m) from each ASU at low tide when water depth was ~ 0.6 m. Samples from unvegetated subtidal sediments were collected a distance of 5 m, measured parallel to the shoreline, from ASUs at low tide, when water depth was ~ 0.4 m. The experimental design in this colonisation study allowed us to assess differences in invertebrate communities between unvegetated shorelines and those with subtidal mangroves but did not permit us to tease apart the effects of shoreline type from spatial variation in assessing the causes of differences found. This reflects natural conditions where unvegetated and mangrove shorelines are spatially separated. We attempted to minimise the effect of spatial variation by choosing sites where the two shoreline types were located in close proximity to each other.

In the laboratory, the epifauna (sampled using sweep nets and hand collection) and infauna (sampled using benthic cores) from each plot were separately washed over a 500 µm sieve and the organisms retained were processed as per the mensurative survey above.

Analyses

Multivariate and univariate permutational analyses of variance (PERMANOVAs; Anderson 2007) assessed spatial variation in infaunal invertebrate communities between: 1) established seagrass patches with and without adjacent intertidal mangrove forest; 2) established mangrove forests with and without adjacent subtidal seagrass beds; and in epifaunal and infaunal communities among 3) ASUs along stretches of shoreline with and without adjacent mangroves, and among ASUs, and adjacent seagrass, subtidal and intertidal habitats. The first two sets of analyses, for the mensurative study, had two factors: adjacent habitat type (two levels, fixed: unvegetated and mangrove for the seagrass analyses, or unvegetated and seagrass for the mangrove analyses) and site (eight levels for the seagrass analysis and six levels for the mangrove analysis, random, nested within adjacent habitat type). The third set of analyses, for the colonisation experiment, had three factors: site (two levels, random: Towra Point and Kurnell), shoreline type (two levels, fixed, nested within site: unvegetated and mangrove) and habitat (four levels, fixed: artificial seagrass (ASU), seagrass, subtidal sediment and intertidal habitat). Multivariate analyses of community structure used Bray Curtis dissimilarities calculated between untransformed samples (Bray and Curtis 1957). Univariate PERMANOVAs were run on total invertebrate abundance and species richness, as well as on key taxa identified by SIMPER analysis to contribute ≥ 5% to multivariate differences among treatments and with dissimilarity to standard deviation ratios ≥ 1.0 for the mensurative study and ≥ 1.3 for the colonisation experiment (Clarke and Warwick 2001). Univariate analyses used Euclidean distances calculated between untransformed samples (Gauch 1982). All analyses were conducted using Primer 7.0.13 and Permanova+ 1 statistical software (Primer-E, 2012).

Results

Mensurative study

In total, 107 benthic macroinvertebrate morphospecies were identified in sediments of established mangrove forests and seagrass beds in Brisbane waters, with 49 unique to seagrass, 12 unique to mangroves and 46 occurring in both habitat types (Fig. 2). Taxa in common between seagrass and mangrove habitats were dominated by bivalves, gastropods, isopods and polychaetes with some amphipods and decapods also occurring in each. Morphospecies appearing exclusively in seagrass habitats were dominated by polychaetes (14), gastropods (7), crustaceans (5) and amphipods (4). Morphospecies sampled only in mangrove habitats were predominantly polychaetes (3) or gastropods (3). Seagrass beds contained the same number of species in common with mangrove habitats (40), irrespective of whether or not they were located adjacent to mangrove forests (Fig. 2). Contrary to expectation, the mangrove forests with adjacent seagrass beds shared fewer (29) morphospecies with seagrass beds than those without adjacent seagrass beds (36) (Fig. 2).

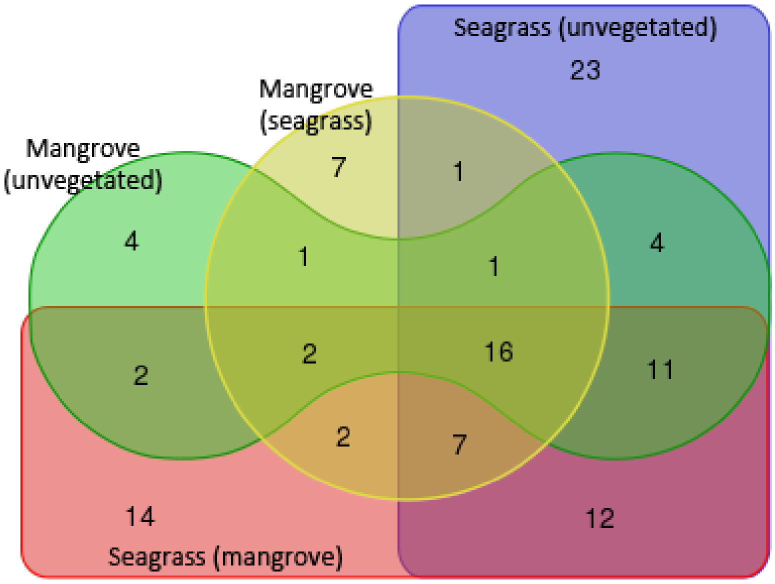

Figure 2. Venn diagram of the number of species found in seagrass patches adjacent to unvegetated and mangrove shorelines and in mangrove forests adjacent to unvegetated and seagrass subtidal areas (adjacent habitat type shown in brackets).

Multivariate analyses of infaunal communities found significant spatial variation among sites within adjacent habitat treatments in both seagrass beds and mangrove forests, above which main effects of adjacent habitat treatment could not be detected (Fig. 3; Supplementary material: Table S1). Similarly, univariate analysis of invertebrate abundance and species richness in seagrass and mangroves revealed significant among-site variation which obscured any main effect of adjacent habitat (Fig. 3; Supplementary material: Table S2). Nevertheless, seagrass sites adjacent to mangrove forests generally had greater infaunal abundances than those adjacent to unvegetated shorelines (Fig. 4). The polychaete *Aglaophamus australiensis* and the bivalve *Mysella vitrea* were identified by SIMPER analysis as the taxa most strongly contributing to the difference between seagrass communities adjacent to mangrove or unvegetated shorelines. The strongest contributor to the difference between mangrove communities adjacent to seagrass or unvegetated subtidal areas was the polychaete

Levinsenia gracilis. However, in all of these cases, significant spatial variation among sites within adjacent habitat treatments meant that no main effect of adjacent habitat type could be detected (Supplementary material: Table S3).

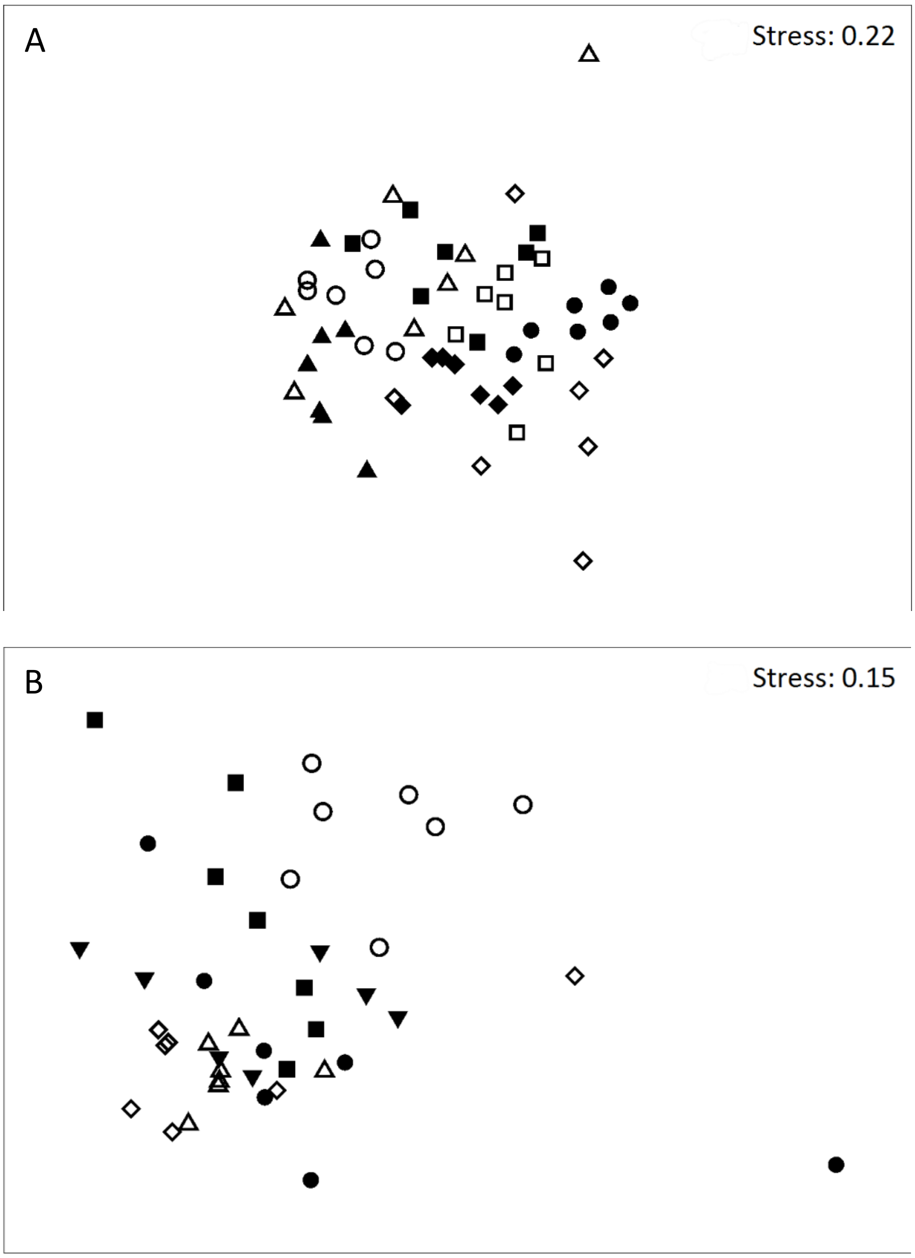

Figure 3. Non-metric multidimensional scaling plots of invertebrate communities in: A) seagrass habitats with (open symbols) and without (closed symbols) adjacent mangroves; and B) mangrove habitats with (open symbol) and without (closed symbols) adjacent seagrass. Different shapes denote different sites, with n=7 samples per site.

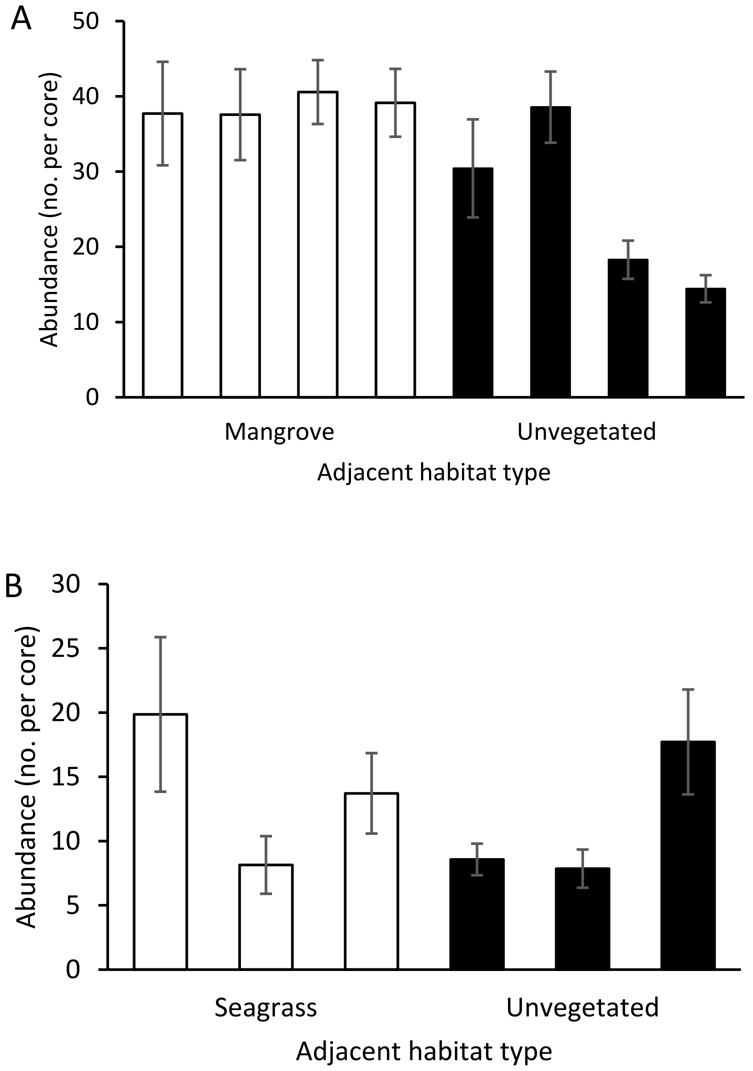

Figure 4. Mean (± SE, n=7) abundance of infauna in: A) sampled seagrass habitats adjacent to mangrove (open columns) or unvegetated shorelines (black columns); and B) sampled mangrove habitats adjacent to subtidal seagrass (open columns) or unvegetated (black columns) sediments.

Colonisation experiment

Individual ASUs contained between seven and 16 infaunal and one and six epifaunal morphospecies each. Across both sites, and all samples, a total of 17 infaunal and 13 epifaunal morphospecies were identified from ASUs adjacent to mangrove shorelines, and 26 infaunal and 13 epifaunal morphospecies were identified adjacent to unvegetated shorelines. Artificial seagrass units shared 19 infaunal and eight epifaunal morphospecies with natural seagrass beds adjacent to unvegetated shorelines as opposed to 17 infaunal and four epifaunal morphospecies near mangrove shorelines. Sampled ASUs shared more common morphospecies with subtidal habitats on unvegetated shorelines (infauna 15, epifauna 8) than on mangrove shorelines (infauna 9, epifauna 5). However, ASUs on unvegetated shorelines shared fewer morphospecies with intertidal habitats on unvegetated shorelines (infauna 10, epifauna 5) than with intertidal habitats on mangrove shorelines (infauna 14, epifauna 10) and ASUs on mangrove shorelines also shared fewer morphospecies with intertidal habitats on unvegetated shorelines (infauna 5, epifauna 5) than with intertidal habitats on mangrove shorelines (infauna 10, epifauna 6) (Fig. 5). Contrary to expectation, on three of the four shorelines sampled for infauna, and on both shoreline types for epifauna, ASUs contained unique morphospecies not found in other habitats. Morphospecies unique to ASUs were always observed in very low numbers (≤ 3) in any single sample, suggesting that these species are relatively rare in the environment. The exception to this occurred in the unvegetated shoreline treatment at Kurnell where 16 *Pyrgulina ceria* occurred in a single ASU sample. However, *P. ceria* was not found in other ASU samples from that shoreline treatment.

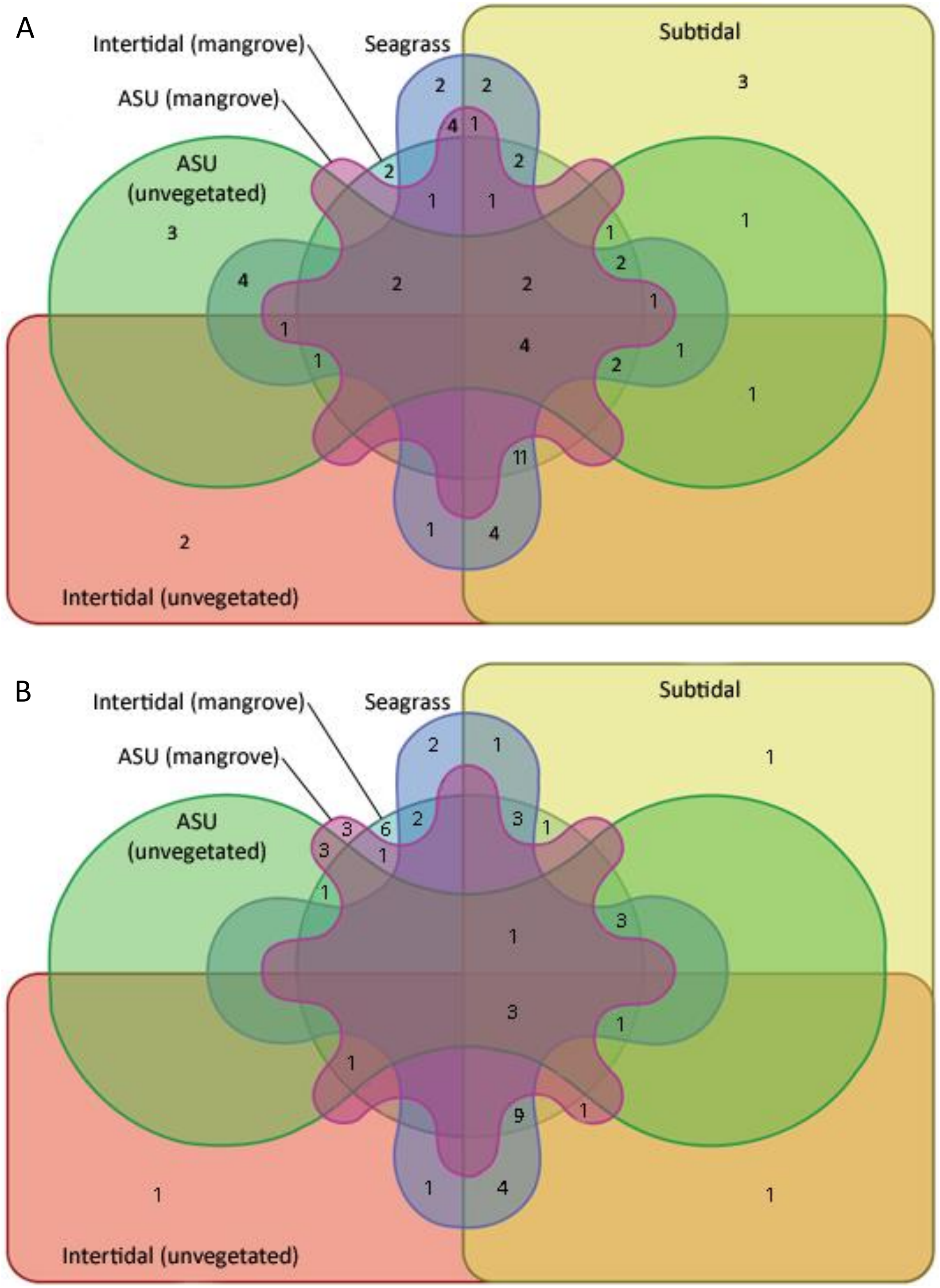

Figure 5: Number of A) infaunal and B) epifaunal morphospecies sampled in artificial seagrass unit and mangrove habitats on unvegetated and mangrove shorelines as well as natural seagrass and subtidal sediments.

Multivariate analyses of both infaunal and epifaunal invertebrate communities showed significant shoreline (site) × habitat interactions (Supplementary material; Table S4). At Towra Point, the infaunal communities of each of ASU, seagrass, subtidal and intertidal habitats differed between unvegetated and mangrove shorelines. However, at Kurnell, only invertebrate communities of ASU and intertidal habitats differed between shoreline types (Fig. 6; *a posteriori* tests: Supplementary material; Table S5). Epifaunal communities in ASU, seagrass and intertidal habitats differed between unvegetated and mangrove shorelines at Towra Point and differed between shoreline types across all habitat types at Kurnell (Fig. 7; *a posteriori* tests: Supplementary material; Table S5).

When infaunal and epifaunal communities of ASUs within levels of shoreline (site) were compared to those of other habitat types, all contrasts were significant except for the infaunal ASU-seagrass comparison for the mangrove shoreline at Towra Point (*a posteriori* tests: Supplementary material; Table S6). Infaunal communities on all shorelines displayed higher abundances in ASU habitat than in natural seagrass, except on the mangrove shoreline at Towra Point where the mean infaunal abundance was extraordinarily high. This was driven by high abundances in two of the five sample cores, and the large variance resulting from this meant that this comparison did not show a significant difference. Within sites, infaunal communities in ASUs showed higher similarity to intertidal communities on mangrove shorelines than on unvegetated shorelines and epifaunal communities in ASUs showed higher similarity to natural seagrass on unvegetated shorelines than on mangrove shorelines (Figs. 6 and 7; Table 1).

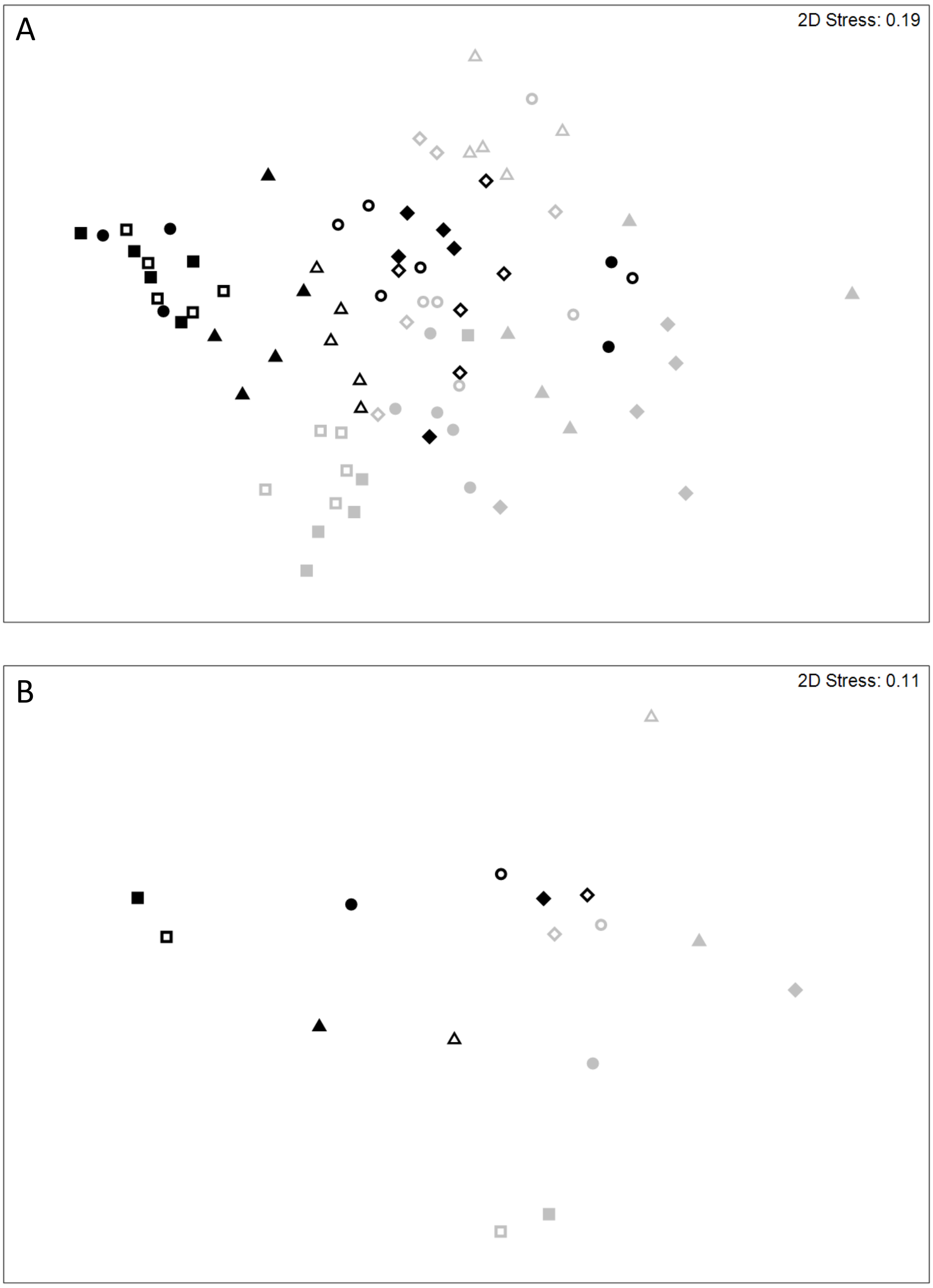

Figure 6: Non-metric Multidimensional Scaling Plots of A) infaunal communities and B) centroids of infaunal communities sampled on unvegetated (grey symbols) and mangrove (black symbols) shorelines at Towra Point (closed symbols) and Kurnell (open symbols). Samples were collected from four habitat types: ASU (squares); seagrass (circles); subtidal sediment (diamonds); and intertidal habitats (triangles); with n=5 samples within each.

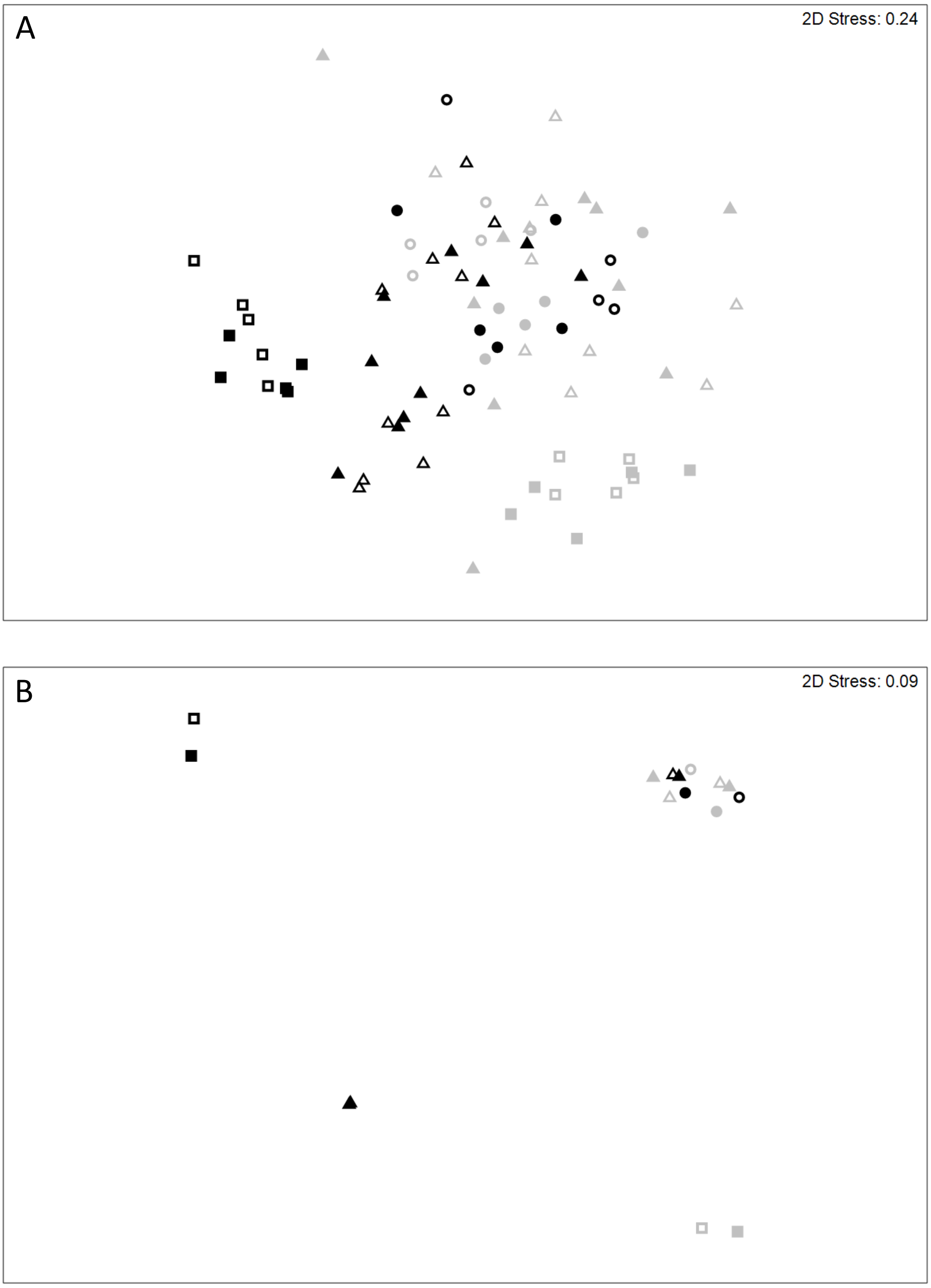

Figure 7: Non-metric Multidimensional Scaling Plots of A) epifaunal communities and B) centroids of epifaunal communities sampled on unvegetated (grey symbols) and mangrove (black symbols) shorelines at Towra Point (closed symbols) and Kurnell (open symbols). Samples were collected from four habitat types: ASU (squares); seagrass (circles); subtidal sediment (diamonds); and intertidal habitats (triangles); with n=5 samples within each.

Table 1. Average similarities between invertebrate communities sampled in ASUs and each of natural seagrass, subtidal sediment, and in intertidal sediment habitats. Comparisons are within unvegetated or mangrove shorelines, within sites.

Faunal type	**Site / Shoreline**	**Comparison**	**Av. Similarity (%)**
Infauna	Towra / Unvegetated	ASU, Seagrass	25.92
		ASU, Subtidal	10.22
		ASU, Intertidal	12.75
	Towra / Mangrove	ASU, Seagrass	42.03
		ASU, Subtidal	11.80
		ASU, Intertidal	36.72
	Kurnell / Unvegetated	ASU, Seagrass	18.38
		ASU, Subtidal	23.79
		ASU, Intertidal	8.75
	Kurnell / Mangrove	ASU, Seagrass	17.33
		ASU, Subtidal	11.53
		ASU, Intertidal	24.50
Epifauna	Towra / Unvegetated	ASU, Seagrass	20.75
		ASU, Subtidal	14.32
		ASU, Intertidal	8.37
	Towra / Mangrove	ASU, Seagrass	15.81
		ASU, Subtidal	13.77
		ASU, Intertidal	23.91
	Kurnell / Unvegetated	ASU, Seagrass	9.76
		ASU, Subtidal	17.59
		ASU, Intertidal	16.93
	Kurnell / Mangrove	ASU, Seagrass	5.34
		ASU, Subtidal	15.67
		ASU, Intertidal	15.03

Infaunal abundance did not vary with habitat type. However, within sites, across all habitat types, infauna was significantly more abundant on mangrove shorelines than on unvegetated shorelines (Fig. 8). Epifaunal abundance showed a significant shoreline (site) × habitat interaction (Supplementary material: Table S7). Within sites, epifaunal abundance in intertidal, but not other types of habitat, was significantly greater on mangrove than unvegetated shorelines (Fig. 8; *a posteriori* tests: Supplementary material; Table S8). At Towra Point, the abundance of epifauna did not vary between ASUs and each of the other habitat types along the unvegetated shoreline, but along the mangrove shoreline epifauna were less abundant in ASUs than in the intertidal zone. At Kurnell, the abundance of epifauna in ASUs was significantly lower than in all other habitat types along both unvegetated and mangrove shorelines, except for the intertidal habitat on the unvegetated shoreline (Fig. 9; *a posteriori* tests: Supplementary material; Table S9).

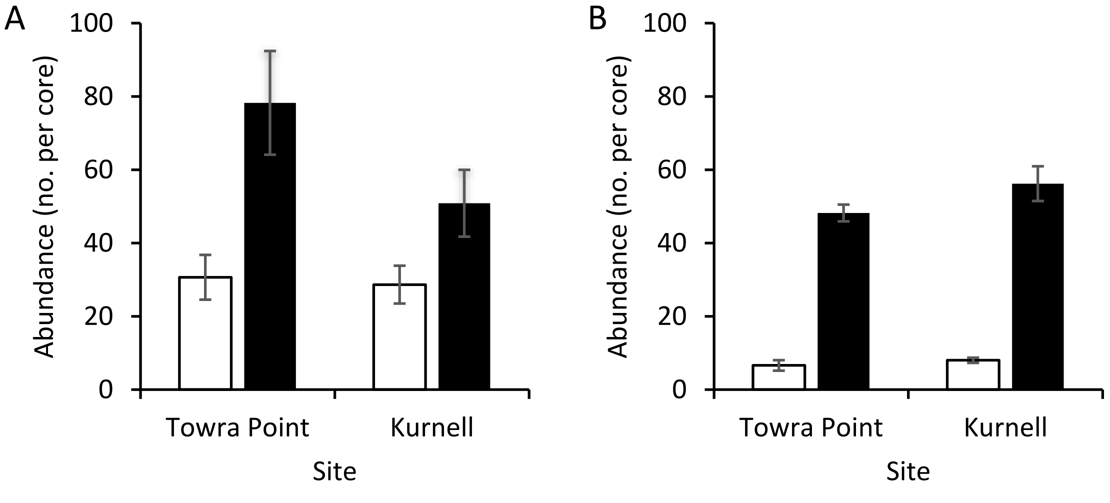

Figure 8: Mean (± SE) abundance of A) infauna across all habitats on unvegetated (open columns) and mangrove (solid columns) shorelines, with n=20 cores per shoreline; and B) epifauna abundance in intertidal habitat on unvegetated (open columns) and mangrove (solid columns) shorelines, with n=5 samples per habitat.

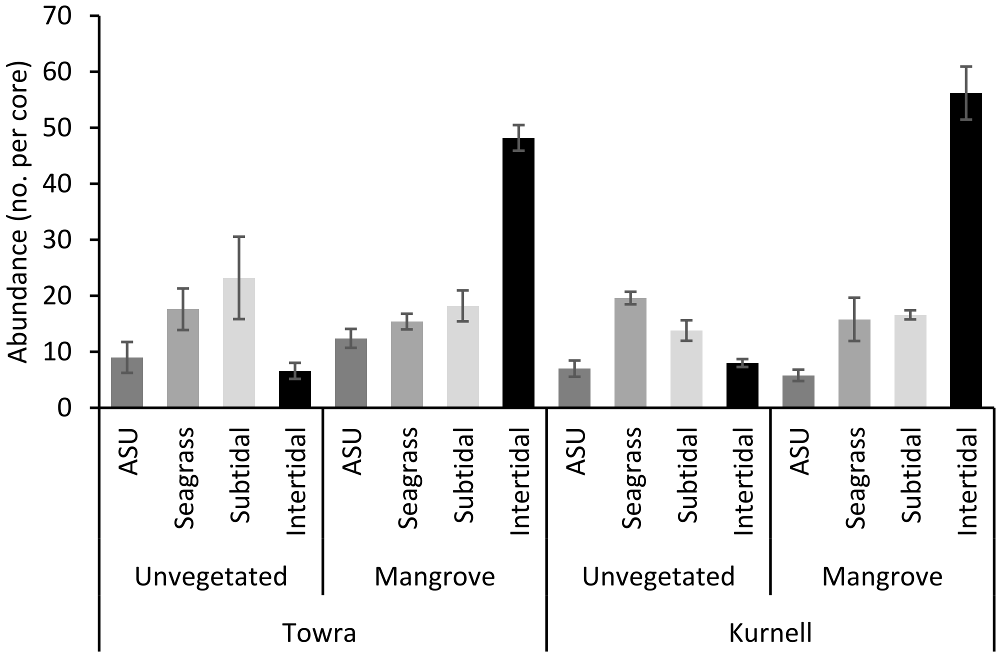

Figure 9: Mean (±SE, n=5) abundance of epifauna sampled in four habitat types across two different shoreline types at each of two sites.

Species richness in both infauna and epifauna showed a significant shoreline (site) × habitat interaction (Supplementary material: Table S7). *Post hoc* testing showed no significant effect of shoreline type on infaunal richness in similar habitat types, except at Towra point where richness in the intertidal habitat was lower on the unvegetated shoreline than on the mangrove shoreline (Fig. 10; *a posteriori* tests: Supplementary material; Table S8). Infaunal richness did not vary between ASUs and other habitat types on the same shoreline at each site, except for the subtidal and intertidal habitats on the unvegetated shoreline at Towra Point and the intertidal habitat on the unvegetated shoreline at Kurnell (Fig. 10; *a posteriori* tests: Supplementary material; Table S9). Epifaunal richness in ASUs was higher on the mangrove shoreline at Towra Point but higher on the unvegetated shoreline at Kurnell and in the intertidal habitat was higher on the mangrove shoreline at Kurnell (Fig. 10; *a posteriori* tests: Supplementary material; Table S8). Species richness among epifauna varied between ASUs and other habitat types on the same shoreline at each site, except for the seagrass and intertidal habitats on the unvegetated shoreline at Towra Point (Fig. 10; *a posteriori* tests: Supplementary material; Table S9).

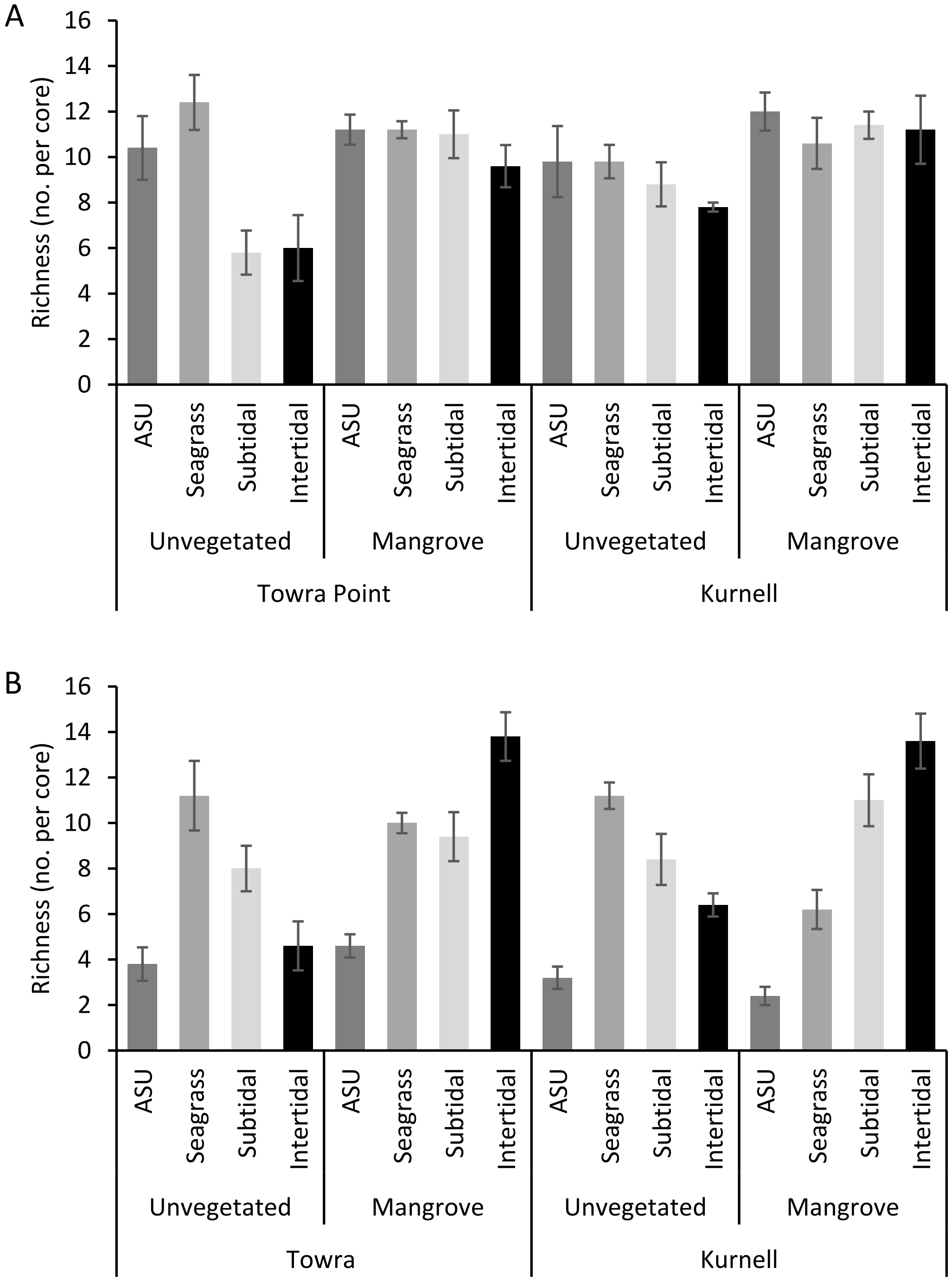

Figure 10: Mean (±SE, n=5) species richness of A) infauna and B) epifauna sampled in four habitat types across two different shoreline types at each of two sites.

The gastropods *P. ceria, Calopia imitata* and *Littoraria luteola*, the bivalve *M. vitrea* and the polychaete *Capitella capitata* were identified by SIMPER analysis as key discriminating species driving differences in infaunal communities among habitats. Across habitat types, *P. ceria* displayed significantly higher abundance on the mangrove than the unvegetated shoreline at both Towra Point and Kurnell (mean ± SE values: Towra Point mangrove shoreline 4.30 ± 1.30 versus unvegetated 0.00 ± 0.00; Kurnell mangrove shoreline 3.15 ± 1.23 versus unvegetated 0.80 ± 0.80). The other key discriminating infaunal species all showed a significant shoreline (site) × habitat interaction (Supplementary material; Table S10). In *post-hoc* testing, the gastropods *C. imitata* and *L. luteola* displayed significantly higher abundance in ASU habitat on mangrove shorelines than on unvegetated shorelines at both Towra Point and Kurnell. Additionally*, C. imitata* was more abundant on the mangrove shoreline than the unvegetated shoreline in subtidal habitat at Towra Point and in intertidal habitat at Kurnell and *L. luteola* more abundant on the mangrove shoreline than the unvegetated shoreline in intertidal habitat at Towra Point. The opposite pattern was generally observed in the bivalve and the polychaete species. *Capitella capitata* was more abundant on the unvegetated shoreline than on the mangrove shoreline in ASU habitat at Kurnell and *M. vitrea* more abundant on the unvegetated than the mangrove shoreline in both ASU and seagrass habitats at Towra Point and in ASU habitat at Kurnell, but less abundant on the unvegetated than the mangrove shoreline in intertidal habitat at Kurnell (*a posteriori* tests: Supplementary material; Tables S11, S12). Among *C. imitata*, *L. luteola*, *M. vitrea* and *C. capitata*, significant differences in *post hoc* pairwise comparisons between ASUs and other habitat types on the same shoreline at the same site consistently showed higher abundance in the ASU habitat, except in ASU-intertidal comparisons in *M. vitrea* on the mangrove shorelines at both Towra Point and Kurnell, where abundance was greater in the intertidal habitat (*a posteriori* tests: Supplementary material; Tables S13, S12).

Amongst epifauna, *M. vitrea, C. imitata* and the polychaetes *Dipolydora socialis, L. gracilis* and *Scoloplos simplex* were identified by SIMPER analysis as key discriminating species. The abundance of *L. gracilis* did not significantly vary with site, shoreline or habitat but all of the remaining key discriminating species showed a significant shoreline (site) × habitat interaction (Supplementary material; Table S14). *Post hoc* tests showed that the abundance of *D. socialis* in similar habtat types did not vary with shoreline type at either site. Abundances of *M. vitrea* were higher on the unvegetated shoreline than on the mangrove shoreline in ASU habitat at both sites but *C. imitata* was more abundant on the mangrove shoreline than the unvegetated shoreline in ASU and intertidal habitats at both Towra Point and Kurnell. The polychaete *S. simplex* in ASU habitat was more abundant on the unvegetated shoreline than the mangrove shoreline at Towra Point and Kurnell but display the opposite pattern in subtidal sediment at Kurnell (*a posteriori* tests: Supplementary material; Tables S15, S16). In pairwise comparisons between ASUs and other habitats on the same shoreline in the polychaetes *D. socialis* and *S. simplex,* significant differences always indicated lower abundances in the ASU habitat as these species did not occur in ASU samples. In *C. imitata,* significant differences between pais of habitats always indicated higher abundances in the ASU habitat. Significant differences in *M. vitrea* between pairs of habitats within unvegetated shorelines showed higher abundances in the ASU habitat, but comparisons within mangrove shorelines showed lower abundances in the ASU habitat (*a posteriori* tests: Supplementary material; Tables S17, S16).

Discussion

Despite a rich literature on how the spatial configuration of biogenic habitat patches determines associated communities of nekton (e.g. Jelbart et al. 2007; Saintilan et al. 2007;

Gain et al. 2017), relatively few studies have addressed how invertebrate communities, which may be dominated by species of lower mobility or smaller body size, respond to patch configuration (but see González-Ortiz et al. 2016; Lefcheck et al. 2016). Our surveys of natural seagrass beds, and of artificial seagrass units of standardised morphology, found differences in invertebrate communities close to and distant from mangrove forests. By contrast, within natural mangrove forests, there was no difference in invertebrate communities between forests close to and away from seagrass beds. Hence, although habitat configuration may be of importance in structuring invertebrate communities, the effects may be asymmetric between the habitat types involved. The timeframe of our colonisation study (over four months) was sufficient to allow comprehensive colonisation of both above- and below-ground portions of the ASUs by macroinvertebrate species from adjacent habitats. Previous studies utilising ASUs have shown epifauna to extensively colonise ASUs within days, reaching asymptotic levels of abundance and richness after 4-8 days, while epifauna have been shown to colonise new sediments to asymptotic levels of abundance and richness within 30 days (Virnstein and Curran 1986; Guerra-García and García-Gómez 2006).

On shorelines with mangroves, the difference between the communities of ASUs and adjacent subtidal sediment was strongly affected by the gastropod *C. imitata*, which was far more abundant in the artificial seagrass than in the surrounding sediment. This pattern may represent high levels of migration to artificial seagrass units by gastropods from adjacent mangrove habitat. Small gastropods have been shown to rapidly colonise artificial seagrass at distances > 15m, albeit with abundance in the new habitat decreasing with migration distance (Virnstein and Curran 1986).

Along unvegetated shorelines, the key driver of dissimilarity between ASUs and surrounding subtidal sediment was a higher density of the bivalve *M. vitrea* in the artificial seagrass units. Bivalves, which are typically more abundant in structurally complex than simple habitat may benefit from the protection from predation that complex habitat provides, or from enhanced trapping of organic matter in structurally complex habitat (e.g. Orth et al. 1984). Bivalves disperse by planktonic spawning, with settlement on ASUs depending on encounter rate (Bologna and Heck 2000). The high numbers of gastropods seen in ASUs on mangrove shorelines are not apparent on unvegetated shorelines, possibly due to the lack of proximal mangrove habitat source populations.

The generally greater abundances of infaunal invertebrates in seagrass beds close to mangroves than in beds spatially separated from mangrove forests in our study mirrors patterns displayed by nekton such as fish and prawns (Skilleter et al. 2005; Jelbart et al. 2007) and is analogous to the results of Grabowski et al. (2005) where the abundance of resident invertebrates in seagrass and saltmarsh habitats was enhanced by the presence of nearby physically complex oyster reef. However, studies of fish communities in seagrass also showed significantly higher species richness near to than distant from mangrove forests, largely driven by the presence of mangrove-utilising species not seen away from mangroves (Jelbart et al. 2007). Our study, by contrast, found no difference in invertebrate richness between patches close to and away from mangroves. Whereas the high mobility of many nektonic species may allow them to migrate freely between proximate habitat patches to forage and/or shelter on time scales as short as tidal cycles or less, infauna and epifauna are typically of reduced mobility (Saintilan et al. 2007). The asymmetry of habitat effects may reflect one serving as a donor and the other as a recipient of larvae and/or other resources. On both unvegetated and mangrove shorelines, the invertebrate communities of artificial seagrass units more closely resembled those of mangrove forests than unvegetated intertidal sediments, suggesting the affinity of key species for structurally complex habitats.

Invertebrate communities in ASUs differed between shorelines with and without mangroves. The artificial seagrass units developed distinct communities with higher infaunal abundance but lower epifaunal abundance than the surrounding subtidal sediments. This conflicted with our initial expectation that the addition of structural complexity both above and below ground would drive increases in both in- and epi-faunal abundances.

Differences in the communities of both natural seagrass beds and ASUs between shorelines with and without mangroves may reflect their proximity to mangroves, or alternatively, may be driven by environmental differences between these places. While our colonisation study was not able to disentangle the effects of shoreline type and spatial separation, the patterns observed were similar to those seen in our earlier mensurative survey, suggesting that the shoreline type was the key driver of differences in invertebrate communities between shoreline types. Within estuaries, spatial variation in the establishment of *A. marina* is largely driven by propagule supply, tidal/wave action and the distribution of interspecific competitors and predators (Clarke and Mysercough 1993). Although stretches of shoreline with and without mangroves were selected on the basis of their otherwise similar environmental conditions, it is possible that the same processes that determined the presence or absence of mangroves produced differences in the communities of seagrass and ASUs between shorelines with and without mangroves. Mangrove clearing or restoration projects would provide the opportunity to distinguish the effects of mangroves from other environmental factors on the community structure of adjacent habitats.

Mangroves may influence the communities of adjacent seagrass by determining the species pool available for colonisation, or via their modification of environmental conditions. Mangroves produce considerable amounts of detrital material, in the form of leaf fall, which organically enriches the sediments of mangroves (Alfaro 2006) and adjacent habitats which trap suspended particles (Skilleter et al. 2005). If differences in the communities of the natural and artificial seagrass between shorelines with and without mangroves reflect differences in the available species pool for colonisation, the species driving this difference would be expected to be those same species that differ in abundance or presence between mangrove and unvegetated habitats. This was not supported by our data as species driving differences in the communities of ASUs between shoreline types were generally found in both intertidal habitat types. Only one species (*C. imitata*) displayed a significant difference in abundance between both ASUs adjacent to unvegetated and mangrove shorelines, and the intertidal habitats themselves. However, of the species driving differences in seagrass communities between shoreline types, most were surface deposit feeders, abundant in mangrove forests. This is consistent with the hypothesis of greater organic matter enrichment of seagrass beds close to than further from mangroves, although we did not explicitly test for this, and may explain the asymmetric effects of the proximity of seagrass and mangrove habitats on the resident invertebrate communities of each.

Conclusion

Globally, physically complex estuarine and inshore marine habitats are being lost due to persistent and increasing anthropogenic pressure (de Juan et al. 2013). Restoration programs, aimed at assisting the recovery of degraded ecosystems, are becoming common, especially in Australia, the USA and Europe (Bayraktarov et al. 2015). However, such programs are expensive to implement (Bayraktarov et al. 2015) and maximising the return on investment is a sound strategy. Maximising the taxonomic abundance and diversity of communities in restored habitats is likely to increase the resilience of those communities to environmental perturbation (Moberg and Rönnbäck 2003). Our study shows the positive effects of proximity to mangrove habitats on seagrass communities. Previous studies have demonstrated benefits to communities in seagrass and reef habitats of connectivity to other habitat types (e.g. Jelbart et al. 2007; Saintilan et al. 2007; Gain et al. 2017). Therefore, it may be beneficial to prioritise protection or restoration in locations adjacent to other types of biogenic habitats in order to maximise resilience in restored communities. Assessments of the risk of collapse in estuarine ecosystems may also benefit from placing greater weight on loss of complex habitats in such locations than on loss of such habitats surrounded by sedimentary matrix.

Our study demonstrates that the structure of estuarine infaunal and epifaunal communities varies according to the spatial configuration of habitat patches. Effects of neighbouring habitats on one another were uni-directional, suggesting that one is the donor and the other the recipient of propagule supply and/or resources. Studies are now needed to investigate the mechanisms by which such effects of habitat configuration arise.

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Appendix: Results of statistical tests

Table S1. Results from multivariate two-factor nested PERMANOVAs testing for differences in community structure between seagrass sites adjacent to mangrove or unvegetated shoreline, and mangrove sites adjacent to seagrass or unvegetated habitat. Statistically significant results (at $\alpha = 0.05$) shown in bold.

Habitat	**Source**	**d.f.**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Seagrass	Adjacent habitat	1	6102.80	6102.80	0.63	0.80	35
	Site (Adjacent habitat)	6	58461.00	9743.50	4.33	**0.01**	85022
	Residual	48	108130.00	2252.70			
Mangrove	Adjacent habitat	1	8.60	8.60	0.85	050	9
	Site (Adjacent habitat)	4	40.38	10.10	3.10	**0.03**	9887
	Residual	36	117.14	3.25			

Table S2. Results from univariate two-factor nested PERMANOVAs testing for differences in the abundance and richness of infauna between seagrass sites adjacent to mangrove or unvegetated shoreline, and mangrove sites adjacent to seagrass or unvegetated habitat. Statistically significant results (at α = 0.05) shown in bold.

Metric	**Habitat**	**Source**	**d.f.**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Abundance	Seagrass	Adjacent habitat	1	2484.40	2484.40	5.67	0.08	34
		Site (Adjacent habitat)	6	2629.80	438.30	2.54	**0.03**	9939
		Residual	48	8268.30	172.26			
	Mangrove	Adjacent habitat	1	66.88	66.88	0.30	0.61	10
		Site (Adjacent habitat)	4	903.62	225.90	2.71	**0.04**	9942
		Residual	36	2997.10	83.25			
Richness	Seagrass	Adjacent habitat	1	5.79	5.79	0.09	0.77	29
		Site (Adjacent habitat)	6	387.93	64.66	6.31	**0.01**	9958
		Residual	48	491.71	10.24			
	Mangrove	Adjacent habitat	1	0.38	0.38	0.01	0.90	10
		Site (Adjacent habitat)	4	124.95	31.24	6.54	**0.01**	9931
		Residual	36	172.00	4.78			

Table S3. Results of two-way nested PERMANOVAs testing for sources of variation in the abundance of key discriminating taxa identified by SIMPER as driving differences between levels of adjacent habitat in seagrass and mangrove habitats. Analyses of species in seagrass habitats had the factors adjacent habitat (2 levels, fixed: mangrove and unvegetated) and site (8 levels, random). Analyses of species in mangrove habitats had the factors adjacent habitat (2 levels, fixed: seagrass and unvegetated) and site (6 levels, random). Statistically significant results (at α = 0.05) shown in bold.

Habitat	**Species**	**Source**	**d.f.**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Seagrass	*Aglaophamus australiensis*	Adjacent habitat	1	9.45	9.45	0.20	0.68	28
		Site (Adjacent habitat)	6	282.96	47.16	4.93	**0.01**	9943
		Residual	48	459.14	9.57			
	Mysella vitrea	Adjacent habitat	1	13.02	13.02	1.40	0.29	18
		Site (Adjacent habitat)	6	55.68	9.28	3.88	**0.01**	9922
		Residual	48	114.86	2.39			
Mangrove	*Levinsenia gracilis*	Adjacent habitat	1	8.60	8.60	0.85	0.50	9
		Site (Adjacent habitat)	4	40.38	10.10	3.10	**0.03**	9887
		Residual	36	117.14	3.25			

Table S4. Results of PERMANOVAs testing for multivariate differences in infaunal and epifaunal communities between Sites (2 levels, random: Towra Point and Kurnell), Shoreline types (2 levels, fixed, nested within Site: mangrove and unvegetated) and among Habitats (4 levels, fixed: artificial seagrass units (ASUs), natural seagrass, subtidal sediment and intertidal sediment). Statistically significant results (at α = 0.05) are shown in bold.

Faunal type	**Source**	**d.f.**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Infauna	Site	1	6470.40	6470.40	3.35	**0.01**	3
	Habitat	3	35518.00	11839.00	3.91	**0.05**	840
	Shoreline (Site)	2	279510	13975.00	7.23	**0.01**	9907
	Site × Habitat	3	9087.70	3029.20	1.57	**0.01**	9917
	Shoreline (Site) × Habitat	6	51709.00	8618.10	4.46	**0.01**	9789
	Residual	64	123640.00	1931.80			
Epifauna	Site	1	1498.50	1498.50	0.77	0.70	9913
	Habitat	3	52790.00	17597.00	7.15	**0.02**	840
	Shoreline (Site)	2	21784.00	10892.00	5.58	**0.01**	9908
	Site × Habitat	3	7386.10	2462.00	1.26	0.13	9888
	Shoreline (Site) × Habitat	6	48676.00	8112.60	4.16	**0.01**	9844
	Residual	64	124880.00	1951.20			

Table S5. Results of *a posteriori* tests for differences in infaunal and epifaunal invertebrate communities in similar habitat types between levels of Shoreline Type (Site). Statistically significant results (at α = 0.05) shown in bold.

Faunal type	**Site**	**Habitat type**	**d.f.**	***t***	***P* (perm)**	**Unique perms**
Infauna	Towra	ASU	1, 8	3.77	**0.01**	126
		Seagrass	1, 8	1.82	**0.01**	126
		Subtidal	1, 8	2.01	**0.01**	126
		Intertidal	1, 8	2.46	**0.01**	126
	Kurnell	ASU	1, 8	4.07	**0.01**	126
		Seagrass	1, 8	1.24	0.12	126
		Subtidal	1, 8	0.97	0.55	126
		Intertidal	1, 8	2.86	**0.01**	126
Epifauna	Towra	ASU	1, 8	3.32	**0.01**	126
		Seagrass	1, 8	1.49	**0.02**	126
		Subtidal	1, 8	1.02	0.39	126
		Intertidal	1, 8	2.05	**0.01**	126
	Kurnell	ASU	1, 8	3.62	**0.01**	126
		Seagrass	1, 8	1.96	**0.01**	126
		Subtidal	1, 8	1.47	**0.02**	126
		Intertidal	1, 8	2.13	**0.01**	126

Table S6. Results of *a posteriori* tests for differences in infaunal and epifaunal invertebrate communities between Artificial Seagrass Units (ASUs) and other habitat types within levels of Shoreline Type (Site). Statistically significant results (at α = 0.05) shown in bold.

Faunal type	**Site / Shoreline**	**Comparison**	**d.f.**	***t***	***P* (perm)**	**Unique perms**
Infauna	Towra, Unvegetated	ASU, Seagrass	3, 8	2.00	**0.01**	126
		ASU, Subtidal	3, 8	2.33	**0.02**	126
		ASU, Intertidal	3, 8	2.13	**0.01**	126
	Towra, Mangrove	ASU, Seagrass	3, 8	1.26	0.35	126
		ASU, Subtidal	3, 8	3.17	**0.01**	126
		ASU, Intertidal	3, 8	2.62	**0.01**	126
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	2.38	**0.01**	126
		ASU, Subtidal	3, 8	2.05	**0.01**	126
		ASU, Intertidal	3, 8	3.57	**0.01**	126
	Kurnell, Mangrove	ASU, Seagrass	3, 8	2.79	**0.01**	126
		ASU, Subtidal	3, 8	3.06	**0.01**	126
		ASU, Intertidal	3, 8	2.97	**0.01**	126
Epifauna	Towra, Unvegetated	ASU, Seagrass	3, 8	2.00	**0.01**	126
		ASU, Subtidal	3, 8	2.18	**0.01**	126
		ASU, Intertidal	3, 8	1.78	**0.01**	126
	Towra, Mangrove	ASU, Seagrass	3, 8	3.02	**0.01**	126
		ASU, Subtidal	3, 8	3.16	**0.01**	126
		ASU, Intertidal	3, 8	3.48	**0.01**	126
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	3.22	**0.01**	126
		ASU, Subtidal	3, 8	2.55	**0.01**	126
		ASU, Intertidal	3, 8	1.82	**0.01**	126
	Kurnell, Mangrove	ASU, Seagrass	3, 8	3.08	**0.01**	126
		ASU, Subtidal	3, 8	2.70	**0.01**	126
		ASU, Intertidal	3, 8	3.39	**0.01**	126

Table S7. Results of PERMANOVAs testing for differences in the total abundance and species richness of infaunal and epifaunal communities between Sites (2 levels, random: Kurnell and Towra Point), Shoreline types (2 levels, fixed, nested within Site: mangrove and unvegetated) and among Habitats (4 levels, fixed: artificial seagrass units (ASUs), natural seagrass, subtidal sediment and intertidal sediment). Statistically significant results (at α = 0.05) are shown in bold.

Faunal type & metric	**Source**	**d.f.**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Infaunal abundance	Site	1	2152.80	2152.80	6.18	**0.01**	9815
	Habitat	3	25906.00	8635.20	10.71	0.09	839
	Shoreline (Site)	2	10541.00	5270.60	15.13	**0.01**	9957
	Site × Habitat	3	2419.90	806.65	2.31	0.08	9954
	Shoreline (Site) × Habitat	6	2446.50	407.75	1.17	0.34	9932
	Residual	64	22301.00	348.46			
Epifaunal abundance	Site	1	19.01	19.01	0.43	0.53	9840
	Habitat	3	4554.40	1518.10	13.30	**0.05**	840
	Shoreline (Site)	2	2215.50	1107.80	25.05	**0.01**	9940
	Site × Habitat	3	342.34	114.11	2.58	0.06	9954
	Shoreline (Site) × Habitat	6	8081.80	1347.00	30.45	**0.01**	9938
	Residual	64	2830.8	44.23			
Infaunal richness	Site	1	20.00	20.00	22.42	**0.01**	8509
	Habitat	3	9.70	3.23	1.29	0.39	617
	Shoreline (Site)	2	24.10	12.05	14.61	**0.01**	9960
	Site × Habitat	3	7.50	2.50	3.03	**0.03**	9953
	Shoreline (Site) × Habitat	6	28.70	4.78	5.80	**0.01**	9943
	Residual	64	52.80	0.83			
Epifaunal richness	Site	1	42.99	42.99	0.50	0.72	9926
	Habitat	3	6248.8	2082.90	12.52	**0.03**	840
	Shoreline (Site)	2	2841.00	1420.50	16.56	**0.01**	9933
	Site × Habitat	3	499.16	166.39	1.94	0.06	9937

Faunal type & metric	**Source**	**d.f.**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
	Shoreline (Site) × Habitat	6	9805.50	1634.20	19.05	**0.01**	9936
	Residual	64	5490.00	85.78			

Table S8. Results of *a posteriori* tests for differences in the total abundance and species richness of infaunal and epifaunal invertebrate communities in similar habitat types between levels of Shoreline Type (Site). Statistically significant results (at α = 0.05) shown in bold.

Faunal type & metric	**Site**	**Habitat**	**d.f.**	***t***	***P* (perm)**	**Unique perms**
Epifaunal abundance	Towra	ASU	1, 8	1.05	0.37	17
		Seagrass	1, 8	0.55	0.71	19
		Subtidal	1, 8	0.64	0.59	39
		Intertidal	1, 8	15.40	**0.01**	36
	Kurnell	ASU	1, 8	0.68	0.58	11
		Seagrass	1, 8	0.94	0.42	20
		Subtidal	1, 8	1.40	0.23	14
		Intertidal	1, 8	10.06	**0.01**	52
Infaunal richness	Towra	ASU	1, 8	2.89	0.08	3
		Seagrass	1, 8	0.00	1.00	6
		Subtidal	1, 8	6.94	**0.01**	9
		Intertidal	1, 8	2.56	0.08	4
	Kurnell	ASU	1, 8	2.68	0.08	4
		Seagrass	1, 8	1.44	0.30	5
		Subtidal	1, 8	1.34	0.40	3
		Intertidal	1, 8	2.68	0.08	4
Epifaunal richness	Towra	ASU	1, 8	2.12	**0.03**	107
		Seagrass	1, 8	1.02	0.42	102
		Subtidal	1, 8	0.83	0.48	119
		Intertidal	1, 8	8.08	0.01	118
	Kurnell	ASU	1, 8	2.39	**0.01**	81
		Seagrass	1, 8	1.62	0.08	111
		Subtidal	1, 8	1.46	0.08	84
		Intertidal	1, 8	6.65	**0.01**	122

Table S9. Results of *a posteriori* tests for differences in the total abundance and species richness of infaunal and epifaunal invertebrate communities between Artificial Seagrass Units (ASUs) and other habitat types within levels of Shoreline Type (Site). Statistically significant results (at $\alpha = 0.05$) shown in bold.

Faunal type & metric	Site / Shoreline	Comparison	d.f.	*t*	*P* (perm)	Unique perms
Epifaunal abundance	Towra, Unvegetated	ASU, Seagrass	3, 8	1.86	0.12	25
		ASU, Subtidal	3, 8	1.81	0.11	35
		ASU, Intertidal	3, 8	0.77	0.60	16
	Towra, Mangrove	ASU, Seagrass	3, 8	1.37	0.27	11
		ASU, Subtidal	3, 8	1.79	0.13	21
		ASU, Intertidal	3, 8	12.58	**0.01**	42
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	6.87	**0.01**	24
		ASU, Subtidal	3, 8	2.92	**0.04**	20
		ASU, Intertidal	3, 8	0.62	0.63	11
	Kurnell, Mangrove	ASU, Seagrass	3, 8	2.50	**0.04**	28
		ASU, Subtidal	3, 8	8.28	**0.01**	22
		ASU, Intertidal	3, 8	10.40	**0.01**	48
Infaunal richness	Towra, Unvegetated	ASU, Seagrass	3, 8	1.02	0.44	5
		ASU, Subtidal	3, 8	5.69	**0.01**	5
		ASU, Intertidal	3, 8	3.46	**0.04**	4
	Towra, Mangrove	ASU, Seagrass	3, 8	0.31	1.00	3
		ASU, Subtidal	3, 8	1.77	0.20	4
		ASU, Intertidal	3, 8	2.13	0.14	4
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	2.19	0.12	5
		ASU, Subtidal	3, 8	2.89	0.08	3
		ASU, Intertidal	3, 8	5.20	**0.01**	5
	Kurnell, Mangrove	ASU, Seagrass	3, 8	1.62	0.23	5
		ASU, Subtidal	3, 8	0.76	0.72	4
		ASU, Intertidal	3, 8	1.13	0.48	4

Faunal type & metric	**Site / Shoreline**	**Comparison**	**d.f.**	***t***	***P* (perm)**	**Unique perms**
Epifaunal richness	Towra, Unvegetated	ASU, Seagrass	3, 8	2.13	0.07	112
		ASU, Subtidal	3, 8	1.85	**0.04**	120
		ASU, Intertidal	3, 8	1.31	0.19	99
	Towra, Mangrove	ASU, Seagrass	3, 8	2.85	**0.01**	91
		ASU, Subtidal	3, 8	2.42	**0.02**	104
		ASU, Intertidal	3, 8	7.11	**0.01**	123
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	5.17	**0.01**	105
		ASU, Subtidal	3, 8	2.91	**0.01**	91
		ASU, Intertidal	3, 8	1.95	**0.01**	68
	Kurnell, Mangrove	ASU, Seagrass	3, 8	2.52	**0.01**	101
		ASU, Subtidal	3, 8	4.83	**0.01**	105
		ASU, Intertidal	3, 8	7.02	**0.01**	121

Table S10. Results of univariate PERMANOVAs testing for differences in the abundance of key discriminating infaunal species identified by SIMPER between Sites (2 levels, random: Towra Point and Kurnell), Shoreline types (2 levels, fixed, nested within Site: mangrove and unvegetated) and among Habitats (4 levels, fixed: artificial seagrass units (ASUs), natural seagrass, subtidal sediment and intertidal sediment). Statistically significant results (at α = 0.05) shown in bold.

Species	**Source**	**d.f.**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Mysella vitrea	Site	1	80.00	80.00	1.04	0.33	9827
	Habitat	3	3298.00	1099.30	21.81	0.06	833
	Shoreline (Site)	2	776.90	388.45	5.04	**0.01**	9935
	Site × Habitat	3	151.20	50.40	0.65	0.59	9960
	Shoreline (Site) × Habitat	6	5339.50	889.92	11.55	**0.01**	9951
	Residual	64	4929.60	77.03			
Capitella capitata	Site	1	1.51	1.51	0.41	0.56	9837
	Habitat	3	78.04	26.01	10.78	0.11	416
	Shoreline (Site)	2	26.83	13.41	3.65	**0.02**	9957
	Site × Habitat	3	7.24	2.41	0.66	0.64	9958
	Shoreline (Site) × Habitat	6	112.68	18.78	5.11	**0.01**	9941
	Residual	64	235.20	3.68			
Calopia imitata	Site	1	2060.50	2060.50	7.51	**0.01**	9849
	Habitat	3	10480.00	3493.40	8.18	0.08	840
	Shoreline (Site)	2	15430.00	7715.00	28.17	**0.01**	9959
	Site × Habitat	3	1281.80	427.28	1.56	0.21	9953
	Shoreline (Site) × Habitat	6	11319.00	1886.50	6.87	**0.01**	9945
	Residual	64	17562.00	274.40			
Littoraria luteola	Site	1	66.61	66.61	1.18	0.29	9851
	Habitat	3	1935.80	645.28	10.43	0.10	420
	Shoreline (Site)	2	1531.50	765.76	13.56	**0.01**	9946
	Site × Habitat	3	185.54	61.85	1.10	0.37	9954

Species	Source	d.f.	SS	MS	Pseudo-*F*	*P* (perm)	Unique perms
	Shoreline (Site) × Habitat	6	2002.00	333.66	5.91	**0.01**	9952
	Residual	64	3614.40	56.48			
Pyrgulina ceria	Site	1	0.61	0.61	0.04	0.84	9797
	Habitat	3	289.84	96.61	3.01	0.17	420
	Shoreline (Site)	2	240.13	120.06	8.43	**0.01**	9950
	Site × Habitat	3	96.34	32.11	2.25	0.08	9961
	Shoreline (Site) × Habitat	6	154.18	25.70	1.80	0.11	9952
	Residual	64	911.60	14.24			

Table S11. Results of *a posteriori* tests for differences in the abundance of key discriminating infaunal species identified by SIMPER in similar habitat types between levels of Shoreline Type (Site). Dashes represent cases where the species did not occur, and test was not possible. Statistically significant results (at α = 0.05) shown in bold.

Species	**Site**	**Habitat**	**d.f.**	***t***	***P* (perm)**	**Unique perms**
Mysella vitrea	Towra	ASU	1, 8	3.12	**0.03**	59
		Seagrass	1, 8	3.93	**0.02**	23
		Subtidal	1, 8	1.69	0.17	9
		Intertidal	1, 8	1.92	0.06	37
	Kurnell	ASU	1, 8	5.06	**0.01**	36
		Seagrass	1, 8	0.81	0.51	13
		Subtidal	1, 8	0.17	0.95	16
		Intertidal	1, 8	3.71	**0.01**	24
Capitella capitata	Towra	ASU	1, 8	2.21	0.01	12
		Seagrass	1, 8	0.89	0.73	3
		Subtidal	1, 8	0.63	1.00	2
		Intertidal	-	-	**-**	-
	Kurnell	ASU	1, 8	2.54	**0.05**	6
		Seagrass	-	-	-	-
		Subtidal	1, 8	0.45	1.00	2
		Intertidal	1, 8	1.00	1.00	1
Calopia imitata	Towra	ASU	1, 8	4.91	**0.01**	35
		Seagrass	1, 8	2.09	0.16	8
		Subtidal	1, 8	3.16	**0.05**	5
		Intertidal	1, 8	6.04	0.01	14
	Kurnell	ASU	1, 8	3.41	**0.01**	58
		Seagrass	1, 8	2.35	0.09	15
		Subtidal	1, 8	0.58	0.79	6
		Intertidal	1, 8	4.06	**0.01**	14

Species	**Site**	**Habitat**	**d.f.**	***t***	***P* (perm)**	**Unique perms**
Littoraria luteola	Towra	ASU	1, 8	2.54	**0.01**	12
		Seagrass	1, 8	1.57	0.44	2
		Subtidal	-	-	**-**	-
		Intertidal	1, 8	3.03	**0.01**	10
	Kurnell	ASU	1, 8	4.65	**0.01**	38
		Seagrass	-	-	**-**	-
		Subtidal	-	-	**-**	-
		Intertidal	1, 8	1.00	1.00	1

Table S12. Mean (SE) abundance of key discriminating infaunal species identified by SIMPER analysis within habitat types on unvegetated and mangrove shorelines within Towra Point and Kurnell sites (n=5 replicates). Dashes indicate no occurrence of the species.

Site	**Shoreline**	**Habitat**	**Species**			
			Mysella vitrea	*Calopia imitata*	*Capitella capitata*	*Littoraria luteola*
Towra	Unvegetated	ASU	41.80 (12.04)	0.80 (0.48)	6.40 (2.89)	-
		Seagrass	11.40 (1.91)	0.40 (0.4)	0.20 (0.2)	-
		Subtidal	1.60 (0.92)	-	0.20 (0.2)	-
		Intertidal	2.80 (0.86)	-	-	-
	Mangrove	ASU	4.00 (1.09)	81.40 (16.39)	-	23.40 (9.21)
		Seagrass	2.60 (1.16)	44.00 (20.81)	0.60 (0.4)	12.20 (7.74)
		Subtidal	3.80 (0.91)	3.00 (0.94)	0.60 (0.6)	-
		Intertidal	15.20 (6.4)	21.00 (3.47)	-	6.40 (2.11)
Kurnell	Unvegetated	ASU	30.00 (4.79)	2.40 (0.87)	3.80 (1.49)	0.60 (0.4)
		Seagrass	4.80 (1.65)	1.60 (1.02)	0.60 (0.4)	-
		Subtidal	5.20 (3.3)	2.80 (0.73)	0.20 (0.2)	-
		Intertidal	1.00 (0.31)	1.80 (0.37)	-	-
	Mangrove	ASU	5.00 (1.18)	44.80 (12.41)	-	26.60 (5.57)
		Seagrass	3.20 (1.06)	6.80 (1.95)	0.60 (0.4)	-
		Subtidal	4.60 (1.12)	2.20 (0.73)	0.40 (0.4)	-
		Intertidal	13.40 (3.32)	7.00 (1.22)	0.20 (0.2)	0.20 (0.2)

Table S13. Results of *a posteriori* tests for differences in the abundance of key discriminating infaunal species identified by SIMPER between Artificial Seagrass Units (ASUs) and other habitat types within levels of Shoreline Type (Site). Dashes represent cases where the species did not occur, and test was not possible. Statistically significant results (at α = 0.05) shown in bold.

Species	**Site / Shoreline**	**Comparison**	**d.f.**	***t***	***P* (perm)**	**Unique perms**
Mysella vitrea	Towra, Unvegetated	ASU, Seagrass	3, 8	2.49	**0.04**	56
		ASU, Subtidal	3, 8	3.33	**0.02**	63
		ASU, Intertidal	3, 8	3.23	**0.03**	56
	Towra, Mangrove	ASU, Seagrass	3, 8	0.88	0.11	10
		ASU, Subtidal	3, 8	0.14	**0.45**	7
		ASU, Intertidal	3, 8	1.72	**0.49**	18
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	4.97	**0.01**	45
		ASU, Subtidal	3, 8	4.26	**0.01**	41
		ASU, Intertidal	3, 8	6.03	**0.01**	20
	Kurnell, Mangrove	ASU, Seagrass	3, 8	1.13	0.33	10
		ASU, Subtidal	3, 8	0.25	0.86	10
		ASU, Intertidal	3, 8	2.38	**0.05**	24
Capitella capitata	Towra, Unvegetated	ASU, Seagrass	3, 8	2.14	**0.02**	16
		ASU, Subtidal	3, 8	2.14	**0.01**	16
		ASU, Intertidal	3, 8	2.21	**0.01**	12
	Towra, Mangrove	ASU, Seagrass	3, 8	1.50	0.44	2
		ASU, Subtidal	3, 8	1.00	1.00	1
		ASU, Intertidal	-	-	**-**	-
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	2.07	0.09	11
		ASU, Subtidal	3, 8	2.38	**0.05**	11
		ASU, Intertidal	3, 8	2.54	**0.05**	6
	Kurnell, Mangrove	ASU, Seagrass	3, 8	1.50	0.45	2
		ASU, Subtidal	3, 8	1.00	1.00	1

Species	Site / Shoreline	Comparison	d.f.	*t*	***P* (perm)**	Unique perms
		ASU, Intertidal	3, 8	1.00	1.00	1
Calopia imitata	Towra, Unvegetated	ASU, Seagrass	3, 8	0.63	1.00	2
		ASU, Subtidal	3, 8	1.60	0.44	2
		ASU, Intertidal	3, 8	1.63	0.44	2
	Towra, Mangrove	ASU, Seagrass	3, 8	1.41	0.17	64
		ASU, Subtidal	3, 8	4.77	**0.01**	62
		ASU, Intertidal	3, 8	3.60	**0.01**	78
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	0.59	0.64	9
		ASU, Subtidal	3, 8	0.35	0.86	8
		ASU, Intertidal	3, 8	0.63	0.71	6
	Kurnell, Mangrove	ASU, Seagrass	3, 8	3.02	**0.02**	60
		ASU, Subtidal	3, 8	3.43	**0.01**	53
		ASU, Intertidal	3, 8	3.03	**0.02**	61
Littoraria luteola	Towra, Unvegetated	ASU, Seagrass	-	-	**-**	-
		ASU, Subtidal	-	-	**-**	-
		ASU, Intertidal	-	-	**-**	-
	Towra, Mangrove	ASU, Seagrass	3, 8	0.93	0.40	27
		ASU, Subtidal	3, 8	2.54	**0.01**	12
		ASU, Intertidal	3, 8	1.80	0.11	39
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	1.50	0.44	2
		ASU, Subtidal	3, 8	1.50	0.45	2
		ASU, Intertidal	3, 8	1.50	0.44	2
	Kurnell, Mangrove	ASU, Seagrass	3, 8	4.77	**0.01**	14
		ASU, Subtidal	3, 8	4.77	**0.01**	14
		ASU, Intertidal	3, 8	4.73	**0.01**	23

Table S14. Results of univariate PERMANOVAs testing for differences in the abundance of key discriminating epifaunal species identified by SIMPER between Sites (2 levels, random: Towra Point and Kurnell), Shoreline types (2 levels, fixed, nested within Site: mangrove and unvegetated) and among Habitats (4 levels, fixed: artificial seagrass units (ASUs), natural seagrass, subtidal sediment and intertidal sediment). Statistically significant results (at α = 0.05) shown in bold.

Species	**Source**	**d.f.**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Dipolydora socialis	Site	1	2.81	2.81	1.61	0.22	9791
	Habitat	3	61.94	20.65	2.94	0.20	825
	Shoreline (Site)	2	2.73	1.36	0.78	0.48	9955
	Site × Habitat	3	21.04	7.01	4.01	**0.01**	9946
	Shoreline (Site) × Habitat	6	54.98	9.16	5.24	**0.01**	9954
	Residual	64	112.00	1.75			
Mysella vitrea	Site	1	2.11	2.11	0.68	0.42	9797
	Habitat	3	3.94	1.31	1.05	0.38	389
	Shoreline (Site)	2	3.03	1.51	0.49	0.63	9957
	Site × Habitat	3	3.74	1.25	0.40	0.75	9940
	Shoreline (Site) × Habitat	6	100.28	16.71	5.39	**0.01**	9954
	Residual	64	198.40	3.10			
Levinsenia gracilis	Site	1	0.31	0.31	0.11	0.75	9798
	Habitat	3	53.84	17.95	2.73	0.25	835
	Shoreline (Site)	2	18.93	9.46	3.21	0.06	9942
	Site × Habitat	3	19.74	6.58	2.23	0.09	9952
	Shoreline (Site) × Habitat	6	19.38	3.23	1.09	0.37	9947
	Residual	64	188.80	2.95			
Calopia imitata	Site	1	7.20	7.20	2.55	0.11	9346
	Habitat	3	96.70	32.23	13.25	**0.04**	794
	Shoreline (Site)	2	254.80	127.40	45.20	**0.01**	9943
	Site × Habitat	3	7.30	2.43	0.86	0.47	9959

Species	Source	d.f.	SS	MS	Pseudo-*F*	*P* (perm)	Unique perms
	Shoreline (Site) × Habitat	6	182.40	30.40	10.79	**0.01**	9950
	Residual	64	180.40	2.82			
Scoloplos simplex	Site	1	0.05	0.05	0.08	0.78	9674
	Habitat	3	19.40	6.47	35.27	**0.02**	725
	Shoreline (Site)	2	2.05	1.03	1.62	0.20	9944
	Site × Habitat	3	0.55	0.18	0.29	0.84	9959
	Shoreline (Site) × Habitat	6	13.75	2.29	3.63	**0.01**	9937
	Residual	64	40.40	0.63			

Table S15. Results of *a posteriori* tests for differences in the abundance of key discriminating epifaunal species identified by SIMPER in similar habitat types between levels of Shoreline Type (Site). Dashes represent cases where the species did not occur, and test was not possible. Statistically significant results (at α = 0.05) shown in bold.

Species	**Site**	**Habitat**	**d.f.**	***t***	***P* (perm)**	**Unique perms**
Dipolydora socialis	Towra	ASU	-	-	**-**	-
		Seagrass	1 ,8	1.98	0.13	5
		Subtidal	1, 8	1.94	0.10	13
		Intertidal	1, 8	1.00	1.00	1
	Kurnell	ASU	-	-	**-**	-
		Seagrass	1, 8	2.08	0.12	7
		Subtidal	1, 8	2.71	0.09	6
		Intertidal	1, 8	1.00	1.00	1
Mysella vitrea	Towra	ASU	1, 8	2.72	**0.03**	8
		Seagrass	1, 8	0.19	1.00	7
		Subtidal	1, 8	1.02	0.60	6
		Intertidal	1, 8	1.90	0.16	9
	Kurnell	ASU	1, 8	6.52	**0.01**	9
		Seagrass	1, 8	1.80	0.10	8
		Subtidal	1, 8	1.10	0.51	3
		Intertidal	1, 8	1.54	0.24	9
Calopia imitata	Towra	ASU	1, 8	11.69	**0.01**	12
		Seagrass	1, 8	1.54	0.27	5
		Subtidal	1, 8	0.80	0.69	6
		Intertidal	1, 8	10.59	**0.01**	11
	Kurnell	ASU	1, 8	4.53	**0.01**	11
		Seagrass	1, 8	0.83	0.57	6
		Subtidal	1, 8	1.42	0.22	6
		Intertidal	1, 8	3.39	**0.01**	10

Species	**Site**	**Habitat**	**d.f.**	***t***	***P* (perm)**	**Unique perms**
Scoloplos simplex	Towra	ASU	-	-	**-**	-
		Seagrass	1, 8	3.79	**0.03**	4
		Subtidal	1, 8	0.78	0.56	7
		Intertidal	1, 8	0.35	1.00	3
	Kurnell	ASU	-	-	**-**	-
		Seagrass	1, 8	6.32	**0.01**	6
		Subtidal	1, 8	0.67	**0.77**	5
		Intertidal	1, 8	0.63	1.00	1

Table S16. Mean (SE) abundance of key discriminating epifaunal species identified by SIMPER analysis within habitat types on unvegetated and mangrove shorelines within Towra Point and Kurnell sites (n=5 replicates). Dashes indicate no occurrence of the species.

Site	**Shoreline**	**Habitat**	**Species**			
			Dipolydora socialis	*Mysella vitrea*	*Calopia imitata*	*Scoloplos simplex*
Towra	Unvegetated	ASU	-	3.60 (1.08)	0.20 (0.2)	-
		Seagrass	0.20 (0.2)	2.40 (0.6)	0.60 (0.4)	1.40 (0.24)
		Subtidal	5.00 (1.70)	2.80 (1.32)	0.80 (0.37)	1.00 (0.77)
		Intertidal	-	0.40 (0.24)	-	0.40 (0.40)
	Mangrove	ASU	-	0.60 (0.24)	6.60 (0.51)	-
		Seagrass	1.60 (0.68)	2.20 (0.86)	1.60 (0.51)	0.20 (0.20)
		Subtidal	1.40 (0.75)	1.40 (0.40)	1.60 (0.92)	1.80 (0.66)
		Intertidal	0.20 (0.20)	2.80 (1.24)	8.60 (0.81)	0.60 (0.40)
Kurnell	Unvegetated	ASU	-	3.80 (0.58)	0.20 (0.20)	-
		Seagrass	0.40 (0.24)	0.80 (0.20)	1.40 (0.75)	2.00 (0.32)
		Subtidal	2.00 (0.63)	1.40 (0.51)	0.40 (0.24)	1.00 (0.45)
		Intertidal	-	0.80 (0.37)	-	0.40 (0.24)
	Mangrove	ASU	-	-	4.20 (0.86)	-
		Seagrass	2.60 (1.03)	3.20 (1.32)	0.60 (0.60)	-
		Subtidal	0.20 (0.20)	0.80 (0.20)	2.20 (1.24)	1.40 (0.40)
		Intertidal	0.20 (0.20)	2.80 (1.24)	6.20 (1.83)	0.20 (0.20)

Table S17. Results of *a posteriori* tests for differences in the abundance of key discriminating epifaunal species identified by SIMPER between Artificial Seagrass Units (ASUs) and other habitat types within levels of Shoreline Type (Site). Dashes represent cases where the species did not occur, and test was not possible. Statistically significant results (at α = 0.05) shown in bold.

Species	**Site / Shoreline**	**Comparison**	**d.f.**	***t***	***P* (perm)**	**Unique perms**
Dipolydora socialis	Towra, Unvegetated	ASU, Seagrass	3, 8	1.00	1.00	1
		ASU, Subtidal	3, 8	2.94	**0.01**	12
		ASU, Intertidal	-	-	**-**	-
	Towra, Mangrove	ASU, Seagrass	3, 8	2.36	**0.05**	5
		ASU, Subtidal	3, 8	1.87	0.16	4
		ASU, Intertidal	3, 8	1.00	1.00	1
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	1.63	0.44	2
		ASU, Subtidal	3, 8	3.16	**0.05**	4
		ASU, Intertidal	-	-	**-**	-
	Kurnell, Mangrove	ASU, Seagrass	3, 8	2.53	0.05	5
		ASU, Subtidal	3, 8	1.00	1.00	1
		ASU, Intertidal	3, 8	1.00	1.00	1
Mysella vitrea	Towra, Unvegetated	ASU, Seagrass	3, 8	0.97	0.46	8
		ASU, Subtidal	3, 8	0.47	0.75	10
		ASU, Intertidal	3, 8	2.90	**0.03**	9
	Towra, Mangrove	ASU, Seagrass	3, 8	1.79	0.17	6
		ASU, Subtidal	3, 8	1.71	0.23	4
		ASU, Intertidal	3, 8	1.74	0.18	8
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	4.87	**0.01**	8
		ASU, Subtidal	3, 8	3.10	**0.04**	8
		ASU, Intertidal	3, 8	4.33	**0.02**	8
	Kurnell, Mangrove	ASU, Seagrass	3, 8	2.43	**0.05**	6
		ASU, Subtidal	3, 8	4.00	**0.05**	3

Species	**Site / Shoreline**	**Comparison**	**d.f.**	***t***	***P* (perm)**	**Unique perms**
		ASU, Intertidal	3, 8	2.26	0.16	4
Calopia imitata	Towra, Unvegetated	ASU, Seagrass	3, 8	0.89	0.72	3
		ASU, Subtidal	3, 8	1.41	0.40	3
		ASU, Intertidal	3, 8	1.00	1.00	1
	Towra, Mangrove	ASU, Seagrass	3, 8	6.93	**0.01**	12
		ASU, Subtidal	3, 8	4.72	**0.02**	13
		ASU, Intertidal	3, 8	2.09	0.11	8
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	1.55	0.30	5
		ASU, Subtidal	3, 8	0.63	1.00	2
		ASU, Intertidal	3, 8	1.00	1.00	1
	Kurnell, Mangrove	ASU, Seagrass	3, 8	3.43	**0.02**	11
		ASU, Subtidal	3, 8	1.32	0.27	11
		ASU, Intertidal	3, 8	0.99	0.48	11
Scoloplos simplex	Towra, Unvegetated	ASU, Seagrass	3, 8	5.72	**0.01**	4
		ASU, Subtidal	3, 8	1.29	0.44	2
		ASU, Intertidal	3, 8	1.00	1.00	1
	Towra, Mangrove	ASU, Seagrass	3, 8	1.00	1.00	1
		ASU, Subtidal	3, 8	2.71	**0.05**	5
		ASU, Intertidal	3, 8	1.50	0.44	2
	Kurnell, Unvegetated	ASU, Seagrass	3, 8	6.32	**0.01**	6
		ASU, Subtidal	3, 8	2.24	0.16	3
		ASU, Intertidal	3, 8	1.63	0.45	2
	Kurnell, Mangrove	ASU, Seagrass	-	-	**-**	-
		ASU, Subtidal	3, 8	3.50	**0.05**	4
		ASU, Intertidal	3, 8	1.00	1.00	1

Chapter 4: Assessing risk of estuarine ecosystem collapse

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Abstract

Estuarine ecosystems are increasingly threatened by coastal development and climate change. The large number of estuaries globally necessitates risk assessment to prioritise conservation efforts. Schemes for assessing risk of ecosystem collapse have been designed around terrestrial ecosystems, often defined by a single characteristic vegetation type, with their applicability to estuaries unclear. Here we consider the causes and symptoms of estuarine ecosystem collapse and assess, using a case study of the Chesapeake Bay, the applicability of ecosystem-level risk assessments to estuarine ecosystems, typified by mosaics of habitats. Functional estuaries are characterised by habitat heterogeneity and connectivity, maintenance of constituent habitats through recruitment, and a complex trophic structure including apex predators. Additionally, primary production and biomass are dominated by benthic, as opposed to pelagic, species. Hence, homogenisation of habitat types, decreased connectivity, recruitment failure, loss of apex predators and a decreased ratio of benthic to pelagic biomass may be symptoms of a trajectory towards collapse. In terrestrial ecosystems, criteria used for assessing risk of ecosystem collapse include declining or restricted distribution of ecosystems, degradation of the abiotic environment, changes in species composition and declining ecological function. As the boundaries of estuaries are typically defined by topography, rarely do significant changes in the area of the ecosystem occur. Furthermore, because the extent of estuaries is typically small, assessments based on area of occupancy may over-inflate risk. Instead, criteria based on abiotic and biotic changes, many of which are documented through monitoring programs, may be most useful for risk assessments of estuarine ecosystems.

Keywords

Biodiversity assessment; Threatening processes; Risk assessment; IUCN Red List of Ecosystems; Habitat mosaic

1. Introduction

As ecotones at the interface of the terrestrial, marine and fluvial environments, estuaries support unique species assemblages and ecological interactions (Remane, 1934, and Elliott and Whitfield, 2011). Estuaries serve as vital nursery areas for many species of commercial importance provide food and raw materials, maintain clean water, sequester carbon, protect shorelines, control erosion, and provide recreational and aesthetic amenity (Barbier et al., 2011). However, due to their high value, estuaries are often under intense pressure from human populations (Hughes et al., 2005, Worm et al., 2006 and Halpern et al., 2008). Conservation strategies are required to maintain estuarine biodiversity and important ecosystem services.

With thousands of estuaries globally and limited conservation funding available, mechanisms are needed to triage potential conservation efforts (Brooks et al., 2006). Biodiversity risk assessments allow decision makers to prioritise critical species and/or areas of need. Risk assessments have traditionally been focussed at the species level (Rodrigues et al., 2006). However, many researchers have suggested that risk assessment at the ecosystem scale may be more efficient than a species-by-species approach and also capture the loss of important functions often not visible in species-based assessments (Nicholson et al., 2009; and Keith et al., 2013). Because of the ease of defining their spatial boundaries, estuaries are commonly used as management units (Imperial and Hennessy, 1996 and Elliott and McLusky, 2002) and may provide a suitable scale for risk assessments.

Several schemes have been advanced for assessing risk of collapse at the ecosystem-scale (Nicholson et al., 2009). The most recent such scheme is the International Union for the Conservation of Nature (IUCN) Red List of Ecosystems. Launched in 2013 (Keith et al., 2013), the Red List of Ecosystems has been widely adopted across continents and ecosystem types (e.g. Keith et al., 2013, Payet et al., 2013, Auld and Leishman, 2015, Clark et al., 2015 and Murray et al., 2015). Risk assessment criteria utilised by such schemes include declining or restricted distribution, degradation of the abiotic environment, changes in species composition and declining ecological function as predictors of ecosystem collapse (Nicholson et al., 2009 and Keith et al., 2013). For the purpose of risk assessment, the distribution of an ecosystem is usually defined by the area of occupancy of a dominant group of foundation species, for example a vegetation type (Keith et al., 2013). This approach works well for terrestrial ecosystems where vegetation maps are available to define and track the borders of ecosystems. This approach may also be applicable to other ecosystems such as coral reefs, which are dominated by a single group of foundation species. However, its applicability to estuarine ecosystems that are often constrained by topography and/or bathymetry, encompass mosaics of different habitat types (e.g. sedimentary bottoms, vegetation patches, shellfish beds) and have upper boundaries defined by the extent of tidal influence (Cameron and Pritchard, 1963), is uncertain. In estuarine ecosystems, the connectivity and persistence of multiple types of habitat patches may be particularly important as many species utilise multiple habitats within a landscape throughout their life history to obtain different resources (Jackson et al., 2001).

Here we consider the applicability of the IUCN Red List of Ecosystems risk assessment criteria to estuarine ecosystems. We examine common causes of decline in estuarine ecosystems and suggest a suite of indicators that are predictive of collapse and that may be used by conservation managers. A retrospective risk assessment of the estuarine ecosystem of Chesapeake Bay, in the eastern United States, conducted for the year 1980, is presented as a proof-of-concept for the proposed indicators. We identify incongruities in applying the proposed indicators to the IUCN Red List of Ecosystems risk assessment criteria, as being representative of the most common criteria proposed in risk assessment schemes and discuss potential solutions to these incompatibilities.

2. State Change in Estuarine Ecosystems

Effective risk assessment of ecosystem collapse requires knowledge of the range of conditions across which ecosystems may be considered functional as well as a defined end-state, beyond which they are no longer functional and collapse has occurred (Keith et al., 2013). An understanding of both functional and collapsed states allows patterns of change that are predictive of collapse at the scale of whole estuaries to be identified.

2.1. Features of Functional Estuaries

Functional estuaries contain a mosaic of distinct habitats, each of which is of sufficient area, complexity and number to support characteristic biota and key ecosystem services and to resist disturbance (Simenstad et al., 2006). Among and within habitat types there is connectivity of resources and species. Functional biogenic habitat patches are maintained by successful recruitment over time, facilitated by connectivity among habitat patches (Fig. 1).

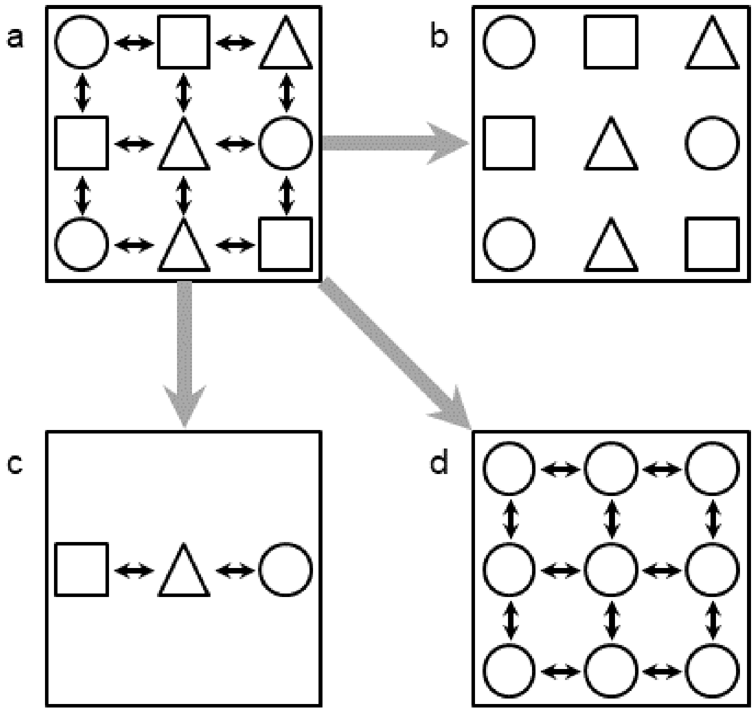

Figure 1. Conceptual diagram of functional (a) and collapsed (b-d) mosaic ecosystems. Shapes represent different habitat types and black arrows represent connectivity. In a functional mosaic ecosystem (a) there is heterogeneity of habitat types, connectivity among and within habitats, and sufficient area and complexity of each habitat type to sustain key species and ecological functions. Collapse of mosaic ecosystems may result from: (b) loss of connectivity between or among habitats, perhaps as a result of the construction of physical barriers such as barrages, breakwaters, or weirs, or the development of environmental barriers such as low dissolved oxygen or altered patterns of currents; (c) reduction in the area or complexity of key habitats, as a result of habitat destruction (shown) or fragmentation, below thresholds required to sustain key biodiversity and its functions; and/or (d) homogenisation of the habitat mosaic.

Functional diversity in estuarine landscapes is a product of both species-diversity within habitats (alpha diversity) and the variation present across the entire habitat-mosaic (beta diversity) (Whittaker, 1960). Alpha diversity is maximised where total habitat area is large and habitat is complex (Hewitt et al., 2005). The majority of physically complex habitat in estuaries is biogenic, such as seagrass meadows, oyster reefs or mangrove forests (Hewitt et al., 2008). These ecosystem engineers modify the abiotic environment by providing substrates, creating habitat and/or altering the flow of nutrients and energy through the system (Jones et al., 1997 and Worm et al., 2006). Beta diversity is driven by the level of differentiation between the habitats present. Different habitat types maintain diverse ecological functions by supporting either different species or differing densities of taxa representative of functional groups (Hewitt et al., 2008). The presence of multiple patches of each habitat type provides potential sources of recolonisation as insurance against environmental perturbations (Loreau et al., 2003).

In functional estuarine ecosystems, there is strong spatial and temporal connectivity within and between the component parts of the habitat mosaic driven by geographic proximity, water currents, energy flows and the migration of organisms (Sheaves et al., 2007). Spatial connectivity facilitates the migration of organisms and reproductive propagules/larvae between habitats, increasing colonisation, gene-flow and trophic relays as well as the range of biotic interactions and processes present in the system (Sheaves, 2009). Strong temporal connectivity facilitates the presence of species that utilise multiple habitats at different times of the day or year and in different phases of their life history (Sheaves, 2009).

In ecosystems, functional groups generally exist within a single trophic level (Hairston, 1960). Therefore, functional diversity is maximised in complex trophic webs comprising multiple levels. The persistence of complex trophic webs relies heavily on benthic primary production to supply energy to higher trophic levels and the presence of efficient pathways for energy flow (Kemp et al., 2001). In functional estuaries, primary production is dominated by benthic taxa such as seagrasses, saltmarsh, mangroves and microphytobenthos (Jackson et al., 2001). Where alpha and beta diversity are high, trophic specialists, who promote trophic transfer of energy, are generally present (Jackson et al., 2001 and Clavel et al., 2011).

Abiotic conditions (such as salinity, water clarity, pH level, oxygen level and temperature) in functional estuaries are dynamic but remain within a range that allows characteristic biota to persist (Hewitt et al., 1997). Some euryhaline and eurythermal species are able to tolerate direct exposure to these variable environmental conditions, but the persistence of others is dependent on the occupancy of less variable microhabitats, provided by ecosystem engineers (Jones et al., 1997 and Stachowicz, 2001) or, if the organism is mobile, migration into more favourable conditions (Barletta et al., 2008).

2.2. Features of Collapsed Estuaries

In collapsed estuaries, the heterogeneity of the habitat-mosaic is generally reduced, and biogenic habitat patches may be insufficiently large, numerous or complex to perform vital ecological functions, such as recruitment, habitat provisioning or nutrient cycling (Eggleston et al., 1999 and Hovel and Lipcius, 2001). Alternatively, habitats may be reduced to a single location, reducing functional resilience (Loreau et al., 2003) (Fig. 1). The prevailing trophic structure is simplified, containing fewer trophic levels and lower species richness, particularly amongst apex predators and trophic specialists (Jackson et al., 2001 and Clavel et al., 2011). Lower species richness reduces ecological functionality and decreases functional resilience to environmental perturbation (Loreau et al., 2003). Often there is a concomitant shift from benthic to pelagic biomass in the trophic web, particularly at the level of primary producers (Wu, 2002, Smith, 2003 and Krause-Jensen et al., 2012) (Fig. 2). Invasive species, particularly in the form of ecosystem engineers or predatory species, are often present and act to alter existing trophic structures (Crooks, 2002). For example, the 1993 introduction of the invasive algae *Caulerpa racemosa* var. *cylindracea* to the Mediterranean coast of Tuscany caused loss of beta diversity in the region (Piazzi and Balata, 2008).

The restricted size of individual estuaries renders them highly vulnerable to perturbations large enough to affect the total ecosystem. Many collapsed estuaries display degraded bottom sediment and water conditions (Diaz, 2001, Smith, 2003 and Baird et al., 2004). Concentrations of pollutants, such as toxins or nutrients, may be enhanced, the latter of which may exacerbate the extent or severity of hypoxic conditions (Diaz, 2001, Kennish, 2002 and Smith, 2003). Water clarity, strongly associated with water quality, may be altered from its characteristic state, generally in a negative direction, altering the penetration of light (Smith, 2003). Minimum, maximum and mean values of salinity, temperature, light, noise and pH may fluctuate outside the tolerance range of characteristic biota or established patterns of temporal heterogeneity may become disrupted (Jackson, 2001). For example, temporal heterogeneity is reduced where Intermittently Closed and Open Lakes and Lagoons (ICOLLs), a subclass of estuary that periodically become disconnected from the ocean by a sandbar, are permanently trained open, causing reduced variability in salinity, temperature and other abiotc conditions (Dye, 2005, Schallenberg et al., 2010 and Garside et al. 2014).

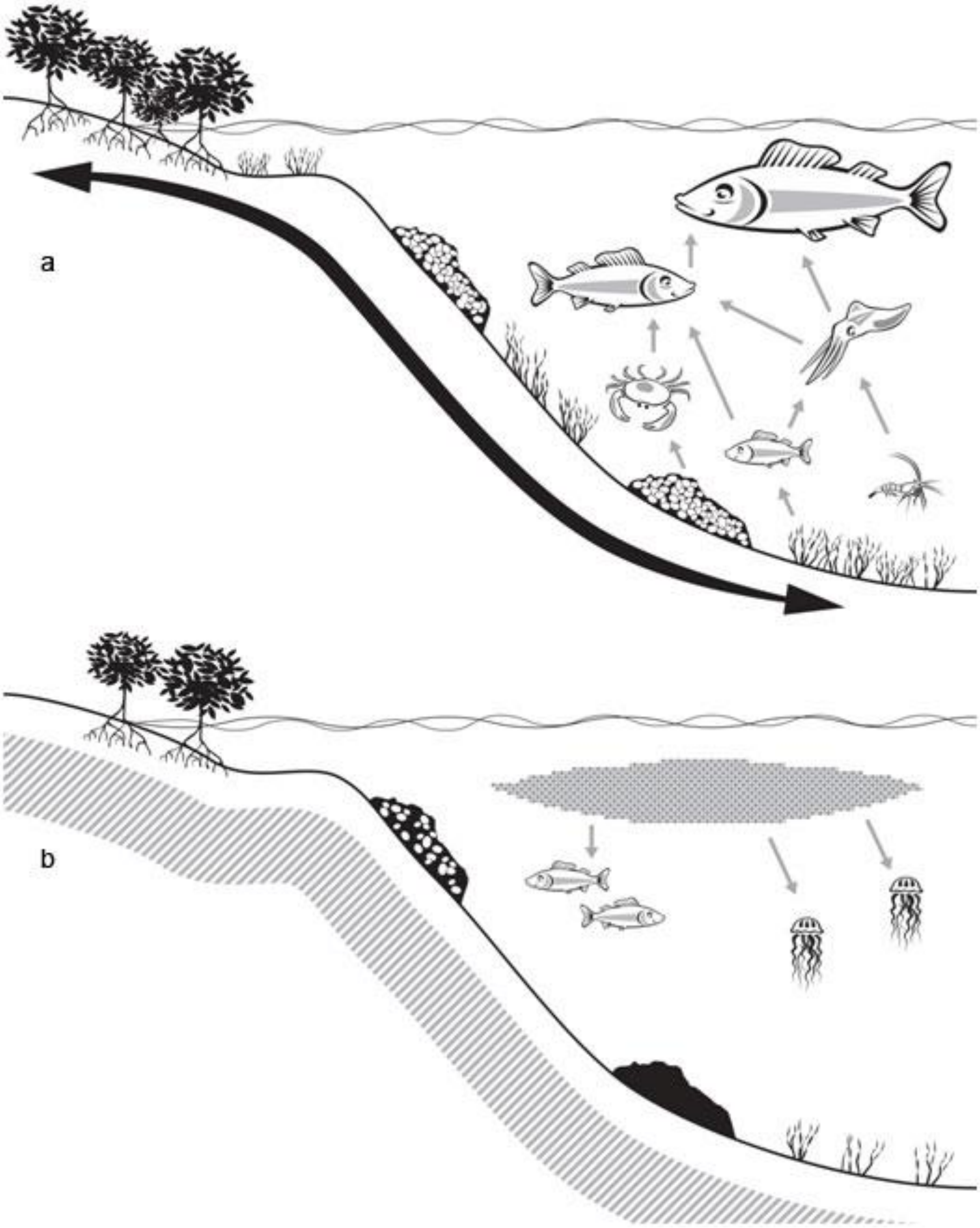

Figure 2. Conceptual diagram of food-web structure in (a) functional and (b) collapsed estuarine, habitat-mosaic, ecosystems. The black arrow indicates connectivity; grey arrows indicate trophic transfer. In functional estuarine ecosystems, production is dominated by benthic taxa and there is a diversity of habitat types which support a food web composed of multiple trophic levels. In collapsed estuarine ecosystems, production is dominated by pelagic taxa and reduced heterogeneity and connectivity of benthic habitats results in vertically compressed food webs.

3. Causes of estuarine ecosystem collapse and relevant indicators

IUCN Red List of Ecosystems uses five criteria to assess the risk of collapse in ecosystems (Keith et al., 2013). Criterion A evaluates risk based on decline in the distribution of the ecosystem. Criterion B is based on the restricted geographical distribution of an ecosystem, with a small area of occupancy enhancing extinction risk, when coupled with evidence of exposure of the estuary to stochastic processes or to ongoing human modification. Criterion C assesses risk based on degradation of local abiotic conditions to which characteristic biota respond. Criterion D uses changes to intra- and inter-specific interactions that disrupt characteristic biota (Keith et al., 2013). The final IUCN criterion (E) differs from the other four in utilising a mathematical modelling approach to quantify the risk of ecosystem collapse.

The high level of complexity inherent in ecosystems precludes the monitoring of all components. Therefore, measurable proxy variables are used as indicators of larger-scale processes within ecosystems (Dale and Beyeler, 2001). Effective indicators for assessing risk of ecosystem collapse may be abiotic variables to which characteristic biota are known to respond in a predictable manner, or metrics of abundance or richness in characteristic biota, whose relationship with community structure are understood (Dale and Beyeler, 2001 and Keith et al., 2013).

As the pathway of collapse is not the same in all estuarine ecosystems, appropriate indicators should be selected based on knowledge of the key local processes, interactions and threats (Keith et al., 2013). In the following sections, we discuss possible causes of estuarine ecosystem decline under each of the assessment criteria, A, B, C and D and discuss potential indicators (Table 1). High quality, long-term datasets are required to determine whether contemporary conditions lie within the bounds of natural variability in the state of an ecosystem or represent a trajectory of change toward collapse (Keith et al., 2013).

Table 1. Examples of indicator variables for use in IUCN Red List of Ecosystems risk assessment of estuaries.

IUCN Criterion	**Degradation process**	**Indicator variable(s)**
A. Decline in distribution	Land reclamation, over-extraction of water, sedimentation	Total area
B. Restricted distribution	Small size, enhancing risk of entire ecosystem being influenced by natural or human perturbations	Total area (only useful in cases where other criteria also show risk of collapse)
C. Degraded abiotic conditions	Modification of freshwater, wave and/or tidal influence by processes such as over-extraction of water, estuarine entrance training, or dredging and sea-level rise, resulting in changes in the mean or variance in environmental conditions that determine species' fundamental niches	Mean (or variation in) salinity, temperature, pH; flushing time; sea-level
	Structural simplification of microhabitats by replacement of complex rocky reefs with seawalls and artificial structures	Perimeter of estuary with shoreline armouring; area of artificial habitats; indices of habitat complexity.
	Contamination of estuary with toxic pollutants from industry (e.g. dioxins, heavy metals, poly aromatic hydrocarbons), agriculture (e.g. herbicides, pesticides) or urban settlements in surrounding catchment; underwater noise and artificial light pollution.	Concentrations of pollutant in water and/or sediments; flux and wavelengths of artificial light; decibels and frequency of underwater noise
	Eutrophication, resulting from agricultural or urban activities, enhancing nutrient inputs.	Chlorophyll-*a*; dissolved oxygen concentrations of bottom waters
	Reduced light penetration as a result of algal blooms, sedimentation or enhanced suspended solids	Turbidity; Secchi depth; concentrations of suspended solids
	Modification of sediment inputs from land-clearing, damming and other mechanisms	Mean (or variance in) sediment grain size; sedimentation rates; sediment organic content
D. Disrupted biotic	Homogenisation of habitats, possibly by replacement of natural	Indices of habitat diversity

IUCN Criterion	Degradation process	Indicator variable(s)
interactions	with artificial substrates, species invasion or habitat destruction	
	Reduction in function of habitat patches, caused by reduction in size, complexity and/or vertical elevation	Size of habitat patches; indices of fragmentation; indices of habitat complexity; vertical elevation of biogenic reefs; density of key structural elements
	Loss of connectivity among habitats, as a result of construction of coastal barriers, altered circulation patterns and/or increased distances among habitat patches	Fluxes; timing, frequency and duration of species movements among habitat patches; genetic diversity of key taxa.
	Alteration of species composition	Species richness; dissimilarity measures that take into consideration species identity; dominance and diversity indices; abundance of keystone or characteristic species.
	Altered trophic structure, as a result of removal of key taxa (i.e. over-harvest of top predators; declines in populations of ecosystem engineers) or altered resource availability	Number of trophic levels; ratio of benthic to pelagic biomass; food web structure; interaction strengths; predator abundance.

3.1. Criterion A: Declining Distribution

Estuarine ecosystems are typically constrained by geomorphology and topography, rather than the distributions of defining biogenic habitats, and respond to few perturbations through decline in area. Some land reclamation activities or loss of freshwater input may lead to a loss of total area. Sea-level rise or shifts in the balance of marine to freshwater inputs may serve to move the landward boundary of estuaries, typically defined as the upper limit of tidal influence or saltwater intrusion (Pritchard, 1967 and Elliott and McLusky, 2002).

3.2. Criterion B: Restricted Distribution

Criterion B of the Red List of Ecosystems, that determines threat status based on restriction in the distribution of an ecosystem (Keith et al., 2013), may conflate assessments of the risk of estuarine ecosystems collapsing. Under criterion B1, an ecosystem with a total area of ≤ 2000km^2 would be assigned the threat status of *Critically Endangered* as would an ecosystem present at only single location, where it is prone to stochastic events or ongoing human impact (Keith et al. 2013). Most assessments done on individual estuaries will fall into this category. For example, only three of the 973 estuaries included in the 1998 Australian National Land and Water Resources Audit have areas larger than 2000km^2 (OzCoasts, 2015). Even the Chesapeake Bay, the largest estuary in the USA, is classified as *Endangered* when evaluated on the basis of restricted distribution alone.

3.3. Criterion C: degradation of abiotic conditions

Criterion C, assessing the risk of ecosystem collapse based on changes in abiotic variables, is likely to be more powerful in estuaries than either Criterion A or B. Because of their proximity to human population centres, estuaries often experience significant collateral damage from coastal development (Kennish, 2002). Land-use changes within catchments can result in increased run-off of sediments, nutrients and other pollutants (Bowen and Valiela, 2001). The causative links between abiotic variables and characteristic biota are well studied for many of the highly urbanised estuaries of the world and, in many estuaries, government-mandated water-quality monitoring programs provide time-series data on relevant abiotic indicators (Table 2).

Pollutants, including greenhouse gases, phosphates and nitrates, heavy metals, plastic debris, polyaromatic hydrocarbons, leachate from acid sulphate soils, as well as sound and light, have been implicated in altering the physico-chemical conditions of estuaries that determine ecosystem structure and function (Tomlinson et al., 1980, Long et al., 1995, Cloern, 2001, Kennish, 2002, Slabbekoorn et al., 2010 and Becker et al. 2013). Pollutants may directly act on estuarine ecosystems or, in the case of greenhouse gases, indirectly, by changing the Earth's climate system. Observed and physico-chemical changes to estuaries as a result of greenhouse gas emissions include increased temperatures, sea-level rise, increased variability in salinity due to and altered local rainfall patterns, changes in local sediment transport regimes, as well as increased frequency of extreme weather events (Sheaves et al., 2007 and Najjar et al., 2010).

Table 2. Abiotic variables relevant to estuarine biota measured under government-mandated water-quality monitoring programs.

Region	**Regulatory framework**	**Monitoring agency**	**Abiotic variables measured**	**Source**
European Union	Water Framework Directive (Annex V)	Individual member nations	Nutrient levels, hazardous substances, organic enrichment, commercial fishing	European Environment Agency, 2015
USA	Federal Water Pollution Control Act (1972) (Section 320)	National Estuary Program	Conductivity (salinity), pH, temperature, dissolved oxygen (DO), turbidity and water level	USEPA, 2015
	National Estuarine Eutrophication Assessment	National Oceanic and Atmospheric Administration + National Ocean Service	Eutrophication levels	National Centers for Coastal Ocean Science, 2016
New Zealand	National River Water Quality Network	National Institute of Water and Atmospheric Research	Dissolved oxygen, temperature, pH, conductivity, visual clarity, turbidity, coloured dissolved organic matter, total and dissolved nitrogen and phosphorus, river flow	National Institute of Water and Atmospheric Research, 2013
Australia	National Water Quality Management Strategy	State and regional governments	Total phosphorus, total nitrogen, chlorophyll-*a*, turbidity, dissolved oxygen, pH, temperature, chemical contaminants or toxicants	Australian Government Department of the Environment, 2015
	National Land and Water Resources Audit	OzCoasts	Geomorphic measurements, anthropogenic modification level, tidal regime	OzCoasts, 2015
India	Water (Prevention and Control of Pollution) Act (1974)	Ministry of Environment and Forests	Temperature, pH, conductivity, dissolved oxygen, toxic metals, persistent organic pollutants	Ministry of Environment and Forests, 2008
Canada	Marine Water Quality	Environment and	Sewage and industrial waste level, agricultural runoff, faecal	Environment and

Region	Regulatory framework	Monitoring agency	Abiotic variables measured	Source
	Monitoring Program	Climate Change Canada	coliform level	Climate Change Canada, 2014
City of Cape Town (South Africa)	Local government authority	Water Quality Monitoring Programme	Conductivity, pH, dissolved oxygen, total suspended solids, nitrogen, total ammonia, un-ionised ammonia, phosphorus, chlorophyll-*a*	City of Cape Town, 2016

Among pollutants, nutrient enrichment, is broadly regarded as one of the greatest threats to estuarine ecosystems (Thrush et al., 2004 and Kennish, 2002). Eutrophication, the over-stimulation of macrophytic growth by enhanced nutrient supply, has been causally linked to the development of hypoxic and anoxic conditions in bottom waters as well as local population extirpations (Breitburg, 2002 and Kennish, 2002). Phytoplankton blooms can block the light available to benthic species and secrete compounds that are toxic to other species (Cloern, 2001 and Breitburg, 2002). The deterioration of bottom-waters by decreased light penetration and development of hypoxia can lead to shifts from benthic to pelagic biomass and altered trophic structures (Harding, 1994 and Breitburg, 2002). Reductions in light availability due to phytoplankton blooms may not only have major impacts on benthic photosynthesis but also predator-prey interactions that depend on visual detection (Steel and Neuhausser, 2002).

In addition to introducing pollutants, urban environments introduce built infrastructure to estuarine environments (Dafforn et al., 2015a). Seawalls, groynes and breakwaters, protect coastal development against erosion and/or inundation, pontoons, wharfs, jetties and pilings support estuarine recreational activities (e.g. boating, swimming) and shipping, fishing, and aquaculture industries, introduce novel structures to estuarine waters (see Dafforn et al., 2015a, b). At the very least, these modify physico-chemical conditions at the site of their construction (Dafforn et al. 2015a), but they can also modify the physico-chemical environment over much larger scales where they interfere with flow and resource transport (Bishop et al., in press). For example, infrastructure, such as dams and weirs, constructed for water and flood management, can modify freshwater flows, and hence associated variables such as salinity and sediment and nutrient supply, as well as water temperature (Ibàñez et al., 1996 and Yang et al., 2006). Changes in the supply of resuspended fine sediments may, like phytoplankton blooms, impact estuarine assemblages by modifying turbidity.

Physico-chemical changes to estuaries may modify their ecosystems both as a consequence of lethal effects, and sub-lethal effects such as behavioural changes, changes in growth rate or reproductive success, and the suppression of immune responses (Kennish, 2002 and Ivar do Sul and Costa, 2013). Lethal effects occur where physico-chemical conditions move outside of the range tolerable by an individual, and the individual is unable to adapt or migrate to more favourable conditions (Breitburg, 2002 and Kennish, 2002). Both lethal and sub-lethal effects of physico-chemical changes may propagate through communities as a consequence of indirect effects, including competitive release from competitive dominants that are negatively affected, alteration of trophic structures and behaviourally-mediated indirect interactions (Sorte et al., 2010, Selleslagh et al., 2012 and Becker et al., 2013). The propensity of heavy metals and some other contaminants to bioaccumulate and biomagnify drives severe impacts at all trophic levels, with these impacts being greatest at higher trophic levels (Bryan, 1971).

Where the dose-response relationship between pollutants and ecological impacts has been causally determined, concentrations of the pollutant in water and/or sediments, the flux and wavelengths of artificial light, or the decibels and frequency of underwater noise may be directly measured as an indicator of the ecological response. In the case of eutrophication, however, increased phytoplankton biomass may be a more appropriate indicator of eutrophication than direct measures of nutrient concentrations as biological systems rapidly assimilate nutrients (Scanes et al., 2007). Phytoplankton abundance is easily tracked by measuring levels of chlorophyll-*a* in the water column and is already utilised as an indicator of eutrophication in many jurisdictions (USEPA, 2008 and Ferreira et al., 2011). In utilising chlorophyll-*a* concentrations as an indicator of eutrophication, it should be noted that concentrations can display considerable natural variability among seasons or wet and dry periods (Ferreira et al., 2011). The use of peak chlorophyll-*a* measures is suggested in systems where high levels persist for extended periods whereas annual mean values may have greater diagnostic power in systems where peak values are experienced only briefly. In deeper sections of estuaries, that are prone to seasonal stratification of water, dissolved oxygen concentration may also be a useful indicator of severe eutrophication.

Secchi discs are an economical method for obtaining robust measures of turbidity and their use requires minimal training (Steel and Neuhausser, 2002). A primary concern in monitoring turbidity should be the length of time when turbidity decreases light penetration below the minimum level at which benthic photosynthesis is possible in the local system. This will require accurate knowledge of the tolerance of local benthic macrophytes, such as seagrass, for light deprivation and their average depth of distribution. Temporal variability in turbidity due to seasonal variation in wind, rainfall or plankton abundance should be considered in sampling regimes. Where relationships between built infrastructure and damage to estuarine ecosystems are well understood, changes through time in the number and/or aerial coverage of such structures may serve as indicators.

3.4. Criterion D: Disrupted biological interactions

Criterion D of the IUCN Red List of Ecosystems examines disruptions in biotic interactions and processes and is potentially the strongest diagnostic tool in estuarine risk assessment, although data sets applicable to Criterion C may be more readily available. Estuarine ecosystems, where high levels of facilitation are common and there is strong top-down trophic regulation, are particularly susceptible to disruption of the biotic compartment of the ecosystem (Jackson et al., 2001, Stachowicz, 2001, Dobson et al., 2006 and Keith et al., 2013). Given the strong effects of resident species on the abiotic environment, changes in biotic communities may precede and drive environmental changes assessed by Criterion C in many estuaries.

Biogenic habitats, such as saltmarshes, mangroves, shellfish reefs and seagrass beds support dense and diverse communities, as a consequence of their provision of structural habitat, and their amelioration of biotic and abiotic stressors (Boström et al., 2011). Degradation of biogenic habitat may lead to biodiversity loss, as a consequence of a decrease in habitat area and/or a decrease in habitat quality and connectivity, for example, as a result of fragmentation (Boström et al., 2011). Below a certain size threshold, individual patches may become too small to be self-sustaining, support significant biodiversity, or to perform their key functional roles in ameliorating biotic and abiotic stressors (Hovel and Lipcius, 2001). Changes in habitat density and morphology may also influence its capacity to ameliorate biotic and abiotic stressors (Boström et al., 2011 and de Juan and Hewitt, 2011). Fragmentation of habitat can result in a loss of connectivity between and among habitats, inhibiting colonisation processes, and thereby reducing resilience to environmental perturbations (Loreau et al., 2003 and Lundquist et al., 2010). Spatial connectivity among estuarine habitat patches may also be lost as a consequence of the introduction of physical barriers (such as hard engineering structures or low water levels) or chemical barriers to migration (such as hypoxic, toxic or hypersaline zones) (Boström et al., 2011, de Juan and Hewitt, 2011 and Bishop et al., in press).

In estuaries, as in other marine systems, over extraction of top predators can also have disproportionate influence on trophic structures (Pauly et al., 1998, Pace et al., 1999, Jackson et al., 2001 and Myers et al., 2007). Loss of top predators results in simplified trophic structures, comprising fewer trophic levels (Pauly et al., 1998) and, particularly in systems where trophic cascades and other indirect interactions are important in determining community structure, result in major regime shifts (Pace et al., 1999 and Myers et al., 2007). For example, overfishing, when combined with hypoxic conditions created by increased microbial biomass, is believed to favour an increase in the abundance of jellyfish in coastal marine ecosystems (Richardson et al., 2009). Jellyfish form a trophic *cul-de-sac* in estuarine ecosystems, acting as an energy sink and further destabilising existing trophic structures (Baird and Ulanowicz, 1989).

Monitoring of the number, identity, patch size and total extent of biogenic habitats comprising the estuarine mosaic is recommended as an indicator in estuarine risk assessment. Where local processes are well understood, it may be possible to restrict monitoring activities to the most important biogenic habitats. Recent improvements in satellite imaging and remote sensing technologies make desktop habitat mapping in shallow estuaries a realistic possibility and facilitate ongoing tracking of distribution changes in estuarine habitat mosaics (Roelfsema et al., 2014). Similarly, new technologies enable remote sensing of changes in the height and density of biogenic habitats. Very-high Resolution Side-scanning Sonar has been used to measure the height of inter-tidal biogenic reef structures in Belgium to a high degree of accuracy (Degraer et al., 2008) while Acoustic Doppler Current Profiler technology has been used successfully to measure the height and density of the seagrass *Zostera marina* in the USA (Warren and Peterson, 2007).

Commercial fisheries catch records can also be useful sources of time-series data about changes in key species (Myers and Worm, 2003). Catch data may be for finfishes, shellfish, such as oysters, mussels and clams that provide important biogenic habitat or other invertebrates such as shrimp and crabs. For example, commercial catch records from Chesapeake Bay showed drastic declines predictive of ecosystem collapse in stocks of both top predator fish species and oysters decades before collapse occurred (Richards and Rago, 1999 and Rothschild et al., 1994). Recreational catch surveys are also available in some regions and have been used in studies (e.g. Pradervand and Baird, 2002). Fisheries data should, however, be treated with caution as the reliability of catch records is dependent on compliance with reporting regulations by fishers (Gezelius, 2006). Furthermore, increased inter-annual variability has been demonstrated in the size in fish populations under harvesting pressure and estimates of abundance based on catch-per-unit-effort may not correctly reflect changes in population size or loss of resilience to environmental change resulting from biotic homogenisation, particularly amongst top predators (Harley et al., 2001).

3.5. Criterion E: Quantitative Risk Analysis

Criterion E presents the possibility for highly accurate risk assessment in the future through the use of mathematical models of ecosystem functioning as predictors of collapse. The application of Criterion E is, however, reliant on the availability of relevant models capable of apprehending and incorporating the interactions between the different components of ecosystem function (Keith et al., 2013). Ecological models exist that incorporate hydrological processes in estuaries (e.g. Webster, 2007). These are useful due to the strong correlation between hydrology and estuarine ecology (Lester et al., 2011). However, a deeper understanding of the major functional groups, abiotic conditions, and interactions in estuaries is required to enable more comprehensive and effective models of biological responses to change (Airoldi et al., 2008).

4. Application of the IUCN risk assessment criteria to an estuarine ecosystem: Chesapeake Bay

To assess the capacity of the IUCN Red List of Ecosystems to provide a meaningful assessment of the risk of estuarine ecosystem collapse, and to test some of the indicators proposed above, we conduct a retrospective risk assessment for the Chesapeake Bay ecosystem for the year 1980. Chesapeake Bay, with an area of 11500km^2, is the largest estuary in the USA, historically supported a thriving fishing industry (Kemp et al., 2005) and is one of the most well studied estuarine systems globally, with established monitoring programs for several environmental variables and historic fisheries catch data. We compare the outcome of a risk assessment that could have been made in 1980 using data available at the time with the subsequent trajectory of change in the Bay's ecosystem. We start by reviewing key processes that sustain the Chesapeake Bay ecosystem and the key threatening processes before providing an assessment.

4.1. Key Ecosystem Processes

The Bay is generally shallow, with the mean depth only slightly exceeding six metres. Freshwater input to the estuary is via more than 100 rivers, although approximately half of the annual fluvial input derives solely from the Susquehanna River. Despite high riverine influence, flushing times in the Bay are generally between 120-300 days (Shen and Wang, 2007).

Stratigraphic evidence from benthic sediments and early eye-witness reports suggest that the biotic compartment of the Chesapeake Bay ecosystem was characterised by extensive biogenic habitat including abundant reefs of the eastern oyster (*Crassostrea virginica*) (Ingersoll, 1881) and seagrasses of several species (Orth and Moore, 1983, 1984 and Kirby and Miller, 2005). At least prior to 1900 (Mann et al., 2009 and zu Ermgassen et al., 2013), water filtration by abundant oyster reefs is posited to have maintained water clarity, allowing sufficient light penetration for submerged aquatic vegetation to persist, and to have moved carbon and nutrients from the pelagic compartment of the ecosystem to the benthic compartment (Newell, 1988 and Kemp et al, 2004) (Fig. 3). In the last decade, however, there has been debate as to the extent that oyster filtration acted as a top-down control on phytoplankton biomass (e.g. Pomeroy et al., 2006, 2007, Cerco and Noel, 2007, Fulford et al., 2007 and Newell, et al. 2007). Seagrass beds likely supported rich communities of infauna, epifauna and fish at significantly higher densities than adjacent unvegetated strata and acted as a nursery ground for many species (Orth, 1977, Orth and Moore, 1983, Baird and Ulanowicz, 1989, Goetz et al., 2004 and Kirby and Miller, 2005). Connectivity would have existed between habitats, with many known resident species utilising different habitats within the Bay at different life stages. For example, blue crabs (*Callinectes sapidus*) are known to recruit to seagrass and saltmarsh habitats but migrate and forage much more widely as adults (Hines et al., 1995) while striped bass (*Morone saxatilis*) forage on benthic prey as juveniles but feed mostly on pelagic food sources as adults (Hartman and Brandt, 1995 and Harding and Mann, 2001). A complex, multi-layered trophic web is thought to have been present with high benthic primary production and levels of herbivory controlled by key local mesopredators such as blue crabs and apex piscivorous predators such as striped bass, bluefish (*Pomatomus saltatrix*), and weakfish (*Cynoscion regalis*) (Murdy et al., 1997 and Kemp et al. 2005).

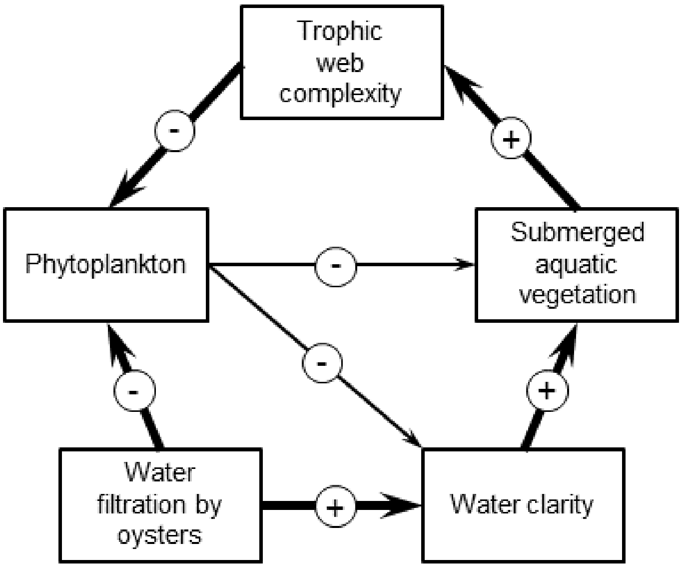

Figure 3. Key ecosystem components and processes in the functional Chesapeake Bay showing positive (+) and negative (-) interactive effects; effect strength indicated by arrow thickness.

4.2. Key Threatening Processes

Since European settlement, there has been extensive land clearing for agriculture and urbanisation within the Chesapeake Bay catchment (Goetz et al., 2004) and proxy evidence from stratigraphic analysis of benthic sediments points to increases in sedimentation rates, turbidity and nutrient loadings across that period (Cooper, 1995). Few direct measures of water quality are available, but multiple environmental proxies indicate a Bay-wide reduction in water quality that would have been apparent as early as 1880, accelerating significantly from around 1920 (e.g. Cooper, 1995, Cornwell et al., 1996, Colman et al., 2002, Kirby and Miller, 2005). Increasing phytoplankton biomass was detected in the system from the early 1900s, with the trend continuing through until the 1970s before stabilising, presumably in response to achieving carrying capacity (Harding, 1994 and Kirby and Miller, 2005). Cooper and Brush (1993) report a shift in the ratio of benthic to pelagic diatom forms in the sediment record, consistent with increasing nutrient levels in the water column, in the middle of the 20th century. Amplified sediment and nutrient inputs resulted in diminished dissolved oxygen concentrations in the bottom waters of the Bay being noted by the 1930s (Newcombe and Horne, 1938). In the 1950s high turbidity and seasonal bottom-water hypoxia became regular occurrences (Kemp et al., 2001, 2005). Proxies in the stratigraphic record suggest that during the early period of European settlement, Chesapeake Bay exhibited lower than current levels of summer hypoxia (Cooper and Brush, 1993).

From the 1870's onward, substantial anthropogenic dredge-harvest of the eastern oyster (*Crassostrea virginica*) caused severe declines in the spatial extent of oyster reef present (Rothschild et al., 1994). This resulted in loss of hard substratum for oyster recruitment and presumably led to a reduction in the water filtering function of oysters, which in turn would increase turbidity and biomass of phytoplankton in the Bay, as filtration and these two variables are negatively correlated (Lenihan and Peterson, 1998, Kirby and Miller, 2005 and zu Ermgassen et al., 2013). Beginning in the 1960s, substantial areas of seagrasses were lost in response to reduced light penetration through the water column, leaving many parts of Bay devoid of seagrasses entirely (Orth and Moore, 1984). The loss of these two important biogenic habitats reduced the complexity of the bottom structure in the Bay and drove the loss of associated species such as the bay scallop (*Argopecten irradians concentricus*) that relies on seagrass beds for recruitment (Orth and Moore, 1984, Lenihan and Peterson, 1998 and Cordero et al., 2012).

Anthropogenic overharvesting resulted in a loss of diversity amongst top local predators such as striped bass (*Morone saxatilis*) and bluefish (*Pomatomus saltatrix)* (Fig. 4). Similarly, the American shad (*Alosa sapidissima*), once an abundant mesopredator in the Bay and a mainstay of the local fishery, declined from the mid-1800s onward due to the damming of rivers and overharvesting, further reducing top-down control of pelagic plankton levels. Local shad stocks reached the point of total collapse in Chesapeake Bay by the 1990s (USFWS, 2014), resulting in catches in the local fishery becoming increasingly dominated by the planktivorous Atlantic menhaden (*Brevoortia tyrannus*) whose numbers have increased in the Bay due to the rise in phytoplankton and reduced predation (Luo and Brandt, 1993, Houde et al., 1999 and Luo et al., 2001).

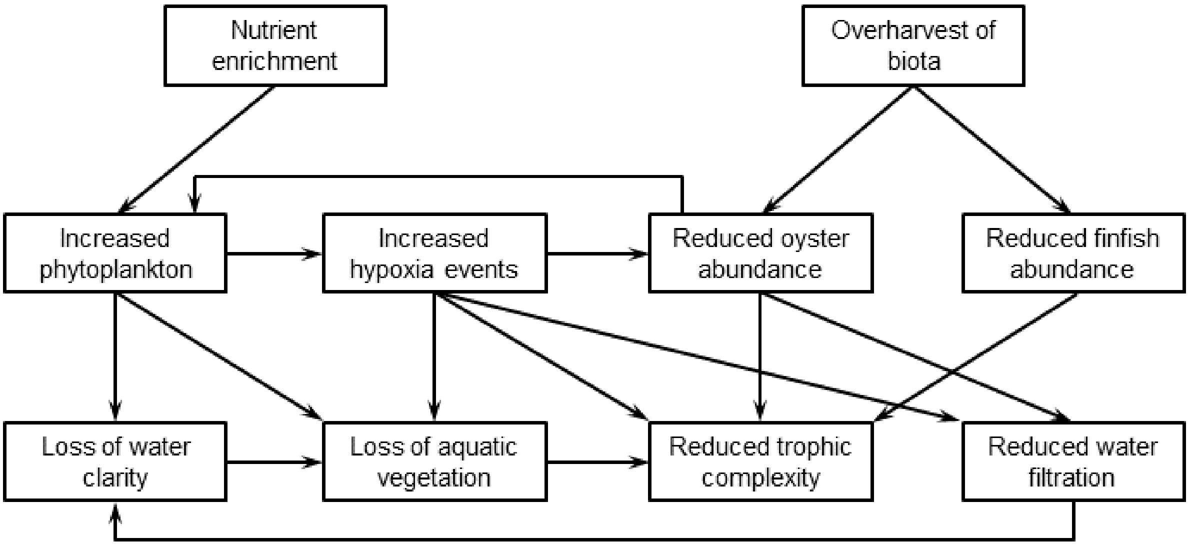

Figure 4. Key threatening processes in the Chesapeake Bay ecosystem with their flow-on effects.

Since the 1960s, there has been an increase in the abundance of gelatinous species in the Bay. Increases in the local Atlantic sea nettle (*Chrysaora quinquecirrha*) have been attributed to greater abundance of zooplankton prey stemming from increased phytoplankton biomass and to an increase in potential settlement areas resulting from dredging activities (Cargo and Schultz, 1967 and Newell, 1988), although this species displays both seasonal and annual fluctuations in density (Feigenbaum and Kelly, 1984). Furthermore, three invasive species of zooplanktivorous jellyfish (*Maeotias marginata*; *Blackfordia virginica* and *Moerisia lyonsi*) were first observed in Chesapeake Bay during the 1960s and '70s (Mills, 2001). Likely introduced by shipping traffic, these jellyfish are now ubiquitous throughout the Bay (Purcell et al., 1999 and Graham and Bayha, 2007).

Increases in zooplankton predation from finfish and jellyfish reduced top-down control of phytoplankton abundance, creating a cycle of positive feedback, driving ecosystem change in the Bay. This has been marked by a decline in the ratio of fishery yield to primary productivity in the Bay (Kemp et al., 2005).

4.3. Ecosystem Collapse

For assessment of risk under IUCN Criteria A and B, collapse is defined as the point where the distribution of the ecosystem declines to zero (i.e. has collapsed throughout its entire range - this may occur without the geographic extent of the waterway reaching zero). For Criterion C, changes in water clarity, chlorophyll-*a* content in surface waters and the level of dissolved oxygen in bottom waters present useful indicators of degraded abiotic conditions in Chesapeake Bay. Collapse, here, is defined as the point where: 1) water clarity declines to the point where submerged aquatic plants are predicted to die (i.e. a median Secchi depth during the local growing season of April-November that is less than 0.82m in regions where salinity is ≤ 5‰, or 1.10m where salinity is > 5‰) (Dennison et al., 1993); or 2) 100% of subtidal bottom waters are hypoxic (dissolved oxygen < 2mg O_2 l^{-1}) for extended periods. Three indicator variables are also identified for use with assessment Criterion D to identify disruptions to biotic processes and interactions: 1) distribution of seagrasses; 2) distribution of oyster reefs; and 3) species richness and evenness of top predators present in the Bay. Collapse under Criterion D is defined as the point where 99% of any key biogenic habitat is lost relative to historical levels, the point of functional extinction (Jackson, 2001 and Beck et al., 2011), or where diversity of top predators declines to zero.

4.4. Assessment Summary

A risk assessment of Chesapeake Bay for the year 1980, conducted using the criteria of the IUCN Red List of Ecosystems (Keith et al., 2013), assigned an overall threat status of *Critically Endangered* based on changes in biotic processes and interactions from 1750 to 1980 (Table 3). For many of the criteria there were insufficient data to permit an assessment, but the confinement of the Chesapeake Bay ecosystem to a single location resulted in a threat status of *Endangered* under sub-criterion B3. No assessments based on Criterion E could be made.

Table 3. Summary of outcomes of the retrospective risk assessment for the Chesapeake Bay for the year 1980, using the IUCN Red List of Ecosystems Criteria, for each of three time periods. Assessment categories: LC = Least Concern; VU = Vulnerable; EN = Endangered; CR = Critically Endangered; DD = Data Deficient; NE = Not Evaluated.

IUCN Criterion	A	B	C	D	E	Overall
Sub-criterion 1 (1930-1980)	LC	EN	VU	EN	NE	CR
Sub-criterion 2 (1980-2030)	LC	LC	DD	DD	NE	
Sub-criterion 3 (1750-1980)	LC	EN	DD	CR	NE	

4.4.1. Criterion A: Declining Distribution

The spatial boundaries of Chesapeake Bay are defined by local geomorphology and exhibit little change over time scales of tens of years. In the absence of major reductions in freshwater inputs or changes in sea-level, Criterion A is, therefore unlikely to predict risk of collapse in this ecosystem across any relevant timescale to conservation. Accordingly, Chesapeake Bay is assessed as being of *Least Concern* under all three sub-criteria.

4.4.2. Criterion B - Restricted Distribution

B1 – Extent of occurrence: The Chesapeake Bay ecosystem features a geographic distribution that is > 2000km^2 but ≤ 20000km^2 and both ongoing declines in environmental conditions and disruptions of biological interactions have been observed (see Criteria C and D below). The status of Chesapeake Bay is, therefore, *Endangered* under Criterion B1.

B2 – Area of occurrence: The superimposition of a 10 × 10km grid over Chesapeake Bay reveals that the Bay occupies 71 grid squares. Given the evidence of ongoing environmental and biotic decline, the Bay is of *Least Concern* under Criterion B2.

B3: Ecosystem exists at: Only at a single location and is prone to the effects of anthropogenic activity and stochastic environmental perturbations. The large size of Chesapeake Bay may, however, provide some buffering to such impacts. The Bay is, therefore, *Endangered* under Criterion B3.

4.4.3. Criterion C: Degradation of Abiotic Environment

C1 – Current decline, 1980: Mean Secchi depths throughout Chesapeake Bay declined by more than 30% between the 1930s and the 1960s, dropping below 1m across the entire salinity gradient (Kemp et al., 2005). Short periods of localised seasonal deep-water hypoxia were first reported in Chesapeake Bay in the 1930s (Newcombe and Horne, 1938). The frequency and extent of hypoxic events in the Bay increased markedly across the next 50 years with hypoxic conditions dominating approximately one third of the Bay for periods of 2-3 months per year (Officer et al., 1984 and Hagy et al., 2004). The Bay is, therefore, classified as *Vulnerable* under criterion C1.

C2 – Future decline: By 1980, the extent of environmental degradation in Chesapeake Bay was becoming understood and restoration activities were in the planning stage. The First Chesapeake Bay Agreement, aimed at reducing eutrophication in the Bay, was endorsed in 1983 (Boesch et al., 2001). River restoration projects designed to reduce sediment and nutrient inputs to the Bay were also introduced in the early 1980s and the number of such projects active in the Chesapeake Bay catchment increased steadily over the next 20 years

(Hassett et al., 2005). Based on catchment management strategies being considered and adopted in the 1980s, improvement in abiotic conditions in the Bay may have been expected into the future. No accurate projections of changes in abiotic conditions, however, were available in 1980 and the Bay is, therefore, classified as *Data Deficient* under Criterion C2.

C3 – Historic decline: Strong anecdotal evidence exists to support the degradation of abiotic conditions in the Bay since 1750. However, no data sets exist that allow direct comparison of environmental conditions in 1980 with those of 1750. Chesapeake Bay is, therefore, *Data Deficient* under Criterion C3.

4.4.4. Criterion D: Altered Biotic Processes and Interactions

D1 - Current decline, 1980: Commercial catches of striped bass, a local keystone predator, peaked in 1973 and then fell by approximately 80% before 1980 in response to overfishing and loss of nursery habitat area (Richards and Rago, 1999). The timeframe of this decline, however, is too short to provide robust analysis (Keith et al., 2013). Taken over the full 50-year period preceding 1980, no decline in striped bass catches was discernible, with record low catches in the early 1930s, followed by population increase in the following decades. Pooled landings of weakfish for the mid-Atlantic coast and Chesapeake Bay also declined by > 90% between 1930 and 1967 (Joseph, 1972). While indicative of a trend, the timeframe of this dataset is also too short to exclude natural fluctuations in abundance.

The distribution of key biogenic habitats in Chesapeake declined significantly across the 50-year period preceding 1980. Annual commercial landings of eastern oysters from Chesapeake Bay declined by ≈33% from approximately 15000 tonnes in 1930 to around 10000 tonnes in 1980 (Rothschild et al., 1994). Of six well-studied areas in the Bay, all experienced declines in the distribution of seagrasses between 1937 and 1980, with two areas becoming completely devoid of submerged vegetation and a third nearly so. The total distribution of seagrass across all parts of Chesapeake Bay declined by ≈67% during that period (Orth and Moore, 1983, 1984). The decline in seagrass habitat area across the 50 years prior to 1980 means that the Bay is *Endangered* under Criterion D1.

D2 - Future decline: By 1980, conservation schemes were being developed to protect key species. A management plan by the Atlantic States Marine Fisheries Commission was introduced in 1981 to curb the overharvest of striped bass. The management plan underwent amendments in 1984 and 1985 specifically aimed at preserving the Chesapeake Bay stocks of striped bass (Weaver et al., 1986 and Richards and Rago, 1999). The Chesapeake Bay Submerged Aquatic Vegetation Management Policy was approved in 1989 in an attempt to protect seagrasses in the Bay (Orth et al., 2002). However, no detailed projections as to the recovery in biotic processes likely to result from these measures were available in 1980. The Bay is, therefore, classified as *Data Deficient* under Criterion D2.

D3 - Historic decline: By 1980, historically abundant intertidal oyster reefs in Chesapeake were effectively extirpated and the vertical height of sub-tidal reefs greatly reduced (Hargis, 1999 and Woods et al., 2005). Commercial harvest of oysters remained high, with the extraction of approximately 10000 tonnes in 1980, but shellfisheries often continue to produce substantial catches beyond the point where 90% of local reef structure is lost (MacKenzie et al., 1997 and Kirby, 2004). Beck et al. (2011) estimate loss of oyster reef habitat of > 90% compared with historical distributions in the Bay and Wilberg et al. (2011) calculate that abundance of the eastern oyster declined approximately 87.5% between the early 1800s and 1980. Accordingly, the Bay is *Critically Endangered* under Criterion D3.

4.5. Chesapeake Bay post-1980

The above analysis indicates that a Red List of Ecosystems assessment of Chesapeake Bay conducted in 1980 would have classified the ecosystem as *Critically Endangered*. So how did this match up to the subsequent trajectory of change in the Bay? By the mid-1990s Chesapeake Bay had, across several decades, transitioned from a classic trophic regime to one dominated by planktonic and microbial activity during significant portions of the year (Jonas, 1997 and Boesch et al., 2001). Under the new environmental regime, Chesapeake Bay exhibited many of the classic ecological end-states for collapsed estuarine ecosystems such as reduced bottom structure, simplified trophic webs with fewer apex predators and a shift from benthic to pelagic biomass. The pathway to collapse occurred largely as expected with eutrophication driving expansion of hypoxic/anoxic zones, and over-extraction of key taxa, including filter feeding oysters and habitat-forming seagrasses, resulting in a shift of the biotic assemblage toward more planktonic and microbial forms. Positive feedback loops then served to increase the pace of environmental change and prevent recovery of the ecosystem to its former state.

5. Conclusion

The numerous, and often interacting, potential causes of collapse in estuaries serve to make risk assessment for conservation management demanding. Key threatening processes occur in both the abiotic and biotic compartments of estuarine ecosystems and are often strongly tied to anthropogenic activities. Estuarine habitat mosaics are, however, interconnected by both environmental and biological factors with pervasive effects, such as water quality and the presence of ecosystem engineering species. Accordingly, many of the causes of collapse share common symptoms that allow the use of indicators with strong predictive power.

The use of risk assessment schemes, such as the IUCN Red List of Ecosystems, is viable at the thematic scale of whole estuaries. The availability of measurable indicator variables predictive of collapse at this scale enables effective assessment of risk, where sufficient data exists. Risk assessment can provide a powerful tool for estuarine conservation managers, informing the prioritisation of conservation efforts among estuarine ecosystems within jurisdictions or bioregions. However, as estuaries are geographically constrained by topology or geomorphology, the applicability of assessment criteria based on declines in spatial distribution may prove to be of limited utility. Furthermore, spatial constraints may result in estuarine ecosystems being small, even when in a functional and stable state, and this may limit the ability of assessment criteria based on restricted distribution to discriminate between estuaries or lead to over-estimation of the risk of collapse.

Assessment criteria based on changes in key abiotic factors and biota are likely to prove the most useful measures of risk in estuarine habitat-mosaics. A detailed understanding of the key processes and interactions at local scales will be needed in order to identify indicator variables relevant to each ecosystem type. Ongoing research into ecological processes and interactions in estuarine mosaic landscapes should, therefore, be a conservation priority. Additionally, too little is known as yet about the synergistic effects of multiple biogenic habitats in estuaries. For instance, there is likely to be an effect of patch arrangement (in addition to patch presence/absence and size) on community structure. For example, investigations of fish assemblages in seagrass habitats showed strong effects resulting from the proximity of saltmarsh or mangrove habitats (e.g. Saintilan et al., 2007).

The lack of high quality, ecologically relevant, long-term datasets is likely to be the most challenging factor in performing risk assessments. In the risk assessment of Chesapeake Bay, a well-studied waterway, an assessment using IUCN Criterion C could only be made for one of the three assessment periods due to a paucity of relevant datasets of sufficient length.

Efforts to obtain existing data from all potential sources should be a key concern for decision makers. Several datasets currently exist (e.g. see Table 2), but these are often not widely publicised or readily searchable. In some jurisdictions, existing monitoring programs are under threat from cuts to funding, compounding the difficulty in accurately assessing risk into the future. The establishment of relevant national or international data repositories is likely to be of great value to conservation managers in the future, and should focus on data archiving methods that are robust to changes in technology such as the use of open standards such as Extensible Markup Language with wide cross-platform support. Where data are not available, ongoing monitoring programs should be implemented as expeditiously as possible to inform future conservation of biodiversity.

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Appendix: Supplemental material

Table S1: Summary of outcomes and evidence used in risk assessment for the Chesapeake Bay for the year 1980. Red List of Ecosystems assessment categories: LC = Least Concern; VU = Vulnerable; EN = Endangered; CR = Critically Endangered; DD = Data Deficient.

Assessment criterion	Assessment category	Data available	Characteristics
A1	LC	Geographic distribution stable over past 50 years	Distribution defined by local geography – may increase due to sea-level rise
A2	LC	Distribution not predicted to decline over next 50 years	
A3	LC	No recorded change in distribution since 1750	
B1	EN	Extent ≤ 20000km^2 and occurs at only one location	Chesapeake Bay considered unique because it is the largest estuary in the USA and possessed of iconic natural beauty
B2	LC	Area of occupancy encompasses > 50 grid squares	
B3	EN	Ecosystem occurs in a single location and is strongly impacted by human activities due to high population	
C1	VU	Water clarity decline and incidence of seasonal hypoxia across ≥ 30% of Bay and of ≥ 80% relative severity	Assessment across historical and future timeframes not possible due to lack of records and uncertainties regarding future human population and activities
C2	DD	Rehabilitation projects operational but no projections of future abiotic conditions available	
C3	DD	No data available for abiotic conditions across entire historical period	
D1	EN	Loss of keystone seagrass habitat across ≥ 50% of Bay and of ≥ 80% relative severity	Loss of critical biogenic habitat caused severe ongoing disruption to ecological processes and contributed to decline in water quality
D2	DD	Rehabilitation projects operational but no projections of future abiotic conditions available	
D3	CR	Loss of keystone oyster reef habitat across ≥ 80% of Bay and of ≥ 80% relative severity	

Chapter 5: Are geomorphological typologies for estuaries also useful for classifying their ecosystems?

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Abstract

1. Due to the large number of estuaries within many jurisdictions, it is not always feasible to develop estuary-specific management plans. Typologies that identify ecologically similar estuaries may assist in delineating groups of estuaries across which common conservation strategies may be developed, where key threatening processes are also similar.

2. Estuarine typologies have been implemented in many countries, but most are based on hydrology and/or geomorphology rather than ecology. This study assessed the extent to which an Australian estuarine ternary classification scheme, which assigns estuaries to geomorphic classes according to wave, tidal and riverine influences, also captures differences in the mosaic of habitat types present.

3. An analysis of 352 Australian estuaries and coastal waterways, for which geomorphological classifications and areas of key habitats were available, revealed strong

differences in habitat mosaics among geomorphic classes. These differences among classes in habitat mosaics were independent of the extent of anthropogenic modification.

4. The areal extent of mangrove and saltmarsh habitats displayed particularly large differences among estuarine geomorphic classes, being greatest in tide-dominated estuaries and deltas, and smallest in wave-dominated estuaries and deltas and strandplains.

5. Overall, results suggest that geomorphic classification schemes may be useful in identifying groups of ecologically similar estuaries, for which common conservation strategies might be developed, depending on stressors. This approach will be particularly useful in developing management strategies for estuaries for which detailed habitat maps are not available.

KEYWORDS

benthos, biological classification, coastal development, conservation evaluation, mangrove, riverine influence, saltmarsh, seagrass, tidal influence, wave climate

1 | INTRODUCTION

Estuaries, broadly defined as semi-enclosed coastal water bodies with at least an intermittent connection to the sea and at least intermittent freshwater influence, support ecosystems of high socio-economic value (Barbier et al., 2011; Pritchard, 1967). Estuarine ecosystems provide food, cycle nutrients, filter water and sequester carbon (Barbier et al., 2011). Estuarine ecosystems are also of high aesthetic and recreational value (Barbier et al., 2011; Farber et al., 2006). Their habitats serve as vital nurseries for many species and are ecotones where aquatic, terrestrial and marine habitats merge and interact, supporting unique species assemblages (Basset et al., 2013; Franco, Elliott, Franzoi, & Torricelli, 2008).

Estuarine ecosystems are increasingly being degraded by the combined effects of coastal development and climate change (Hoegh-Guldberg & Bruno, 2010; Lotze et al., 2006). Estuaries have long been centres of human settlement and the resultant urbanization, industrial and commercial activities heighten the risk of degradation or collapse of their ecosystems (Lotze et al., 2006; Small & Nicholls, 2003). Management strategies are urgently needed to protect estuarine ecosystems and their important functions. The development of effective strategies for conserving estuarine habitats requires knowledge of their spatial extent and occurrence, as well as the processes that threaten them. Management plans often revolve around the protection of habitats, with the rationale that protection of habitats will protect dependent species (Gladstone, 2007; Jones, Srinivavan, & Almany, 2007; Malcolm, Jordan, & Smith, 2010). Additionally, changes to the overall estuarine habitat mosaic, or key components of such, may act as an early warning of ecosystem collapse (Keith et al., 2013). Yet, with estuaries numbering in the hundreds, or even thousands in some jurisdictions (e.g. Australia, USA), it may not be feasible to develop individual management strategies for every estuary and it is costly to map habitat configurations in each.

The habitats present within estuaries, and their spatial configuration display marked inter-estuary variation reflecting variability in the spatial extent of estuaries and their catchments, their climatic setting and human influences (Gray, McElligott, & Chick, 1996). Categorization of estuaries according to the types of habitats they support might assist in the development of management strategies. Although a variety of typologies are available that classify estuaries according to their geomorphological, hydrological and/or physico-chemical properties (Table 1), it is unclear how these relate to the extent and identity of component habitats.

Table 1. Estuary classification schemes by country of use and grouping factors. GEO = geomorphology; HYD = hydrology; PHC = physicochemical

Country	Classification scheme	GEO	HYD	PHC	Source
Australia	Ternary Classification of Coastal Systems	✓	✓		OzCoasts, 2013
Canada	British Columbia Estuary Mapping Scheme	✓	✓	✓	Hunter, Jones, Wayne, & Pendergast, 1983
Europe	Water Framework Directive		✓	✓	European Commission, 2003
New Zealand	Estuary Environment Classification	✓	✓		Hume, Snelder, Weatherhead, & Liefting, 2007; NIWA, 2013
South Africa	Conceptual Estuary Classification	✓	✓		Harrison, Cooper, & Ramm, 2000
South Korea	Korean Estuary Classification		✓		Jang & Hwang, 2013
United Kingdom	Joint Nature Conservation Committee	✓	✓		Davidson et al., 1991
USA	Marine and Estuarine Ecosystem and Habitat Classification	✓	✓		Levinton, 1995; NOAA, 2012, 2013

As local geomorphological and hydrological forcing regulates physico-chemical regimes (Roy et al., 2001), it might be expected that the component habitats of estuaries co-vary with geomorphology. Nevertheless, local ecology is determined not only by abiotic, but also by biotic factors (Post, Doyle, Sabo, & Finlay, 2006). For example, ecosystem engineers, such as mangroves, saltmarshes and seagrasses in estuaries, can modify the abiotic environment by adding structural habitat, dampening currents, and stabilizing sediments, making it more or less habitable for other organisms (Jones, Lawton, & Shachak, 1997; Worm et al., 2006). Competitive interactions may also influence local-scale distributions of species (Roughgarden, 1983). For example, on temperate and sub-tropical shorelines, mangrove encroachment into saltmarsh is reducing the abundance of the latter (Saintilan & Williams, 1999). Additionally, in some instances, effects of local habitat disturbance may swamp the effects of physical processes in determining habitat mosaics. Hence, explicit tests of the relationship between estuarine geomorphology and component habitats are required, in both largely unmodified and highly modified estuaries.

Australia has more than 1000 estuaries along its 34,000 km of coastline. Here the ability of a classification scheme developed for Australian estuaries, which is based on hydrology and geomorphology, to also categorize the habitat types and areas present in each estuary is examined. Specifically tested are the hypotheses that: (1) component habitats differ predictably among geomorphic classifications; and (2) these differences are persistent even in anthropogenically modified waterways. Additionally, key environmental correlates of variation in habitat mosaics among estuaries are identified.

2 | METHODS

2.1 | Estuary classifications

Currently, the classification of Australian estuaries is based upon a geomorphic typology that divides estuaries into six classes on the basis of wave, tidal and riverine forcing (after Dalrymple, Zaitlin, & Boyd, 1992; see Figure 1). During the Australian National Land and Water Resources Audit (NLWRA), Geoscience Australia utilized aerial photographs, Landsat imagery, existing scientific literature, and compiled data for wave, tide and river power to categorize Australian estuaries nationally (Harris & Heap, 2003; Heap, Bryce, & Ryan, 2004). The typology has been validated through a numerical analysis of 721 estuaries across Australia (Harris et al., 2002).

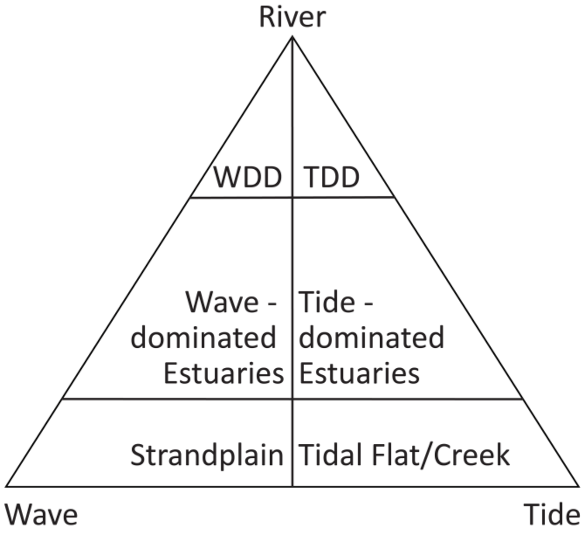

Figure 1. Typology of Australian estuaries (based on Dalrymple et al., 1992, Figure 3, p. 1132). The six classifications are based on the relative magnitude of river, wave and tidal influences as well as local geomorphology. Abbreviations used: WDD = wave-dominated deltas. TDD = tide-dominated deltas

Wave-dominated deltas (WDD), *wave-dominated estuaries* (WDE) and *strandplains* all have greater wave than tidal influences (Figure 1). Wave-dominated deltas are coastal river outlets with bow-shaped shorelines. Wave-dominated estuaries commonly have transverse sandbanks at the entrance, leading to low energy inner conditions and display low turbidity and poor mixing of the water column. Coastal lagoons fall within the WDE classification and are not distinguished from the WDE classification in this paper's analyses. Strandplains have minimal fluvial input and typically receive freshwater only as runoff from their immediate surrounds. They occur along prograded coastlines and often become, at least temporarily, cut off from the ocean by accumulated sediment.

Tide-dominated deltas (TDD), *tide-dominated estuaries* (TDE) and *tidal flats/creeks,* by contrast, have greater tidal than wave influence and are typically well mixed with high turbidity (Figure 1). Tide-dominated deltas are littoral accumulations of fluvial sediment. Tide-dominated estuaries are often characterized by longitudinal sandbanks and extensive intertidal areas. Tidal flats occur in macrotidal regions and areas with low geographic relief. They consist of accumulations of fine sediment and are usually intersected by small tidal creeks.

In addition to these six categories, a seventh category, *other,* was used by the NLWRA assessment. This category includes coastal embayments that conform to broader definitions of estuaries, but do not fit within the scope of the Dalrymple et al. (1992) typology (Natural Heritage Trust, 2002).

2.2 | Estuary condition assessment

The NLWRA also assessed the condition of each estuary as near pristine, largely unmodified, modified, or extensively modified on the basis of land usage within the catchment, impacts from invasive species, human use of the estuary itself and resulting impacts on local estuarine community assemblages and ecological processes (NLWRA, 2008).

Estuaries in near pristine or largely unmodified condition have high levels of catchment vegetation cover (>90% for near pristine and >65% for largely unmodified) and limited anthropogenic modification. No significant modifications to fluvial or tidal hydrological forcings or to flood regimes are present. Natural ecological communities and processes are intact, or mostly so, with minimal invasive species and only sustainable extractive activities present (Heap et al., 2001).

By comparison, modified and extensively modified estuaries show one or more significant ecological problems. Natural vegetation cover within their catchment areas is severely reduced and natural riverine or tidal flows may be heavily modified. Wetland areas have been largely cleared of vegetation, altering flood patterns. Ecological communities and processes are often degraded by the presence of invasive species, overharvesting of biota, and/or habitat loss or modification (Heap et al., 2001).

2.3 | Estuary habitat area

The areal extents of *intertidal flat*, *mangrove*, *saltmarsh/saltflat*, *tidal sandbank*, *rocky reef*, *coral*, *bedrock* and *floodplain* present in individual estuaries were obtained from Condition Assessment Reports prepared under the NLWRA between 1997 and 2008 (NLWRA, 2008; OzCoasts, 2013). These areas were obtained from digitization of existing maps as well as satellite and airborne remote sensing and facies interpretation. The aerial extent of *seagrass* in each estuary was determined from the Australian Estuary Database (Digby et al., 1998) which used aerial and satellite photographs to measure its area.

Intertidal flats, tidal sandbanks, and rocky reef habitats are areas of unconsolidated sediments with minimal habitat-forming benthic cover (NLWRA, 2008; OzCoasts, 2013;

Radke, Brooke, Ryan, Lahtinen, & Heap, 2006). Intertidal flats and tidal sandbanks are formed of sand-mud sized sediments where rocky reef habitats consist of gravel-boulder sized fractions. Intertidal flats are periodically uncovered by tidal movement, but tidal sandbanks are generally continuously submerged and are not bank-attached. Rocky reef habitats may be either inter- or sub-tidal. Bedrock habitats are formed of consolidated substrate and may be inter- or sub-tidal. Saltmarsh/saltflat habitats consist of salt-tolerant vegetation communities occurring in the highest parts of the intertidal zone, above mean spring-tide level, as well as supratidal saline mudflats. Mangrove, coral and seagrass habitats display >10% cover of the relevant taxonomic group (>5% for seagrass). Where multiple taxonomic groups are present, the habitat is defined by the dominant taxon. Floodplain habitat consists of alluvial sediments laterally connected to estuaries only intermittently during flood events (NLWRA, 2008; OzCoasts, 2013; Radke et al., 2006).

2.4 | Estuary environmental data

For each estuary, the perimeter, catchment area, water area (as measured at the annual mean high water mark), maximum length, maximum width, entrance length, entrance width, mean wave height, mean wave period, maximum wave height, maximum wave period, tidal range, longitude, and latitude was obtained from NLWRA Condition Assessment Reports. Annual means, maximums and minimums of air temperature (°C), solar exposure (MJ/m^{-2}) and rainfall (mm) were estimated for each estuary based on Australian Bureau of Meteorology records from the nearest weather station to each (Bureau of Meteorology, 2017). Estuaries where the nearest weather station was located at a distance >25km were excluded. Maximums and minimums were annual means of all available daily maxima or minima.

2.5 | Statistical analyses

A two-way orthogonal permutational multivariate analysis of variance (PERMANOVA; Anderson, Gorley, & Clarke, 2007), with the factors estuarine *classification* and *condition*, assessed: (1) the extent to which among-estuary variation in estuarine habitats followed geomorphic categorizations; (2) whether the relationship between estuarine geomorphology and habitats was modified by estuarine degradation; and (3) whether some estuarine geomorphological types were more susceptible to habitat degradation than others. The factor classification had seven levels, as per the NLWRA estuaries typology. The factor condition had two levels: (1) *unmodified* which included estuaries listed by the NLWRA as near pristine or largely unmodified; and (2) *modified*, which included estuaries listed as modified or extensively modified in the NLWRA database. NLWRA categories for condition were combined so as to provide sufficient statistical power in the analysis. The analysis included the 352 Australian estuaries for which a classification, condition and full set of habitat data were available.

The analysis used Bray Curtis measures of dissimilarity (Bray & Curtis, 1957) of habitat types among estuaries. Permutation of residuals was calculated under a reduced model with 9999 permutations. Where significant treatment effects were found (at $\alpha = 0.05$), these were followed by pairwise *a posteriori* tests to assess sources of differences. Permutational analysis of dispersion (PERMDISP, Anderson 2006) assessed the extent to which any significant treatment effects were driven by heterogeneity in dispersion. Habitat types that were key contributors to multivariate differences among estuarine classifications or modifications, with a dissimilarity to standard deviation ratio ≥ 1.3, were identified using the SIMPER (similarity percentages) routine (Clarke & Warwick, 2001). Two-way univariate PERMANOVAs, of analogous design to the multivariate PERMANOVA, were run on habitat types identified as good discriminators. These used Euclidean distance matrices, with all other procedures as per the multivariate PERMANOVA.

The environmental variables best explaining variation in habitat mosaics among estuaries were assessed using BIOENV analysis (Clarke & Ainsworth, 1993). The analysis searches for the combination of environmental variables that produces a Euclidean distance matrix most closely correlated (via Spearman’s rank) to the dissimilarity matrix of an ecological data set. The analysis included the environmental variables: estuary perimeter, catchment area, water area, entrance width, mean wave height, mean wave period, tidal range, mean annual temperature, mean solar exposure, mean annual rainfall, longitude, and latitude as preliminary analyses indicated the other variables (listed under *Estuary Environmental Data*) were highly correlated to one or more of these. Analyses were conducted to identify key environmental correlates of the Bray Curtis dissimilarity matrix produced from the full, multivariate, suite of habitat data, and on Euclidean distance matrices produced from single habitat types identified by SIMPER as key discriminators among estuarine classifications. Only estuaries (n = 290) for which a full environmental data set was available were included in the analysis. Environmental variables were standardized prior to analysis. Relationships between each of mangrove and saltmarsh/saltflat habitats and individual environmental variables identified by BIOENV as key correlates were further examined using univariate Spearman’s rank-order correlations.

All analyses were run using Primer 6.1.15 and Permanova+ 1.0.5 (Primer-E, 2012), except univariate Spearman’s correlations, which were run using SPSS 24.0.0.2 (IBM, 2016).

3 | RESULTS

Of the nine habitat types considered, seven (intertidal flat, mangrove, saltmarsh/saltflat, tidal sandbank, rocky reef, floodplain and seagrass) were found in all estuarine types. Bedrock habitats were not present in strandplain or tidal flat/creek estuaries and coral habitats were absent from strandplain, tide-dominated and wave-dominated estuaries (Supplemental material, Table S1).

Estuarine habitat mosaics differed among estuaries according to the interacting effects of classification × condition (PERMANOVA, Pseudo-$F_{6, 338}$ = 1.3547, P (perm) = 0.0413). Among unmodified estuaries, significant differences in habitat mosaics were found in 17 of the 21 possible comparisons between estuarine types (*a posteriori* tests; Supplemental material, Table S2). Among modified estuaries, 14 of 21 pairs of classification showed significant differences in habitat mosaics according to *a posteriori* tests (Supplemental material, Table S2). Within levels of estuary classification, significant differences between modified and unmodified condition were found only for the tidal flat/creek classification (*a posteriori* tests; Figure 2). This interaction was driven by a greater dispersion among modified than unmodified estuaries for tidal flats/creeks, but not for the other estuarine classes (Supplemental material: Table S3; Figure 2).

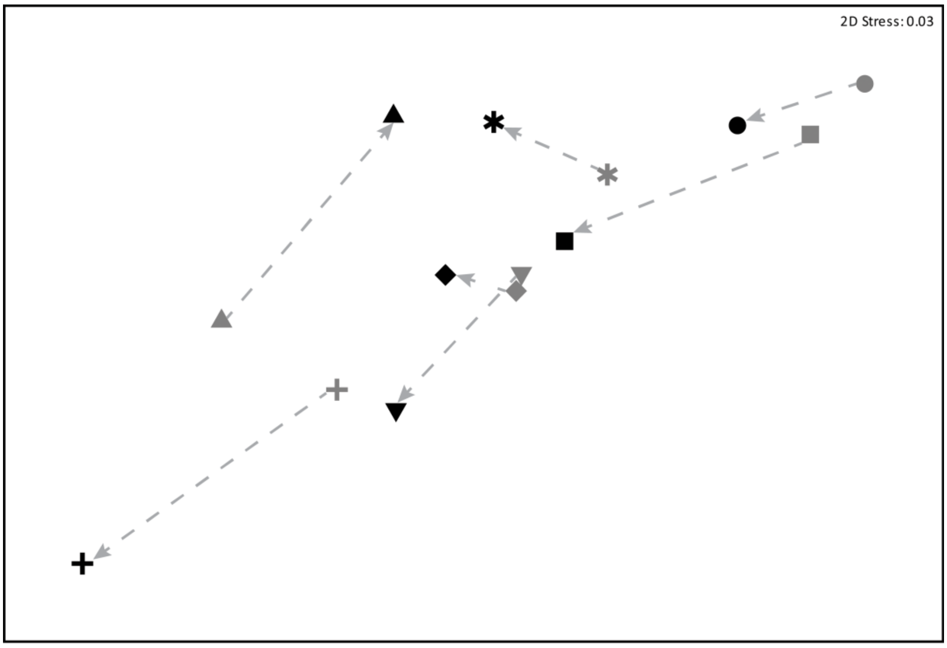

Figure 2. nMDS ordination plot of centroids for areas of habitats present in each of seven estuarine classifications, under modified (black) and unmodified (grey) conditions. Arrows indicate trajectory from unmodified to modified condition. Symbols used: triangle = wave-dominated estuary; inverted triangle = wave-dominated delta; circle = tide-dominated estuary; square = tide-dominated delta; diamond = tidal flat/creek; cross = strandplain; asterix = other

SIMPER analysis showed that the area of mangrove and saltmarsh/saltflat habitats were the key drivers of dissimilarity in habitat mosaics among levels of estuary classification, in both unmodified and modified estuaries (Supplemental material: Tables S4, S5). The area of mangrove habitat differed among estuarine classes (PERMANOVA, main effect of classification: Pseudo-$F_{6,\,338}$ = 6.1901, P (perm) = 0.0042; Figure 3(A)) irrespective of estuarine condition (PERMANOVA, non-significant classification × condition interaction: Pseudo-$F_{6,\,338}$ = 1.0142, P (perm) = 0.3789). Of the seven geomorphic classes, tide-dominated estuaries, tide-dominated deltas and the ‘other’ category displayed the greatest mean area of mangrove habitat, and wave-dominated and strandplain estuaries, the least (*a* *posteriori* tests, Figure 3(A)). The area of saltmarsh/saltflat habitat, likewise, varied significantly among levels of classification (PERMANOVA, Pseudo-$F_{6, 338}$ = 3.0848, P (perm) = 0.0234; Figure 3(B)), irrespective of condition (PERMANOVA, non-significant classification × condition interaction: Pseudo-$F_{6, 338}$ = 1.0142, P (perm) = 0.3789). As with mangrove habitat, the area of saltmarsh/saltflat was greatest in tide-dominated estuaries and tide-dominated deltas, and smallest in wave-dominated estuaries (Figure 3(B)). There was no significant difference in the area of either mangrove or saltmarsh/saltflat habitats between levels of estuarine condition (Mangrove: PERMANOVA, Pseudo-$F_{1, 338}$ = 2.549, P (perm) = 0.0917; saltmarsh/saltflat: PERMANOVA, Pseudo-$F_{1, 338}$ = 2.9775, P (perm) = 0.0652; Figure 4). Nevertheless, SIMPER analysis showed that the area of saltmarsh/saltflat habitat present was the key driver of dissimilarity between unmodified and modified condition tidal flat/creek estuaries (dissimilarity/standard deviation ratio = 1.45).

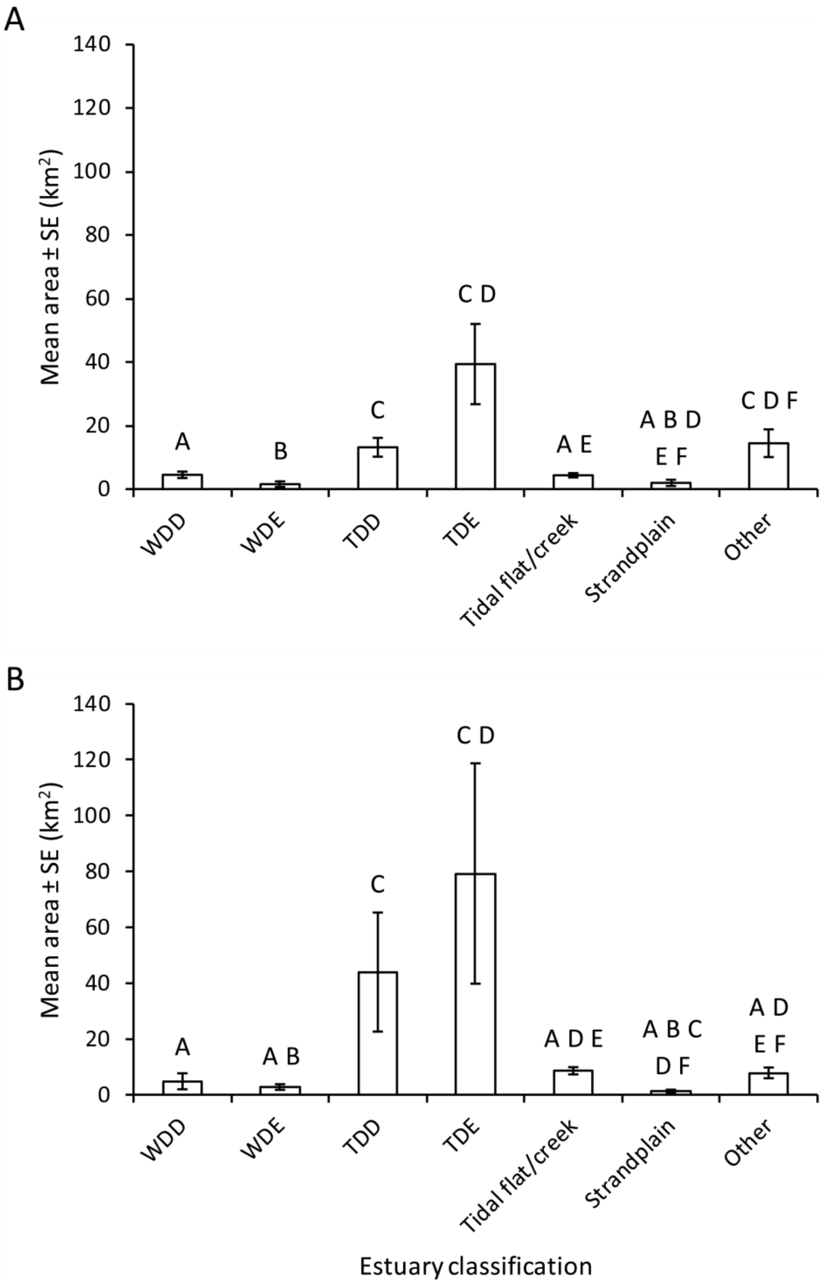

Figure 3. Mean (± SE) area of (A) mangrove, and (B) saltmarsh/saltflat habitat present in each of seven estuary classifications. Letters above columns indicate groupings from *a posteriori* pairwise tests. Abbreviations used: WDD = wave-dominated deltas. WDE = wave-dominated estuaries. TDD = tide-dominated deltas. TDE = tide dominated estuaries

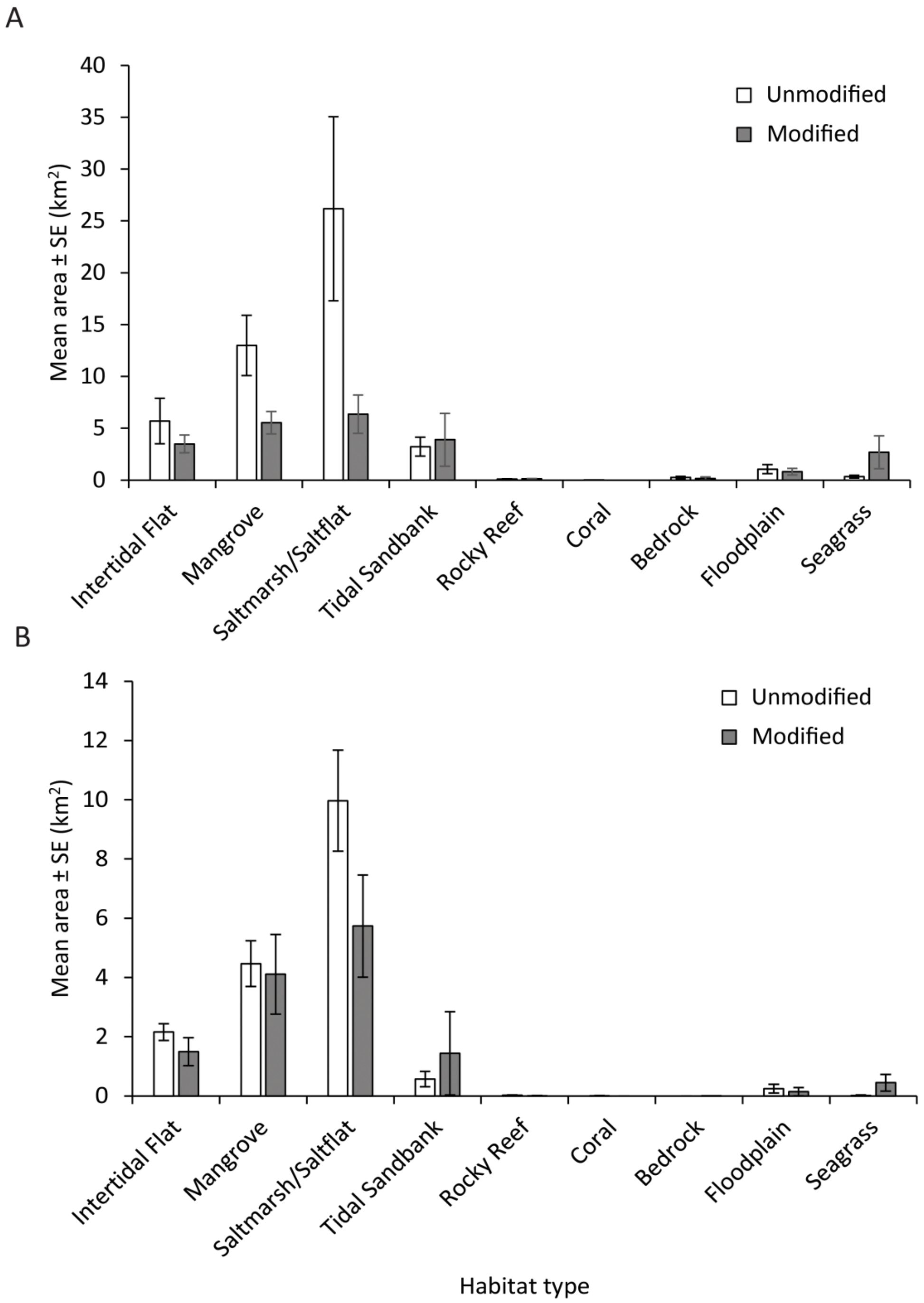

Figure 4. Mean (± SE) area of estuarine habitats present in unmodified and modified estuaries when (A) all estuary classifications are combined, and (B) the tidal flat/creek classification is considered separately

Of the 12 environmental variables considered, BIOENV analysis showed solar exposure alone to best explain multivariate differences among estuaries in habitat mosaics, accounting for 32% of the total variation. Patterns in the distribution of mangrove habitat were best explained by the combination of annual mean rainfall, catchment area, entrance width, tidal range, and latitude, which jointly explained 58.2% of variation. Each of these variables displayed a positive relationship with mangrove habitat area, with the exception of latitude, which displayed a negative relationship (Supplemental material; Table S6). Patterns in saltmarsh/saltflat habitat were most related to the environmental variables annual mean temperature, catchment area, entrance width, and tidal range, which collectively accounting for 56.6% of variation, and each of which individually displayed a positive relationship with saltmarsh/saltflat habitat area (Supplemental material; Table S6).

4 | DISCUSSION

Analysis of 352 Australian estuaries revealed significant spatial variation among estuaries in habitat mosaics that followed estuarine geomorphic classes. Similar relationships between geomorphic classes and component habitats were apparent irrespective of the level of anthropogenic modification. These results suggest that the geomorphic classification scheme for Australian estuaries might also be useful for classifying estuaries according to the habitats they provide.

Mangrove and saltmarsh/saltflat habitats displayed the strongest differences in area among habitat classes. In both modified and unmodified estuaries, each was more abundant in the tide- than wave-dominated estuaries. Both mangroves and saltmarsh are known to be highly responsive to geomorphic and hydrological dynamics (e.g. Allen & Pye, 1992; Thom, Wright, & Coleman, 1975). In this study, the area of these key habitat types increased with estuary entrance width, tidal range, and catchment area. Tide-dominated estuaries generally have wide entrances, enhancing the penetration of seawater, as opposed to wave-dominated estuaries which tend exhibit more constricted entrances (Nicolas et al., 2010). The frequency and duration of tidal inundation has been shown to be crucial to the biomass of vascular saltmarsh plants, where wave action erodes and scours these habitat areas (Balke, Stock, Jensen, Bouma, & Kleyer, 2016; Mudd & Fagherazzi, 2016). Plant productivity has been observed to increase with tidal range, presumably due to greater rates of flushing and the consequent renewal of nutrients (Defne & Ganju, 2016; Morrisey et al., 2010). Furthermore, the major sediment movement that occurs in tide-dominated estuaries can redistribute sediment to support mangrove and saltmarsh accretion (Mudd & Fagherazzi, 2016; Woodroffe, 1995). By contrast, turbid water within tide-dominated estuaries largely precludes the growth of subtidal benthic macrophytes, such as seagrasses (Roy et al., 2001).

However, the strong relationship between estuarine geomorphic classes and habitat mosaics was driven not only by geomorphology and hydrology, but climate as well. Unsurprisingly, as climate drives estuarine geomorphology through its influences on waves and catchment runoff, and tides vary at regional scales, the distribution of the seven estuarine categories around Australia displayed considerable zonation (Harris et al., 2002). Whereas the southern coastline contained predominantly wave-dominated environments, the northern coast was tide-dominated (Harris & Heap, 2003). This latitudinal zonation of geomorphic classes meant that they not only differed according to the wave, tide and river forcing on which they were defined, but also variables such as light, temperature, and precipitation that are important determinants of plant growth (Admiraal, 1976; Beck et al., 2001; Saintilan, 2009). Among-estuary variation in each of mangrove and saltmarsh area was positively correlated with at least one of these climatic variables, and mangrove habitat area was negatively correlated to latitude. The coarse taxonomic resolution of this analysis was, however, unable to capture the opposing patterns of decreasing mangrove species richness and increasing saltmarsh species richness with increasing latitude (Adam, Wilson, & Huntley, 1988, Duke, Ball, & Ellison, 1988). Similarly, it did not consider how, at smaller scales, mangrove expansion is often at the expense of saltmarsh/saltflat area (Saintilan & Williams, 1999).

The lack of a statistically significant difference in habitat mosaics between modified and unmodified in most geomorphic estuary classifications was despite more than 85% of the Australian human population occupying the coastal zone, negative relationships between urbanization and saltmarsh and seagrass area adjacent to major Australian cities (e.g. Cambridge & McComb, 1984; Mitchell & Adam, 2009; Walker & McComb, 1992), and a positive relationship between sedimentation from land clearing and mangrove area (Rogers, Wilton, & Sanitilan, 2006). Where a signal of modification was seen, it was due to greater variability among modified than unmodified tidal flat/creeks, rather than a difference in median (Supplemental material, Table S1). However, it also possible that many Australian estuaries have not yet surpassed the threshold of degradation required to produce major ecological change (Borja et al., 2008; Lotze et al., 2006). Australian estuaries adjacent to major cities accounted for a fairly small proportion of the modified category, which was instead dominated by estuaries impacted by agriculture or smaller settlements. Modified Australian estuaries have a relatively short history of exploitation compared to many northern hemisphere estuaries and comparatively low anthropogenic nutrient inputs (Scanes, Coade, Doherty, & Hill, 2007). Nevertheless, the weak though non-significant trend for smaller areas of key habitats in modified than unmodified estuaries suggests that monitoring of habitat areas may potentially be a useful indicator of estuarine degradation.

Frameworks for the classification of marine habitats based on geophysical features of the environment have previously been proposed for Australia and other jurisdictions (e.g. Bax & Williams, 2001; European Commission, 2003; Galparsoro et al., 2015; Ramos, Puente, & Juanes, 2016; Roff & Taylor, 2000). The present research indicates that such an approach may be applied to estuaries too. Nevertheless, before other classification schemes based on hydrology and/or geomorphology are used to inform conservation and management (see Table 1), a relationship between their classes and estuarine habitat mosaics needs to be empirically verified as dominant habitat types vary among jurisdictions, and may vary in their sensitivity to climatic and hydrological forcing. While mangrove and saltmarsh/saltflat habitats were key discriminators between geomorphic estuary classifications in Australia, mangroves are notably absent from large portions of the North and South American coastlines and are not found in Europe (Giri et al., 2011). Instead, in these regions, saltmarshes are more abundant, extending to lower elevations on the shoreline that are more frequently inundated (Mudd & Fagherazzi, 2016; Radke et al. 2006). This is likely to accentuate the pattern seen in Australia of greater areas in tide- than wave-dominated estuaries. Furthermore, in areas where anthropogenic impacts, rather than climate and hydrology limit habitat types, geomorphic typologies may be poor predictors of habitat mosaics.

A typology of the habitat configurations that different types of estuary support will provide an ecological framework that supports estuarine conservation and management at the national scale. First, such typologies may, in combination with information on threats and risks to estuaries, be used to identify estuarine ecosystems most at risk of degradation. This would enable the resources required for more detailed habitat mapping and planning to be directed at these estuaries most at risk. Second, such typologies may be useful in identifying groups of ecologically similar estuaries across which similar approaches to management and conservation may be applied, and learnings shared. For example, an adaptive management approach may be applied across estuaries within a group, whereby the success of particular management strategies in one estuary is used to inform the application of management strategies to others in which key threatening processes and socio-economic values are also similar.

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Appendix: Supplemental material

Table S1. Mean (SE) area (in km^2) of habitat types present in unmodified and modified estuaries, of each of seven classes. WDD = wave-dominated delta; WDE = wave-dominated estuary; TDD = tide-dominated delta; TDE = tide-dominated estuary.

Estuary classification	Estuary condition	No.in analyses	Intertidal Flat	Mangrove	Saltmarsh/ saltflat	Tidal sandbank	Rocky reef	Coral	Bedrock	Floodplain	Seagrass
WDD	unmodified	25	0.57	5.49	9.58	1.21	0.02	0.07	0.06	0.09	0.02
			(0.038)	(0.394)	(1.266)	(0.183)	(0.002)	(0.010)	(0.012)	(0.011)	(0.002)
	modified	31	0.60	3.68	0.94	0.36	0.02	-	-	0.61	0.15
			(0.019)	(0.169)	(0.062)	(0.020)	(0.002)			(0.064)	(0.011)
WDE	unmodified	36	1.24	0.68	1.90	0.26	0.07	-	0.05	-	0.61
			(0.070)	(0.093)	(0.157)	(0.038)	(0.006)		(0.009)		(0.049)
	modified	61	2.63	2.07	3.28	7.23	0.10	-	0.39	1.36	2.55
			(0.163)	(0.174)	(0.192)	(0.887)	(0.003)		(0.050)	(0.106)	(0.120)
TDD	unmodified	17	5.90	14.32	77.99	3.30	0.01	0.06	-	2.82	-
			(0.606)	(1.203)	(9.734)	(0.495)	(0.003)	(0.014)		(0.669)	
	modified	16	3.55	11.94	7.78	1.41	0.03	-	0.01	1.16	0.51
			(0.308)	(0.804)	(0.552)	(0.164)	(0.008)		(0.002)	(0.111)	(0.097)
TDE	unmodified	26	5.31	46.34	95.9	13.46	0.12	-	0.29	4.59	0.27
			(0.329)	(3.390)	(10.835)	(0.917)	(0.011)		(0.055)	(0.482)	(0.036)
	modified	11	7.41	22.91	39.94	5.58	0.05	-	-	0.49	-

Estuary classification	Estuary condition	No.in analyses	Intertidal Flat	Mangrove	Saltmarsh/ saltflat	Tidal sandbank	Rocky reef	Coral	Bedrock	Floodplain	Seagrass
			(1.092)	(3.384)	(7.505)	(0.733)	(0.009)			(0.117)	
Tidal flat/creek	unmodified	45	2.16	4.47	9.97	0.57	0.02	0.01	-	0.25	0.02
			(0.042)	(0.115)	(0.255)	(0.039)	(0.001)	(0.001)		(0.022)	(0.003)
	modified	22	1.49	4.11	5.74	1.44	0.01	-	-	0.15	0.45
			(0.101)	(0.288)	(0.368)	(0.300)	(0.001)			(0.029)	(0.061)
Strandplain	unmodified	8	0.68	2.92	1.47	0.17	-	-	-	0.02	0.00
			(0.117)	(0.488)	(0.284)	(0.049)				(0.005)	(0.000)
	modified	4	0.14	0.03	0.72	0.05	0.01	-	-	-	0.00
			(0.030)	(0.014)	(0.358)	(0.023)	(0.003)				(0.000)
Other	unmodified	28	23.41	20.35	9.06	4.43	0.39	0.01	1.21	0.55	1.18
			(2.660)	(1.403)	(0.578)	(0.646)	(0.036)	(0.001)	(0.147)	(0.073)	(0.139)
	modified	22	10.50	6.91	6.27	3.75	0.49	-	0.11	0.31	12.31
			(1.023)	(0.527)	(0.420)	(0.413)	(0.053)		(0.018)	(0.050)	(2.515)

Table S2. *P*(perm) values for PERMANOVA pairwise *post-hoc* tests examining differences in habitat mosaics between estuarine classifications, in unmodified (n = 185) and modified (n = 167) estuaries. Significant results shown in bold. Abbreviations used: WDD = wave-dominated delta, WDE = wave-dominated estuary, TDD = tide-dominated delta, TDE = tide-dominated estuary.

	WDD	WDE	TDD	TDE	Tidal flat/creek	Strand-plain
Unmodified						
WDE	**0.001**	-				
TDD	**0.017**	**0.001**	-			
TDE	**0.001**	**0.001**	**0.011**	-		
Tidal flat/creek	**0.001**	**0.001**	0.052	**0.001**	-	
Strandplain	0.844	**0.011**	0.065	**0.001**	**0.001**	-
Other	**0.002**	**0.001**	**0.008**	**0.001**	**0.001**	0.084
Modified						
WDE	**0.001**	-				
TDD	**0.001**	**0.001**	-			
TDE	**0.010**	**0.001**	0.168	-		
Tidal flat/creek	**0.045**	**0.001**	**0.023**	0.063	-	
Strandplain	0.132	0.192	**0.001**	**0.026**	**0.018**	-
Other	**0.016**	**0.004**	**0.003**	0.199	0.059	0.105

Table S3. Results of Permutational Analyses of Dispersion (PERMDISP) testing for heterogeneity in dispersion between modified and unmodified estuaries, within classifications. Significant results shown in bold. Abbreviations used: WDD = wave-dominated delta, WDE = wave-dominated estuary, TDD = tide-dominated delta, TDE = tide-dominated estuary.

Classification	*t*	*P*(perm)
WDE	0.73	0.516
WDD	0.12	0.911
TDE	2.38	0.053
TDD	1.73	0.170
Tidal flat/creek	3.77	**0.005**
Strandplain	0.12	0.920
Other	1.78	0.097

Table S4. SIMPER analysis for unmodified estuaries examining the contribution of habitats to Bray Curtis dissimilarity measures between estuarine classes. Dissimilarity to standard deviation ratios are presented, with habitats with values ≥ 1.3 (highlighted in bold) considered good discriminators. WDD = wave-dominated delta; WDE = wave-dominated estuary; TDD = tide-dominated delta; TDE = tide-dominated estuary.

	Intertidal flat	Mangrove	Saltmarsh/ saltflat	Tidal sandbank	Rocky reef	Coral	Bedrock	Floodplain	Seagrass
WDE – WDD	0.81	1.21	1.21	0.51	0.50	0.30	0.24	0.38	0.58
TDD – WDD	0.94	**1.39**	**1.40**	0.57	0.27	0.29	0.18	0.41	0.29
TDD – WDE	1.08	**1.44**	**1.46**	0.58	0.50	0.23	0.16	0.37	0.50
TDE – WDD	0.85	**1.71**	**1.63**	0.90	0.51	0.19	0.24	0.61	0.40
TDE – WDE	0.93	**2.23**	**1.80**	0.94	0.65	-	0.28	0.59	0.54
TDE – TDD	0.87	**1.42**	**1.49**	0.81	0.53	0.16	0.24	0.59	0.32
Strandplain – WDD	0.94	**1.45**	1.16	0.52	0.27	0.28	0.20	0.44	0.43
Strandplain – WDE	1.03	1.14	1.25	0.61	0.55	-	0.17	0.39	0.60
Strandplain – TDD	1.03	**1.35**	**1.32**	0.59	0.28	0.22	-	0.38	0.23
Strandplain – TDE	0.90	**1.79**	**1.66**	0.91	0.56	-	0.26	0.60	0.36
Tidal flat/creek – WDD	0.93	**1.41**	**1.51**	0.50	0.37	0.25	0.19	0.31	0.24
Tidal flat/creek – WDE	1.12	**1.49**	**1.69**	0.60	0.47	0.15	0.17	0.26	0.57
Tidal flat/creek – TDD	0.99	1.25	**1.52**	0.61	0.31	0.21	-	0.39	0.12
Tidal flat/creek – TDE	0.88	**1.55**	**1.39**	0.85	0.56	0.11	0.25	0.60	0.36
Tidal flat/creek – Strandplain	1.00	**1.40**	**1.49**	0.60	0.29	0.14	-	0.27	0.17
Other – WDD	0.92	**1.31**	1.09	0.54	0.47	0.26	0.34	0.44	0.32

	Intertidal flat	Mangrove	Saltmarsh/ saltflat	Tidal sandbank	Rocky reef	Coral	Bedrock	Floodplain	Seagrass
Other – WDE	1.21	0.85	1.18	0.48	0.61	0.14	0.32	0.40	0.57
Other – TDD	0.92	1.27	1.19	0.58	0.40	0.20	0.28	0.39	0.28
Other - TDE	0.77	**1.69**	**1.34**	0.85	0.46	0.11	0.29	0.60	0.33
Other – Strandplain	1.09	1.28	1.28	0.52	0.46	0.13	0.31	0.52	0.32
Other – Tidal flat/creek	1.00	**1.35**	1.22	0.53	0.47	0.16	0.30	0.29	0.32

Table S5. SIMPER analysis for modified estuaries examining the contribution of habitats to Bray Curtis dissimilarity measures between estuarine classes. Dissimilarity to standard deviation ratios are presented, with habitats with values ≥ 1.3 (highlighted in bold) considered good discriminators. WDD = Wave-dominated delta; WDE = Wave-dominated estuary; TDD = Tide-dominated delta; TDE = Tide-dominated estuary.

	Intertidal Flat	Mangrove	Saltmarsh/ Saltflat	Tidal Sandbank	Rocky Reef	Coral	Bedrock	Floodplain	Seagrass
WDE - WDD	0.83	0.93	0.86	0.54	0.42	-	0.13	0.40	0.55
TDD – WDD	0.96	**1.75**	1.16	0.83	0.34	-	0.25	0.70	0.38
TDD – WDE	0.97	**2.10**	1.15	0.63	0.44	-	0.15	0.70	0.55
TDE – WDD	0.67	**1.47**	**1.46**	0.82	0.26	-	-	0.44	0.35
TDE – WDE	0.71	**1.34**	**1.43**	0.71	0.29	-	0.12	0.45	0.39
TDE - TDD	0.79	**1.60**	**1.30**	0.83	0.40	-	0.21	0.68	0.27
Strandplain – WDD	0.84	1.04	0.83	0.79	0.32	-	-	0.34	0.53
Strandplain – WDE	0.98	0.44	1.04	0.53	0.47	-	0.13	0.23	0.59
Strandplain – TDD	1.00	**2.82**	**1.30**	0.88	0.40	-	0.26	0.71	0.35
Strandplain – TDE	0.70	**1.43**	**1.55**	0.86	0.27	-	-	0.47	0.24
Tidal flat/creek – WDD	0.71	1.28	1.01	0.48	0.27	-	0.21	0.34	0.37
Tidal flat/creek – WDE	0.78	1.10	1.05	0.38	0.40	-	0.13	0.27	0.57
Tidal flat/creek – TDD	0.90	**1.53**	1.17	0.64	0.32	-	0.26	0.69	0.43
Tidal flat/creek – TDE	0.68	**1.55**	**1.36**	0.73	0.23	-	0.17	0.48	0.24
Tidal flat/creek – Strandplain	0.79	1.25	1.22	0.40	0.31	-	0.22	0.37	0.33
Other – WDD	1.01	1.07	1.01	0.62	0.57	-	0.35	0.34	0.45

	Intertidal Flat	Mangrove	Saltmarsh/ Saltflat	Tidal Sandbank	Rocky Reef	Coral	Bedrock	Floodplain	Seagrass
Other – WDE	1.04	0.86	0.99	0.55	0.57	-	0.24	0.30	0.62
Other – TDD	0.91	**1.49**	1.12	0.71	0.70	-	0.37	0.66	0.43
Other - TDE	0.83	**1.32**	1.29	0.75	0.33	-	0.30	0.48	0.33
Other – Strandplain	1.14	0.90	0.93	0.60	0.79	-	0.37	0.40	0.47
Other – Tidal flat/creek	0.91	1.16	1.01	0.54	0.64	-	0.35	0.49	0.47

Table S6. Results of Spearman's correlation tests (all $n = 290$) between key habitat types identified by SIMPER analysis as driving differences between estuarine classifications and correlated environmental variables identified by BIOENV analysis.

Habitat Type	Analysis Result	Mean Temperature	Mean Annual Rainfall	Catchment Area	Entrance Width	Tidal Range	Latitude
Mangrove	*Rho*	-	0.271	0.249	0.597	0.567	-0.737
	P	-	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Saltmarsh/Saltflat	*Rho*	0.512	-	0.355	0.602	0.453	-
	P	< 0.001	-	< 0.001	< 0.001	< 0.001	-

Chapter 6: A test of zeta-diversity as a metric for assessing loss in estuarine habitat mosaics.

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Abstract

Biodiversity monitoring is a key tool for conservation managers. Accurate monitoring data may inform risk assessments that allow decision makers to prioritise conservation targets or provide data with which to assess the success of previous interventions. Estuarine ecosystems are formed from mosaics of disparate habitat types distributed throughout a seascape. Biodiversity conservation in estuaries is strongly tied to the diversity and amount of physically complex habitats present within the ecosystem. Here we test the utility of zeta-diversity, a recently developed metric that describes the incidence patterns of species to reflect changes in the habitat mosaic present in estuaries. Using GIS, we generated samples of the habitats present in three different sizes of randomly placed quadrats in Nelson Bay estuary. We then simulated the loss of 10% and 30% of selected key biogenic habitat types and repeated the sampling procedure. Plots of the decay in zeta-diversity for different quadrat sizes, numbers of samples and levels of habitat loss were tested for the discriminatory power to identify homogenisation in the estuarine habitat matrix. This method would provide a valuable tool for conservation managers to monitor habitat loss. Zeta-diversity curves were able to distinguish between 30% and 10% or 0% levels of habitat loss but lacked the power to distinguish 10% habitat loss from the baseline data. This may be due to the low numbers of habitat types present in out model compared with the number of species usually present in ecological sampling.

Key words: Habitat monitoring; conservation planning, presence/absence; zeta-diversity; estuarine ecosystem; habitat mosaic

Introduction

Biodiversity is the total variability in assemblages of living organisms, including variation among and within species and, at the genetic level, among individuals (Pereira & Cooper 2006; Mace et al. 2012). Within ecosystems, high biodiversity provides redundancy for ecological functioning, increasing resilience to environmental perturbations (Tscharntke et al. 2005; Reich et al. 2012). Biodiversity is currently undergoing global decline and is expected to decline further into the future (Ceballos et al. 2015; Martin 2016). The aim of conservation management is to preserve biodiversity (Soulé 1985). However, conservation managers must also consider the distribution of organisms within the landscape and the pattern of habitats present in order to maximise biodiversity (Noss 1990).

Estuarine ecosystems generally encompass patches of multiple types of physically complex habitats that vary in both space (i.e. size, shape and arrangement) and time (in response to seasonal fluctuations or disturbance events), set within a sedimentary matrix (Gain et al. 2017). Biodiversity in estuarine ecosystems is expected to be strongly tied to the types and abundance of physically complex habitats present within the landscape and their pattern of spatial distribution (Mahoney & Bishop 2017). Therefore, estuarine conservation management must be concerned with preserving habitat heterogeneity.

Habitat mapping in estuarine ecosystems is suggested as an effective management tool but is often expensive and logistically challenging (Mahoney& Bishop 2017). While some schemes exist to monitor estuarine habitat mosaics (e.g. Creese et al. 2009), these are predominantly implemented in developed countries across temperate regions (McGeoch et al. 2010; Martin et al. 2012) and seldom provide long-term data suitable for tracking change over time (McGeoch et al. 2015). A method for assessing the loss of valuable physically complex habitats in estuaries requiring sampling of only subsets of entire estuaries and that provided a visual representation of change over time would be a valuable tool for conservation management in regions where funding for such activities is limited.

Zeta-diversity (Hui & McGeoch 2014) is a recent metric that robustly describes biodiversity patterns based on overlapping species in incidence records. Zeta-diversity is a measure of the mean number of species common to groups of *i* samples. The number of common species declines with *i* where ζ (zeta) is the mean species richness of all individual samples. Zeta-diversity is able to scale with grain and distance, making it useful for comparisons of biodiversity in ecosystems of varying spatial extent. Plots of the decay in zeta-diversity provide a visual representation of the incidence of species in multiple samples across an area of interest (Supplemental material; Fig. S1). Repetitive sampling across time would allow the comparison a time-series of decay curves, potentially visually demonstrating change in species richness across time.

Here, we examine the use of zeta-diversity for rapid assessment of habitat homogenisation in habitat-mosaic ecosystems, using a temperate Australian estuary as a study system. We use zeta-diversity to assess the loss of complex habitats from the habitat mosaic based on presence or absence of habitat types, rather than species, in sampling quadrats within the estuary. Specifically, we test the ability of a series of zeta-diversity decay curves, representing different levels of loss in key physically complex biogenic, to provide a visual representation of change in the estuarine habitat mosaic sufficiently powerful for conservation management.

Methods

Study system and design

We used Nelson Bay, a temperate, semi-diurnal estuary located approximately 200km north of Sydney, New South Wales, Australia, as a study system. The estuary has a total area of approximately 139km^2 and contains a variety of habitat types of varying degrees of physical complexity set within a sub- and inter-tidal sedimentary matrix (New South Wales Department of Primary Industries 2018). We identified the main habitat types present in the Nelson Bay estuary (Table 1) using a GIS habitat distribution map of the area (New South Wales Department of Primary Industries 2018) and images from the Google Earth Pro Version 7.1.5.1557 software package (Google Inc. 2018). While Nelson Bay contains substantial areas devoted to oyster aquaculture, these areas were not included as a habitat type as they are not naturally occurring.

Table 1. Main habitat types present in the Nelson Bay estuary and their total spatial extent. Seagrass habitats are separated by the genus or mix of genera present.

Habitat type	Area present (km^2)
Saltmarsh/saltflat	31.92
Mangrove	20.02
Seagrass: *Halophila*	0.07
Seagrass: *Posidonia*	3.56
Seagrass: *Posidonia/Zostera*	0.19
Seagrass: *Posidonia/Zostera/Halophila*	0.32
Seagrass: *Zostera*	11.65
Seagrass: *Zostera/Halophila*	0.36
Intertidal flats	11.99
Tidal sandbank	8.20
Subtidal sediments	42.46
Rocky reef	1.36
Bedrock	1.91

Data collection

We used the ArcGIS Version 10.3.1software package (ESRI Inc. 2017) to generate random points within the estuary with a minimum spacing from each other of 71m. These points formed the centres of non-overlapping sampling quadrats of 50m × 50m. Within each quadrat, the habitats present were identified using shape file layers present in the GIS map and Google Earth Pro images. We sampled the estuary three separate times, using 20, 40 and 60 sample quadrats. We then repeated the procedure using 250m × 250m quadrats with a minimum spacing between centre points of 354m and 500m × 500m quadrats with a minimum spacing of 708m. The nine differing sampling regimes used encompassed between 0.036% and 10.79% of the total area of Nelson Bay (Table 2).

Table 2. Proportion of the total area of Nelson Bay estuary directly appraised under nine different sampling regimes.

Quadrat size	Number of quadrats sampled		
	20	40	60
50m × 50m	0.00036	0.00072	0.00108
250m × 250m	0.00899	0.01799	0.02698
500m × 500m	0.03597	0.07194	0.10791

To simulate habitat loss in the estuary, we manipulated individual shape files in the GIS map, haphazardly removing 2km^2 of mangrove area from the estuary (a reduction of 10%), replacing this lost area with intertidal flats habitat. We also haphazardly removed 10% of each type of seagrass habitat present, replacing these lost habitat areas with subtidal sedimentary habitat. We then repeated our full sampling procedure for each of the three levels of quadrat size and three levels of sample number. Finally, we further manipulated the original GIS shape files to simulate a haphazard reduction of 30% in the areas of mangrove and seagrass habitats present before repeating our sampling process again in full.

Data analysis

The mean number of habitat types (ζ) shared across i quadrats (i.e. ζ_i) was calculated using an exact analytical solution (Latombe et al. 2018). This is equivalent to calculating the mean number of habitat types shared across all possible combinations of i quadrats from the set of quadrats. For each sampling regime, zeta-diversity of order 1 (ζ_1) is equivalent to mean number of habitat types across all quadrats (n = 20, 40 or 60). Normalised zeta-diversity was calculated by dividing each zeta-diversity value for each order by ζ_1 (i.e. ζ_i / ζ_1). To visually assess the effects of quadrat and sample size, we plotted the decay curves for normalised zeta-diversity for each level of sample size across levels of quadrat size and for each level of quadrat size across levels of sample size. We also plotted the decay curves for normalised zeta-diversity with n = 60 across all levels of habitat loss for each level of quadrat size. For each level of habitat loss in 500m × 500m quadrats with n = 60 samples, we used linear regression to calculate the slope, and its corresponding standard error, of that portion of the data where the value of normalised zeta was between one and zero (i.e. pre-asymptotic). Data were log transformed to achieve linearity prior to regression analyses. Calculated linear regression slopes for the three levels of habitat loss were compared for significant differences (at $\alpha = 0.05$) using the method of Kleinbaum et al. (1978). Intertidal flats and subtidal sedimentary habitats were excluded from analyses as they were considered to be the matrix setting in this estuary, with which lost complex habitats would be replaced, and their inclusion may mask the effects of habitat loss in our analyses. All calculations were done using the base installation of R version 3.4.2 (R Core Team, 2017).

Results

The frequency distribution of the number of habitats per quadrat and of the occurrences of habitat types across quadrats varied with the sampling regime (size and number of quadrats) employed (Supplemental material; Figs. S1, S2). Larger quadrat sizes produce slower rates of decay in normalised zeta-diversity. However, the effect of increasing quadrat size is influenced by sampling effort. The disparity between rates of decline of normalised zeta-diversity in 50m × 50m quadrats and larger quadrat sizes is clear at n = 20 quadrats but differences between 250m × 250m quadrats and 500m × 500m quadrats are not apparent at n = 20. At n = 40 quadrats, there is a visible distinction between 250m × 250m quadrats and 500m × 500m quadrats, but this pattern is not made more apparent by an increase of sampling effort to n = 60 quadrats (Fig. 1). However, at any size of quadrat, simply varying the number of quadrats sampled has little effect on the decay of zeta-diversity (Fig. 2).

At the maximum number of samples, n = 60 quadrats, there was no clear visible distinction between the plotted rates of decay of normalised zeta-diversity among levels of habitat loss using 50m × 50m or 250m × 250m quadrats. Even 500m × 500m quadrats failed to distinguish between the unmodified estuarine habitat configuration and the10% habitat loss treatment, although the 30% habitat loss treatment was visibly different to the other treatment levels (Fig. 3). Comparisons among linear regression slopes of the log-transformed zeta-diversity curves from 500m × 500m quadrats with n = 60 samples showed significant differences for the 0% vs. 30% and 10% vs. 30% levels of habitat loss, but not for the 0% vs. 10% comparison (Table 3).

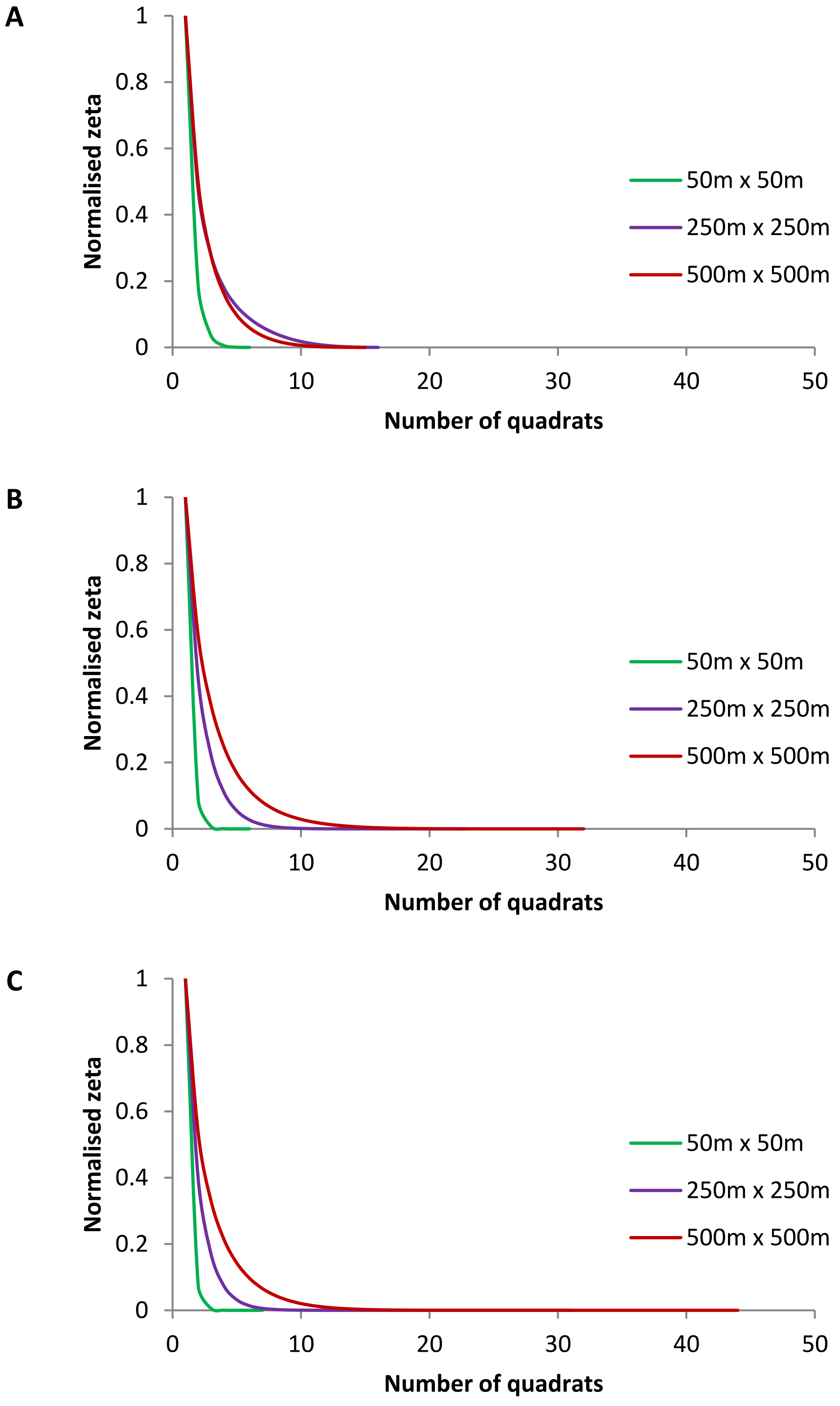

Figure 1. Normalised zeta-diversity curves from nine sampling regimes in original estuary habitat configuration (no habitat loss). Each graph shows sampling at three different quadrat sizes. Separate graphs show sampling using different numbers of quadrats: A) 20 quadrats; B) 40 quadrats; and C) 60 quadrats.

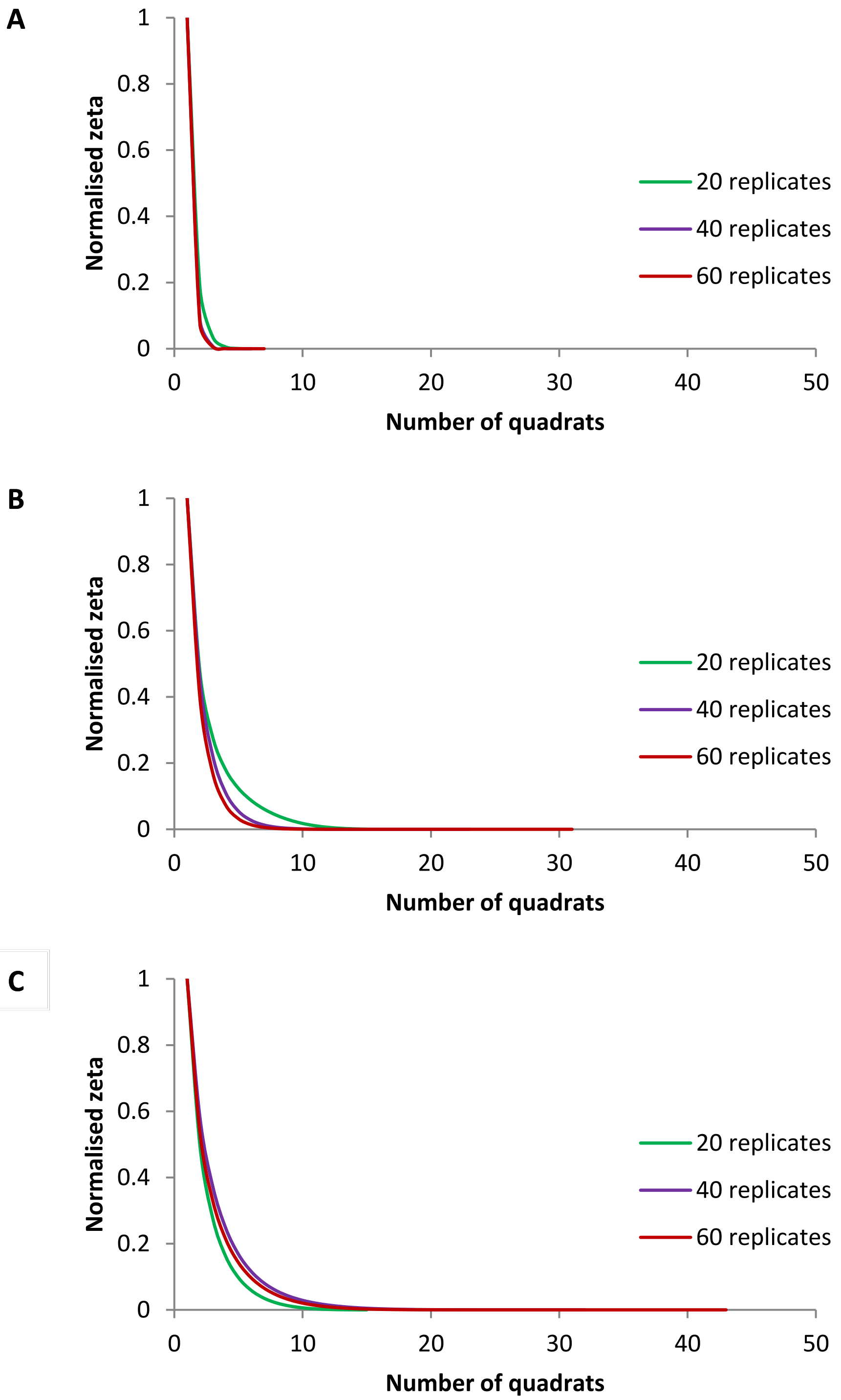

Figure 2. Normalised zeta-diversity curves from nine sampling regimes in original estuary habitat configuration. Each graph shows sampling of three different numbers of quadrats of the same dimensions. Separate graphs show sampling using different sized quadrats: A) 50m × 50m; B) 250m × 250m; and C) 500m × 500m.

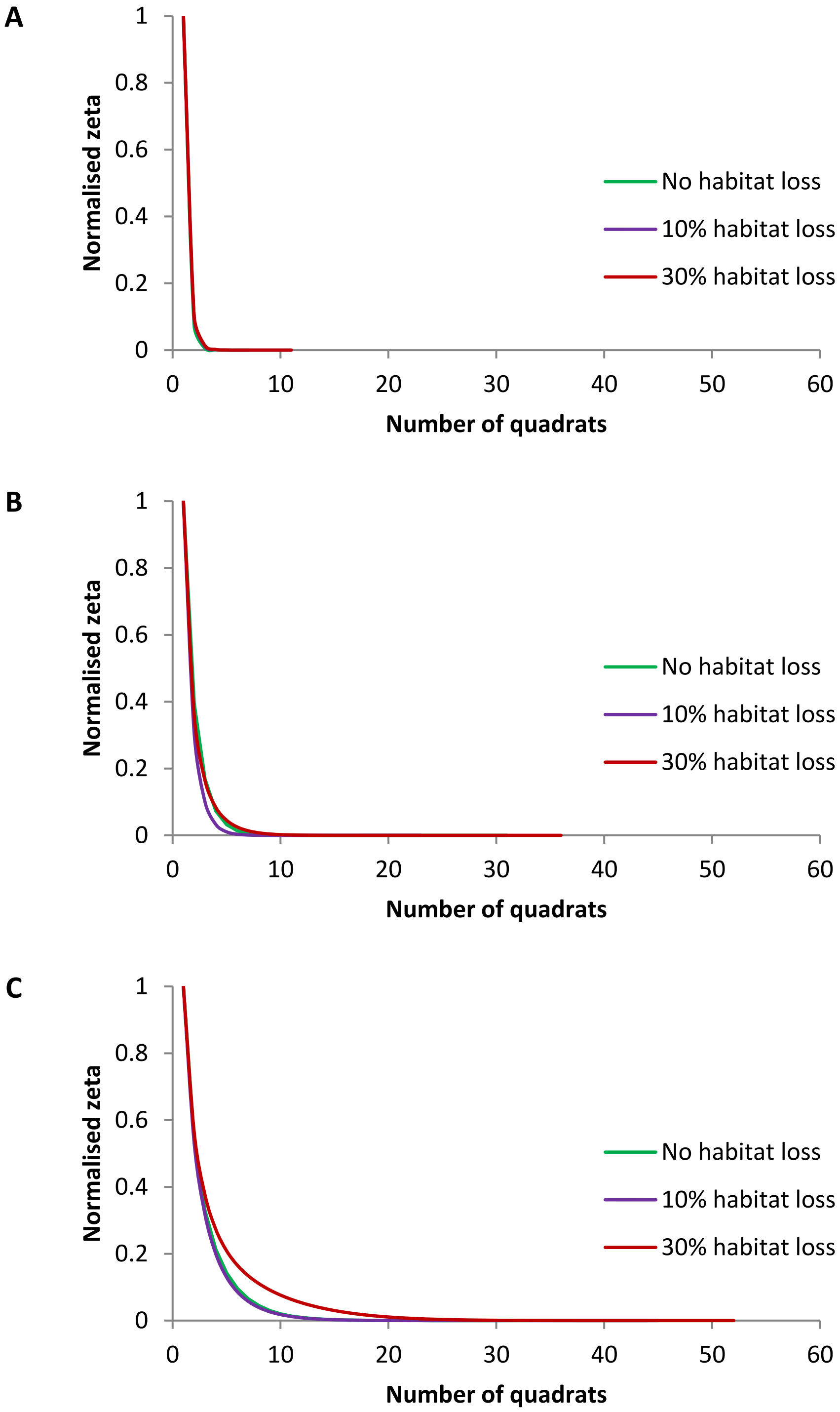

Figure 3. Normalised zeta-diversity curves from different sampling regimes in Nelson Bay. Each graph shows sampling (n = 60 quadrats) under the original estuary habitat configuration and two simulated habitat loss scenarios (10% and 30% loss of key biogenic habitat types). Separate graphs show sampling using different sized quadrats: A) 50m × 50m; B) 250m × 250m; and C) 500m × 500m.

Table 3. Results of statistical tests for differences in tests for differences between regression slops of log-transformed decay curves among levels three levels of habitat loss (0%, 10% and 30%) for 500m × 500m quadrats with n = 60 replicates. Significant results (at $\alpha = 0.05$) shown in bold.

Habitat loss levels compared	Regression slopes compared	$SE_{b1 - b2}$	z	p
0% vs. 10%	0.561, 0.378	0.138	1.322	0.186
0% vs. 30%	0.561, -0.057	0.115	5.368	< **0.001**
10% vs. 30%	0.378, -0.057	0.091	4.800	< **0.001**

Discussion

Zeta-diversity failed to capture the loss of complex physical habitats in our estuarine habitat-mosaic to an extent that would make it an effective conservation management tool. The concept is partially vindicated by the fact that, at very large sample sizes (500m × 500m quadrats), we were able to visually distinguish a 30% reduction in key mangrove and habitat types from the unmodified estuary state using plotted zeta-diversity curves. However, we were unable to distinguish a 10% reduction in those key habitats from the original habitat configuration. This visual pattern is mirrored by our statistical tests where the regression slope for 30% habitat loss was significantly different to the slopes for 0% or 10% habitat loss, but there was no difference between regression slopes for 0% and 10% habitat loss scenarios. Effective habitat monitoring for conservation management is likely to require a more sensitive tool. However, it should be noted that this theoretical trial of zeta-diversity for the purpose of monitoring the loss of physically complex habitats in mosaic seascapes is a first attempt to apply the metric in this manner and has not been trialled in the field. We are not aware of any use of zeta-diversity in the field for any monitoring purpose to date and would recommend trials of the concept in real-world situations.

As with all metrics of biodiversity, zeta-diversity is sensitive to the size of the sampling grain employed, as larger sampling units are able to capture greater target richness (Scheiner et al. 2011). A potential factor in the failure of zeta-diversity to capture habitat loss in our test system was the low total number of habitats present. Zeta-diversity was originally proposed by Hui & McGeoch (2014) for use in comparing species richness across multiple sites. Our zeta-diversity calculations used 11 habitat types, a realistic representation of the diversity of habitat types found in temperate estuaries, but a low number in comparison to the species richness present in many ecosystems. This may have resulted in the low diagnostic power observed. Our study utilised available habitat monitoring data. In estuaries, such datasets (where available) tend to focus on vegetated habitats to the exclusion of soft sediments. The dataset utilised here grouped all soft sedimentary areas into only three categories: intertidal flats, tidal sandbanks and subtidal sediments. This approach overlooks the diversity of environments present in soft sediments, where different sediment grain sizes and levels of bioturbation may result in a great diversity of biotic communities (Wang et al. 2010; Pratt et al. 2014). Mapping of differing soft sediment habitats would have increased the number of habitat types in our analyses and, potentially, the diagnostic power of our analyses.

The use of larger sampling quadrats may yield more discriminatory power by capturing more habitat types in each sample, but the effect of increasing quadrat size is likely to achieve an asymptote at some size level and may reduce the ability to effectively sample small arms and embayments in estuaries. Additionally, increased sample sizes are likely to significantly increase the logistical difficulties and expense of sampling in estuaries and other aquatic environments. However, sampling via GIS and satellite mapping data may, with some limited amount of ground-truthing, make larger sampling quadrats feasible. The use of larger quadrat sizes may also be feasible in terrestrial habitat mosaics of sufficient size to permit such grain.

As zeta-diversity is also sensitive to the number of samples employed and the distance between each sample (Hui & McGeoch 2014), estuarine ecosystems with smaller total areas than Nelson Bay may yield more power to discriminate between levels of habitat loss. In a geographically constrained area such as an estuary, sample number and distance are related, with either a larger number of samples or a smaller total sampling area resulting in less distance on average between each. However, a monitoring tool suited only to estuaries with very limited geographic distributions is unlikely to be adopted by conservation managers responsible for a diverse range of estuaries.

Biodiversity monitoring is likely to assume greater importance in the face of ongoing biodiversity loss globally (Pereira et al. 2010; Ceballos et al. 2015). The increasing gap between the cost of fully protecting biodiversity and the funding available to meet that expense (McCarthy et al. 2012; Martin 2016), will demand more cost-effective methods of performing conservation tasks such as the monitoring of changes in habitat mosaics. Metrics of community structure may yet be developed that make this process easy and affordable and the development of such theoretical models should be a priority for ecologists into the future.

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Appendix: Supplemental material

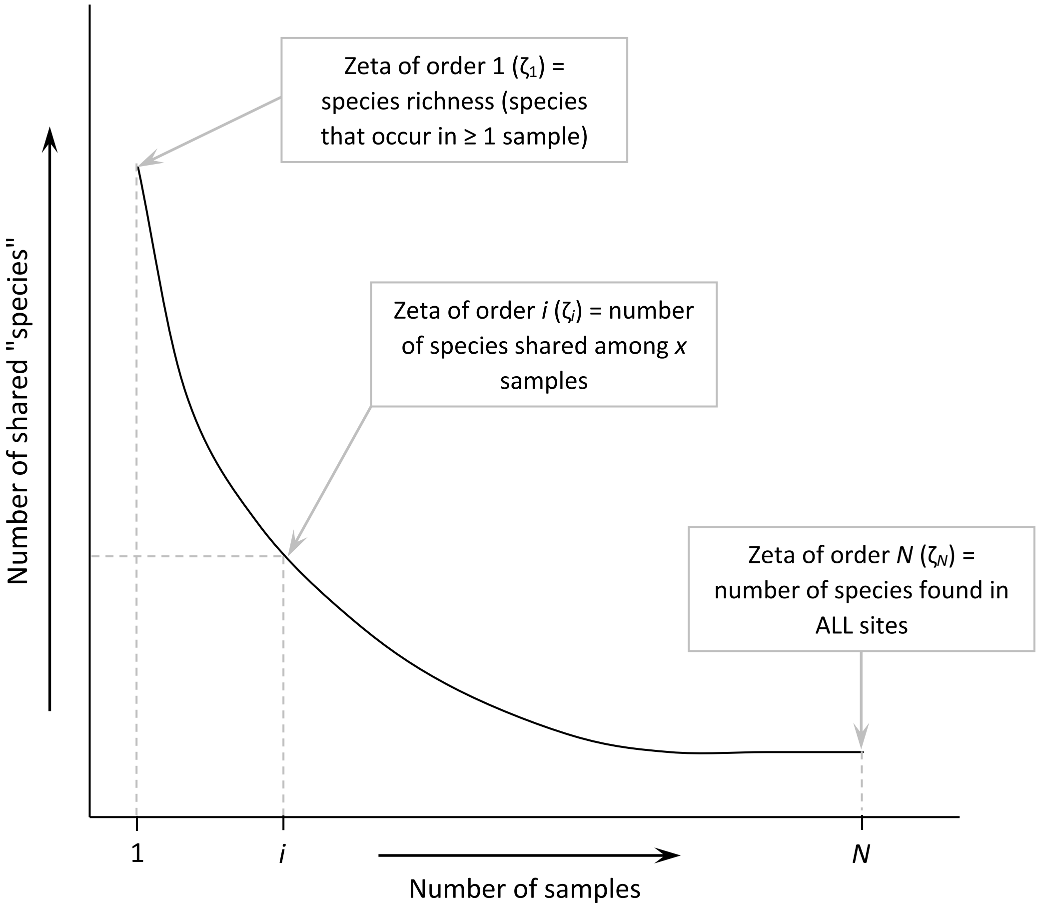

Figure S1. Annotated example of a zeta-diversity plot explaining how points on the curve are defined. Zeta (ζ) commonly declines as the number of samples increases. However, if all species were common to all samples then zeta-diversity would be represented by a horizontal line. As used in this scenario, species are replaced with habitat types within an estuary.

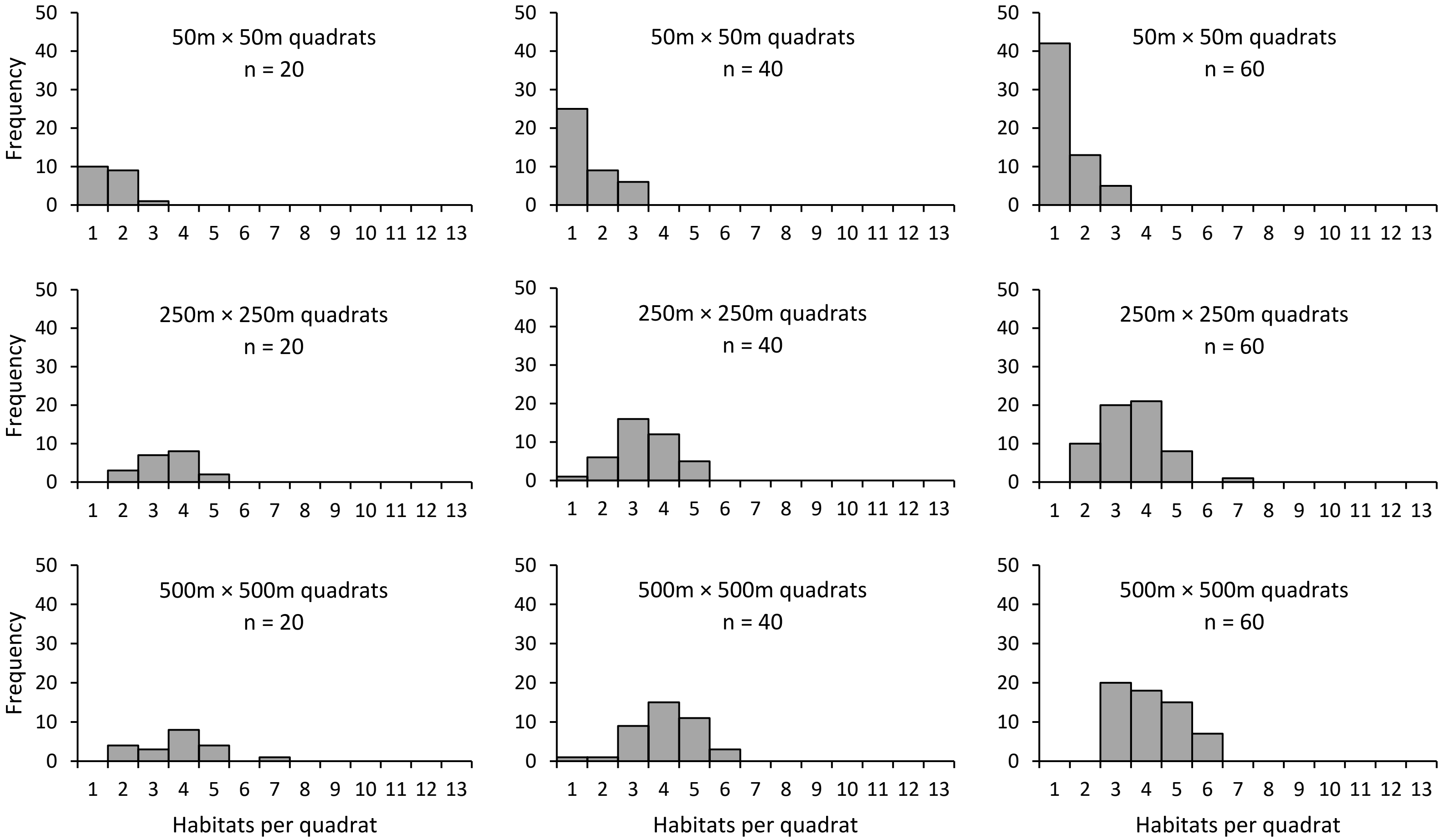

Figure S2. Frequency of differing numbers of habitats occurring in randomly positioned, non-overlapping quadrats in Nelson Bay estuary under multiple sampling regimes. Number of quadrats increases from left to right and quadrat size increases from top to bottom.

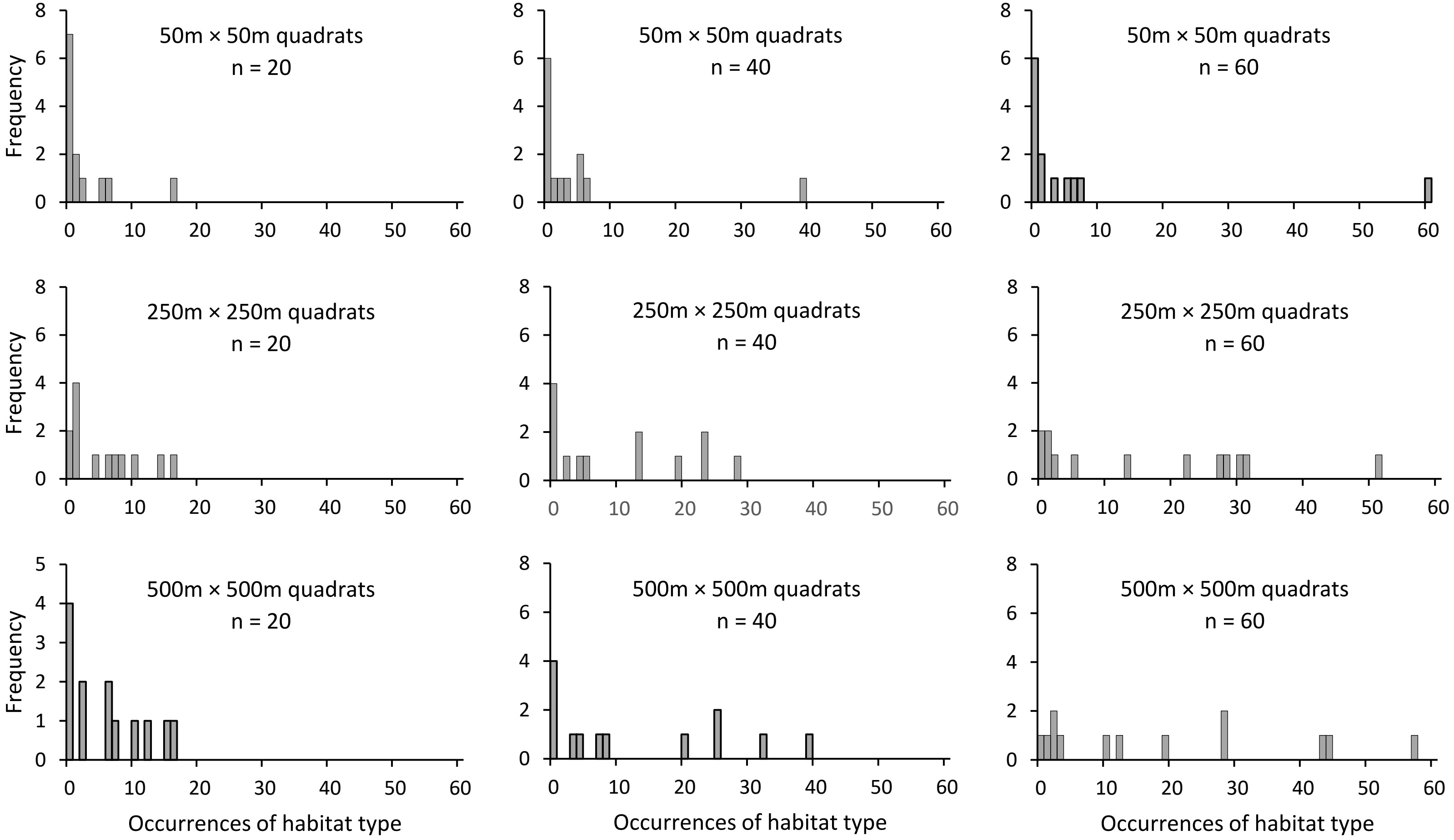

Figure S3. Frequency of occurrence of individual habitat types across randomly positioned, non-overlapping quadrats in Nelson Bay estuary under multiple sampling regimes. Number of quadrats increases from left to right and quadrat size increases from top to bottom.

Chapter 7: Discussion

Key findings

Estuarine ecosystems provide a wide range of valuable services such as food provision, water filtration, shoreline buffering and carbon sequestration, as well as aesthetic enjoyment and recreational opportunities (Barbier et al., 2011). Persistence of the range of unique ecosystem services provided by estuaries is underpinned by local biodiversity (Costanza et al. 2014), and hence depends on the conservation of that biodiversity. Globally, estuarine biodiversity is increasingly threatened, directly by anthropogenic activities that alter the abiotic environment, destroy key habitats or harvest species, and indirectly via anthropogenic climate change (Lotze et al. 2006; Worm et al. 2006; Halpern et al. 2008).

This thesis examined estuarine conservation management at two different thematic scales: 1) the fine grain of habitat patches and populations; and 2) the larger grain of whole ecosystems. At the finer scale, I tested the applicability to the estuarine environment of ecological theories describing the composition and functioning of populations and communities. At the ecosystem-scale, I assessed the effectiveness of key conservation management tools underpinned by those theories and tested a new idea for monitoring habitat heterogeneity across entire estuaries.

Island biogeography theory (MacArthur and Wilson 1963, 1967) forms the structural underpinning of much conservation planning in estuarine environments. My meta-analysis of studies testing for an effect of patch size or isolation on the taxonomic richness of associated communities (Chapter 2) showed only equivocal support for the application of island biogeography theory to estuarine seascapes. My observational studies of benthic invertebrate communities (Chapter 3) demonstrated that more recent theories of landscape ecology and the role of facilitation may be more valuable to estuarine conservation planning than island biogeography.

At the ecosystem-scale, I demonstrated that assessment criteria used to predict the risk of ecosystem collapse are of variable utility in estuaries (Chapter 4). These assessment criteria are designed around terrestrial ecosystems, usually centred around one foundational habitat type, whereas estuaries consist of a mosaic of physically complex habitats set within a sedimentary matrix. I showed that existing typological schemes designed to describe abiotic environmental factors such as geomorphology and hydrology in estuaries, also accurately reflect the habitat types present in estuaries (Chapter 5). Thus, existing typologies can be used to integrate conservation management with other management functions.

Monitoring changes in the composition of estuarine habitat mosaics is essential, both as a predictive tool for risk assessment and to measure the effectiveness of prior conservation interventions. In Chapter 6, I unsuccessfully tested a potential new method for monitoring habitat mosaics and assessment of habitat homogenisation. My findings support the importance of maintaining and maximising physically complex habitats, especially of biogenic origin, if we are to retain estuarine biodiversity.

Ecological theories underpinning estuarine conservation planning

Island biogeography theory explains the structure of terrestrial floral and faunal communities on oceanic islands as being structured by the independent and opposing forces of island size and isolation (MacArthur & Wilson 1963, 1967). This seminal ecological theory has been widely applied to estuaries, with habitat patches being considered as functional analogs for oceanic islands, with resident communities controlled by patch size and distance from the nearest neighbouring patch of similar habitat (Diamond et al. 1976; Harrison and Bruna 1999). This paradigm has informed the planning of conservation reserves and habitat restoration projects for several decades (Diamond 1975; May 1975; Gilpin & Diamond 1980). While I have some evidence from the synthesis of published studies to support a positive effect of patch size on taxonomic richness of associated communities in estuaries, the effect size was not constant among different habitat types and taxonomic groups (Chapter 2). The effect of patch size was statistically significant in coral habitats, but not in seagrass, shellfish or macroalgal habitats, and was significant among benthic, but not nektonic, taxa. The drivers behind these differences remain uncertain. Contrary to expectations, I found no evidence to support the theory that patch isolation influences community richness in estuarine habitats.

There are crucial differences between MacArthur and Wilsons' original concept of oceanic islands and estuarine habitat mosaics that may explain the lack of consistent support for patch size and isolation in estuaries. Among the studies used in my meta-analysis, there was no certainty that the communities sampled had reached the point of equilibrium envisaged by MacArthur and Wilson. Such non-equilibrium states are likely to occur in locations that have recently undergone habitat fragmentation, as is the case in many estuaries (Lotze et al. 2006). MacArthur and Wilsons' model assumed that the matrix surrounding and separating islands was totally hostile to species migrating among islands. However, the matrix between estuarine habitat patches is not completely hostile to aquatic organisms. The fact that benthic taxa showed a significant effect of patch size in the meta-analysis, where nektonic taxa did not, may indicate differing levels of patch fidelity driven by the relative abilities of the groups to move freely between habitat patches. For example, Jelbart et al. (2007) demonstrated that fish and shrimp freely move from one habitat to another for food or shelter at different tidal stages. The lack of a significant effect of patch isolation on community richness may have resulted from the very low number of published studies of this relationship. However, that such a fundamental principle is so poorly tested in estuarine ecosystems is, in itself, a surprising finding and highlights a gap in our understanding of how estuarine environments function.

In observational studies of benthic communities in two Australian estuaries, I have shown that the presence of mangrove habitats adjacent to seagrass beds increased the total abundance of organisms associated with the seagrass habitat (Chapter 3). This adds to the growing body of evidence that seascape configuration plays a role in structuring estuarine communities (e.g. Boström et al. 2011). Beyond the effect of habitat provision and the modification of the environment, patches of complex habitat within a seascape may further benefit biodiversity as the result of their pattern of spatial distribution (Robbins & Bell 1994; Micheli & Peterson 1999). Such patterns may alter the flow of propagules, water, nutrients and/or energy through the ecosystem (Clarke & Allaway 1993; Skilleter et al. 2005). The abundance of fish, crustacea and other invertebrate species varies in estuarine seagrass or intertidal oyster reef habitats in response to their proximity to patches of other habitat types (Saintilan et al. 2007; Lefcheck et al. 2016; González-Ortiz et al. 2016; Gain et al. 2017). Similarly, I have shown that the presence of intertidal mangroves may facilitate greater abundance of benthic invertebrates in nearby seagrass patches by providing additional nutrients. Such facilitation by complex biogenic habitats may extend the realized niche of associated species within estuaries (Bruno et al. 2003).

Assessment of conservation tools and implications for biodiversity management

My research shows that management tools, often designed for terrestrial environments or purposes other than conservation, are useful for planning conservation interventions in estuarine environments. Key tools in conservation planning include ecosystem risk assessment, which allows the prioritisation of conservation interventions, typological schemes that inform relevant comparison of conservation targets, conservation reserves that protect ecosystems from direct human impacts and monitoring schemes which provide raw data to inform risk assessments and measure the success of previous management activities (Chapters 4, 5, 6). The implications of this thesis for these key conservation tools are discussed below.

Risk assessment

Risk assessment is a widely used conservation management tool in terrestrial, aquatic and marine environments. In recent decades, there has been a move from species-based assessment of risk to community- and ecosystem-scale assessment, incorporating interspecies interactions and interlinakges between environmental conditions and ecological functioning. Risk assessment at these broader scales is rooted in metapopulation and landscape ecology theories. This shift in focus is demonstrated by the development of species sensitivity distribution models, which use multivariate species abundance data to predict safe levels of environmental contamination, and in the development of ecosystem-level schemes to assess risk of collapse such as that underpinning the International Union for the Conservation of Nature (IUCN) Red List of Ecosystems (Hewitt et al. 2009; Keith et al. 2013).

In this thesis I conducted a risk assessment of Chesapeake Bay (in the eastern United States) to assess the utility of the IUCN Red List of Ecosystems assessment criteria to estuarine ecosystems. To the best of my knowledge, the only previous application of the IUCN criteria in an estuarine ecosystem was in the Coorong estuary in South Australia (see Keith et al. 2013, Appendix S2, pages 185-197). The main assessment criteria of the Red List of Ecosystems are not equally applicable to estuarine environments (Chapter 4). The IUCN Criteria A and B focus on declining or limited distribution of the spatial extent of the ecosystem (Keith et al. 2013). Application of these criteria to estuaries, which tend to have small geographical size and ecosystem boundaries largely fixed by local geomorphology, may lead to inaccurate estimation of collapse risk and misinform management decisions. As with assessment findings in Chesapeake Bay, the assessment of the Coorong system found Criterion A to produce low estimates of risk but Criterion B to predict very high risk of ecosystem collapse. Risk assessments in both locations assumed that the ecosystems were unique, occurring in only a single location. Assessment Criterion B would classify these ecosystems as *Critically Endangered*. However, it should be noted that estuaries with similar gepmorphological and hydrological conditions are likely to demonstrate comparable ecological functioning (Chapter 5) and this may inform risk assessment where managers are responsible for multiple estuarine ecosystems. Criteria C and D, which focus on declines in the abundance of species and the resulting loss of key abiotic functions within ecosystems, are likely to be a far stronger indicator of risk in estuaries. In particular, the loss of biogenic habitat-forming species such as seagrass and mangroves are strong indicators of risk. In both Chesapeake Bay and Coorong, Criteria C and D proved to be the most effective predictors of ecosystem collapse. Interestingly, loss of seagrass habitat was a major predictor of ecosystem collapse in both estuaries, despite abiotic environmental changes being very different between the two locations.

As in estuaries, many ecosystem types contain mosaics of different structurally complex habitats set within a matrix of sediment or soil. It has been proposed that whole habitat mosaics represent the appropriate management unit for conservation (Law & Dickman 1998). Therefore, conservation management in other habitat-mosaic ecosystem types, such as playas, tropical lowland forests, floodplains and successional communities, is also likely to benefit from ecosystem-scale risk assessment methodologies, despite assessment criteria being largely designed around ecosystems dominated by a single habitat type. However, as many habitat-mosaic ecosystem types are geographically constrained by topology or geomorphology and may limited in geographic extent, even when in a functional and stable state, assessment criteria based on declines in spatial distribution or area of occupancy should be interpreted with caution, as in estuaries.

Typological schemes

Typological schemes facilitate the collective management of multiple locations and the triage of conservation interventions between similar ecosystems. Numerous classification schemes exist to classify geographic units for management purposes in estuaries (Chapter 5) and other environments (Turak & Koop 2008; Berg et al. 2014). However, to be effective for the conservation of biodiversity, typologies must reflect the ecology present. The several estuarine classification systems in use globally are based on the geomorphological, hydrological or physico-chemical factors of waterways, without reference to the resident ecology (e.g. Jang & Hwang 2013). While there are reasons to expect that estuarine ecology would be tied to local abiotic factors, this has never been empirically demonstrated, making the use of such typologies in biodiversity conservation uncertain. In an analysis of 352 Australian estuaries, I have demonstrated that the Australian estuarine typological scheme does adequately capture the mosaic of habitats present and does this well enough to allow conservation managers to identify similar estuarine types (Chapter 5).

This finding is likely to apply to estuaries in other countries where classification schemes are based on abiotic factors (e.g. Canada, New Zealand, UK, USA and South Africa), although analyses should be conducted to confirm that for each region or country. By extension, this finding is likely to apply to non-estuarine habitat-mosaic ecosystems where typlological schema are rooted in abiotic factors, provided that the abiotic variables measured are strongly related to resident ecological functioning. Furthermore, this finding has implications for the design of biodiversity offsets. While less effective in the conservation of biodiversity than avoidance or reduction of anthropogenic impacts, biodiversity offsets offer some mitigation of such habitat damage, provided that offsets are ecologically equivalent to impacted areas (Kiesecker et al. 2010). Therefore, effective planning of biodiversity offsets requires robust assessments of ecological comparability between sites (Quétier & Lavorel 2011), as demonstrated in Australian estuaries in this thesis.

Conservation reserves

Reserves are a widely used tool in the preservation of biodiversity in terrestrial, aquatic and marine environments across all climate zones (Margules & Pressey 2000). The design of reserves is largely rooted in island biogeography theory and species-area curves underlying that theory. While I show qualified support for this approach in estuaries (Chapter 2), there is a need to move beyond these basic principles in designing reserves for biodiversity conservation. MacArthur and Wilsons' seminal theory is now over a half century old and many factors other than simple patch size and isolation have been demonstrated to play key roles in determining patch quality and therefore associated biodiversity in terrestrial and marine settings.

Patch shape and volume are strongly correlated with patch area in many situations and are difficult to tease apart experimentally, and effects such as density and rugosity are difficult to control in natural settings. Accordingly, few studies to date have accounted for these conflated variables (but see Jelbart et al. 2006 and Hattori & Shibuno 2015 for examples of the disentanglement of patch area from shape and volume, or Bell & Westoby 1986 and Nanami & Nishihira 2003 for examples of manipulations of patch density and rugosity). It may even be that decoupling patch area from these other variables is not biologically meaningful. Gratwicke and Speight (2005) suggest a composite 'habitat assessment score' for shallow marine habitats that incorporates patch area, patch volume, surface rugosity, the variety of forms, and the size categories of interstitial spaces. Trials with this metric in tropic marine environments show it to explain 71% of the variation in observed species richness. The dispersal mechanisms and abilities of ecologically important species have been shown to influence connectivity within landscapes. For example, current and wind direction may affect connectivity between habitat patches as strongly as does geographical distance in terrestrial, riverine and marine ecosystems (Stoeckel et al. 1997; Soons et al. 2005; Almany et al. 2009). This may be highly important in estuarine and marine ecosystems where the spatial scale of propagule transport is often greater than in terrestrial systems (Carr et al. 2003).

While intended more for biodiversity enhancement than protection, habitat rehabilitation and restoration programs may also benefit from consideration of factors such as patch shape, physical relief and positioning within the wider landscape. Incorporation of these factors in the planning of rehabilitation and restoration projects may ensure that outcomes include not only the regeneration of lost or degraded habitat but also the enhancement of biodiversity in both analogous and dissimilar patches of connected habitat by the multilateral provision of additional nutrients and sources of colonisation.

Environmental and ecological monitoring schemes

Environmental and biodiversity monitoring schemes are essential for the planning, assessment and refinement of conservation interventions. Effective monitoring programs may also provide early warning of invasive species, reducing the costs of eradication or control programs and increasing the likelihood of these programs succeeding (Lindenmayer et al. 2012). However, while the need for monitoring schemes is widely acknowledged, current monitoring efforts are highly heterogeneous and often poorly designed, producing incomplete or inadequate datasets that impair planning and negatively impact conservation outcomes (Rondinini et al. 2006). Ecosystem-scale risk assessments of the Cheaspeake Bay and

Coorong estuaries both produced ratings of *Data Deficient* in several assessment categories, despite those two estuaries being relatively well studied in comparison with many estuarine systems globally. In general, terrestrial environments are more thoroughly studied than estuarine and marine realms and, for various reasons, even terrestrial monitoring effort is not consistent across different environments, countries and ecosystems (Brooks 2010; Lindenmayer et al. 2012). The distribution of vegetation types is generally well monitored due to the development of remote sensing technology, as is the distribution of many avian species due to the high involvement of citizen science groups. Similarly, the distribution and abundance of charismatic animal species such as pandas, African elephants and Australian macropods are well studied due to the popular support and availability of funding for such projects. However, monitoring of invertebrate species and communities is less common, except in cases of commercially valuable species such as bees and beetles involved in crop pollination.

In estuarine and coastal ecosystems, habitat monitoring data are more readily available for vegetated habitats such as seagrass beds and mangrove forests than for non-vegetated habitats. Non-vegetated habitats such as oyster reefs, mussel beds, tube worm mats, sponge gardens and rhodoliths are generally not well monitored, especially in subtidal areas where they are not highly visible. This presents a major research gap in the field that needs to be addressed urgently. Even different grain sizes and levels of bioturbation in estuarine soft sediments can represent distinct habitats with differing characteristic biota (Wang et al. 2010; Pratt et al. 2014). Mapping and preserving these distinct sedimentary habitats may prove crucial for the conservation of estuarine biodiversity but presents significant logistical challenges.

The final conservation tool tested in this thesis was the use of zeta-diversity curves as a method for monitoring changes in the composition of habitat mosaics (Chapter 6). This new metric was designed to describe declines in patterns of co-occurring species within randomly chosen sampling areas in an ecosystem (Hui & McGeoch 2014). Here I adapted the method to measure patterns of habitat incidences. As used, the method lacked sufficient discriminatory power to detect subtle changes in habitat mosaics, probably resulting from the relatively small variety of habitats for which mapping data were available. Accurate mapping of a wider range of subtidal habitat types, particularly if different sediment compositions were included, may well make this method a reliable monitoring tool.

Future directions

My thesis highlights several key areas of weakness in current estuarine conservation strategies (Chapters 2, 3, 4). To date, empirical evidence for many of the ecological theories explaining community structure is lacking for estuarine and marine environments. Even such foundational ideas as the effect of patch isolation on connectivity in estuaries have seldom been tested using estuarine habitat types and characteristic biota, despite being well investigated in the terrestrial realm (Chapter 2). Among published studies investigating these ideas, the majority are observational in nature. Such studies may establish correlation but are not able to assess causation. Without experimental evidence demonstrating a causal link, we cannot be confident that the correlation between patch size and community structure observed in many studies and predicted by MacArthur and Wilson (1963, 1967) is not caused by a third factor influencing both variables. Thus, there is a strong need for experimental investigations of all aspects of how patch morphology and position within the seascape of different habitat types affect community structure within the whole ecosystem. Experiments that isolate specific aspects of patch morphology such as area, volume, and density or rugosity will enable a fuller understanding of the actual effect of patch size. Of particular importance will be manipulated tests of patch isolation on communities across a range of taxa with varying modes of larval or juvenile dispersal and differing degrees of mobility as adults.

That habitat pattern affects the distribution of biodiversity in estuaries is now well demonstrated (González-Ortiz et al. 2016; Gain et al. 2017). This effect is the result of facilitation or mutualism between elements of the habitat mosaic. The stress gradient hypothesis (Bertness & Callaway 1994) predicts that such positive interactions are likely to become more common in estuarine ecosystems with increasing levels of environmental stress. However, the mechanics of this phenomenon are not yet well understood. Potential causative factors for the effects of habitat mosaic patterns include: 1) differing habitats providing a larger pool of species to potentially colonise adjacent habitats than would be available in monocultures; 2) changes in the current flow through estuaries caused by differing types of physical structure; and 3) varying inputs of nutrients within the overall habitat mosaic from differing habitat forming species.

Experiments investigating the effect of seascape configuration have, to date, largely looked at bilateral relationships between pairs of habitat types (Chapter 3). Multilateral experiments incorporating three or more types of complex physical habitats may allow researchers to tease apart the direction and nature of facilitations or mutualisms in the broader seascape. However, such experiments will inevitably involve complex logistics and require significant resources.

An eventual goal for estuarine conservation should be the creation of comprehensive functional mathematical models of ecosystem functioning. Such models are mandated by the International Union for the Conservation of Nature in risk assessment Criterion E of the Red List of Ecosystems and would inform conservation interventions across a wide range of scenarios and provide a strong planning tool (Keith et al. 2013). Some steps have already been taken in this direction (e.g. Webster 2007) but an understanding of the key ecological processes and interactions in estuaries discussed above is still lacking in many areas.

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