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**Influence of seasonal variability and salinity gradients on
benthic invertebrate assemblages in tropical and subtropical
Australian estuaries**

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Statement of the Contribution of Others

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Supervision

- Professor Richard Pearson
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Abstract

I examine the influences of three key factors (habitat type, climatic regimes, floods and associated salinity regime changes) on the structure of benthic invertebrate assemblages of tropical estuaries.

I compared the habitat-specific invertebrate assemblages of the full spectrum of habitat types available in one region of Deluge Inlet, a near-pristine estuary. There were distinct faunal assemblages associated with particular habitat types that related to sediment size and presence/absence of seagrass. The results of this study laid the foundation for the following studies in establishing the need to sample a single habitat type to facilitate spatial comparisons. Consequently, I selected bare sand for subsequent sampling because this substrate type was available in all estuaries and estuary regions studied.

I then examined the influenced of climatic regimes (wet tropics, dry tropics and dry sub-tropics) on estuarine benthic invertebrate assemblages. The benthic assemblage in wet tropic estuaries differed from assemblages in dry sub-tropic estuaries, with many taxa only recorded in wet tropics estuaries and vice versa. There was little overlap of species between climatic regimes, particularly in upstream transitional zones (i.e. areas at the estuary/freshwater interface subject to substantial seasonal variation in physical conditions). However, a common pattern seen in all ten estuaries studied was distinct differences in faunal assemblages between the mouth and upstream transitional assemblages.

In the third part of this thesis I examined the effect of wet-season floods and how changes in salinity regimes along the downstream gradient of estuaries affected invertebrate assemblages. Following the seasonal flood, upstream assemblages underwent radical restructuring ranging from the total loss of taxa from some sites to significant decreases in diversity and abundances at other sites. The recovery of faunal assemblages after the flood varied between sites and appeared to be mainly a function of the location of the site in relation to freshwater input (i.e., sites closest to freshwater

input were more adversely affected than sites further away from the source of the freshwater input). Clearly, although flooding is a natural occurrence in tropical estuaries, it can have a profound effect on macrobenthic invertebrate assemblages by greatly reducing and/or eliminating taxa, particularly in the upstream reaches at times of low salinity.

These studies provide detailed understanding of benthic assemblages in a range of North Queensland estuaries, of the differences in mouth and transitional zones and of how assemblages respond and recover after a flood. Understanding these patterns and processes is essential in order to understand the ecological functioning of the systems and as a precursor to effective management.

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Chapter 1: General introduction

This thesis addresses several broad questions regarding the spatial and temporal dynamics of the benthic fauna of tropical estuaries. Although there is increasing understanding of the ecology of tropical estuarine fishes (Kathiresan 2014, Lacerda et al. 2014, Reis & Santos, 2014, Sheaves et al. 2014c, Arevalo-Frias & Mendoza-Carranza 2015) there is much less knowledge about other components of the ecosystem. Such knowledge is required for a more comprehensive understanding of food webs that are important to natural ecosystems and to recreational and commercial fisheries. Without such knowledge effective management may not be possible, particularly in the face of anthropogenic pressure such as modified flows, pollution and climate change.

Estuaries and their surrounding littoral landscapes are places of transition between land and sea and between freshwater in the upper reaches and saltwater from the ocean (Levin et al. 2001). These salinity gradients are one of the main features characteristic of any estuarine ecosystem (Telesh and Khlebovich 2010) and are one of the major drivers of variations in floral and faunal patterns and ecological processes along estuaries (Skylar and Browden 1998). Estuaries are among the most productive ecosystems in the world and they provide many ecosystem services and functions including erosion control, filtration of water as it flows from land to sea, regulation and cycling of nutrients, and habitat for plants and animals (Levin et al. 2001, Winkler et al. 2003, Telesh & Khlebovich 2010).

Estuaries and Transitional Wetlands

By definition, estuaries share a suite of uniting features: they are partly enclosed coastal bodies of water within which there is a measurable variation of salinity due to the mixture of sea water with fresh water derived from adjacent land (Day 1980). Some important details were added to the definition of an estuary by recognising that estuaries can be subdivided into three regions: (1) a freshwater zone characterized by lack of ocean salinity but subject to tidal rise and fall of sea level (only apparent in estuaries with year-round freshwater inflow); (2) a transition zone, where freshwater from the upper reaches mixes with saltwater from the downstream reaches; in the dry season, the transition zone may only occupy a short span in the estuary, but in the wet

season it can be extensive, impacting greatly on the marine organisms in the estuary; and (3) a mouth zone that maintains salinity around that of seawater, except during large river-flow events (Kennish 2002). While estuaries share a number of features in common, they also can vary considerably in, for example, the length of the estuary, size of catchment area, modifications to estuary (e.g. dams and weirs), the amount of development around the estuary, pollution, nutrient input and differences in taxa (Kennish 2002). While there are many definitions and parameters used to try to define an estuary, there is no one single definition that suits all; however, one feature that is clear is that freshwater flow has a major impact on the estuarine fauna. Seasonal floods are a feature of many tropical estuaries and can be a major driver of change. Many parts of the tropics display strong seasonal alternation of weather patterns. Rather than variable year-round rainfall, tropical areas often have an extended dry season when little or no rain falls, followed by an intense monsoon-driven wet season. The seasonal change is usually rapid, with the dry season drought broken by intense rainfall events often resulting from cyclonic disturbances. The impact of this seasonal change is most extreme in the transition zone (Gillanders & Kingsford 2002) (Figure 1.1). At the end of the dry season salinities in transition zones are often around that of seawater or are even hypersaline (Sheaves 1996a). The rapid influx of freshwater from the intense seasonal flooding results in a substantial reduction in salinity, often altering the salinity in transition zones from marine or hypersaline to freshwater in a matter of minutes.

Estuarine invertebrates are integral in the structure, health and functioning tropical estuaries. For example, many benthic invertebrates are important in estuarine detrital food chains (MacFarlane et al, 2000). By processing detritus, they play an important role in carbon and nutrient cycling and in the transfer of energy to higher trophic levels (Camilleri 1992). In addition, burrowing by estuarine invertebrates aerates the soil, and creates conduits for water and nutrient exchange as well as providing habitats for other organisms (Ridd 1996). Furthermore, many estuarine invertebrates are of significant commercial importance, for example the mud crab *Scylla serrata* (Meynecke et al. 2012) and *Penaeus* prawns (Vance et al. 1990).

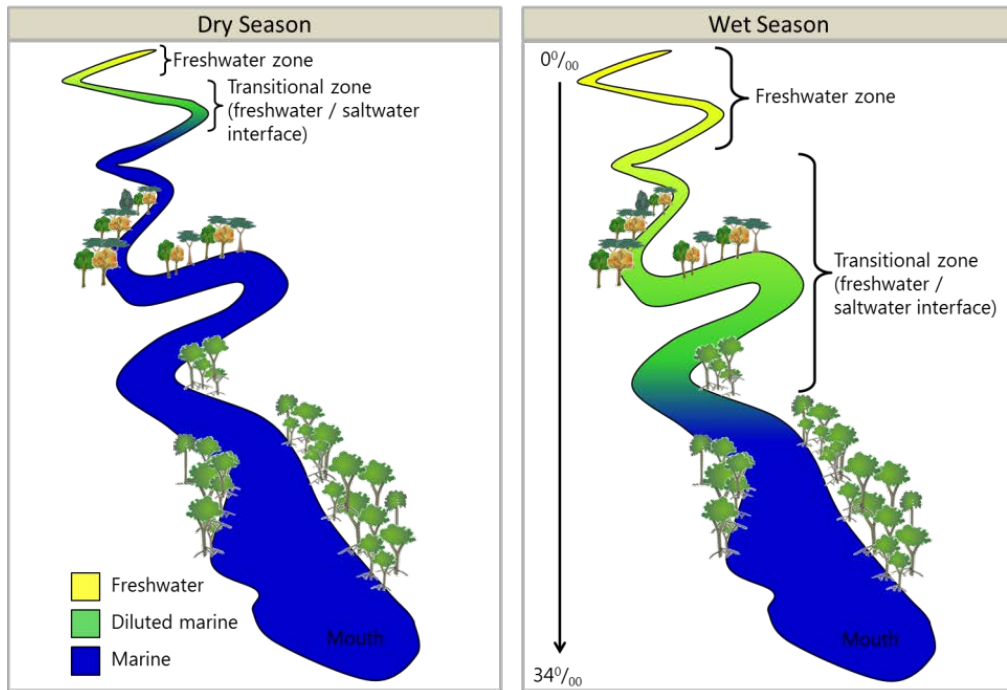


Figure 1.1. Changes in freshwater and transitional zones and salinities from the dry season to the wet season.

Impacts of Catastrophic Salinity Change on Fauna

Many studies of tropical and temperate estuaries document changes in taxa along the estuarine salinity gradient (Boesch 1977, Engle & Summers 1999, Attrill & Rundle 2002, Gimenez et al. 2005b, Barros et al. 2012). This gradient is highly dynamic in tropical estuaries, particularly in the estuary transition zone. The intense seasonality of many tropical estuaries leading to catastrophic salinity changes means the inhabitants of transition zones are in a constant state of flux, driven by flood-driven extinction of fauna dependent on marine conditions, followed by faunal recovery, then on to another sequence of flood-driven extinction. Fish and motile invertebrates, such as prawns, are able to respond to these changes by migrating downstream where conditions are more favourable and then returning upstream when conditions improve, with the extent of this migration depending on species-specific factors (Sheaves 1996a). In contrast, most benthic invertebrates have little or no ability to relocate during floods; therefore, they bear the brunt of rapidly changing salinities usually resulting in greatly reduced abundance and diversity following flooding events (Moverley et al, 1986, Kanandjembo et al. 2001). Substantial wet-season-driven changes to transition-zone benthic

invertebrate assemblages propagate throughout the food web to have major impacts on fauna at higher trophic levels areas because many fish rely on benthic invertebrates as the primary food source (Davis et al. 2014a).

Despite the widespread occurrence of intense seasonal change in the tropics, there is considerable variation in the timing, duration and magnitude of freshwater flow events – variation that is likely to have far reaching impacts on estuarine assemblages (Drinkwater & Frank 1994, Gillanders & Kingsford 2002) For example, at the most basic level, the tropics can be divided into wet and dry tropics, based on differences in the distribution and amount of rainfall received. The result of this variability is highly variable flooding patterns and differences in the duration of freshwater input. The geomorphological setting of an estuary can also have an impact on its rainfall regime. For example, in Australia, estuaries along the north-east coast of Queensland are backed by the mountainous Great Dividing Range that tends to channel freshwater flows into distinct drainage systems, resulting in relatively rapid runoff to the sea. In contrast, the Gulf of Carpentaria has a broad floodplain extending hundreds of kilometres inland, so that monsoonal rainfall floods extensive areas of flat plains leading to long retention of floodwaters across the floodplain. These contrasting situations are likely to have quite different consequences for the benthic fauna of estuaries. There are also variations the amount of rainfall received from year to year, and more extremely so in dry tropics areas. These variations in the strength of the wet season may be linked to differences in the number of extreme events, such as cyclones, that are often the initiators of major rainfall.

Climate change has the potential to exacerbate these differences, with predictions for Australia of increases in rainfall variability and in the number of severe cyclones – situations that are likely to lead to more intense, but more unpredictable, flooding (Kang et al, 2015). This potential increase in the extent, duration and periodicity of change has substantial implications for both the inhabitants of estuaries and estuary functioning. For example, increased rainfall variability may result in many wet tropics streams moving towards dry tropics flooding patterns for years at a time, preventing

them from maintaining their characteristic wet tropics seasonal flow patterns. This is likely to result in fundamental changes in faunal assemblage and ecosystem function.

Ecosystem Effects

There has been little study of the benthic infauna of the transition zones of tropical estuaries (Davis et al. 2014a). As a result, there is no detailed understanding of how seasonal changes influence tropical infauna. However, based on evidence from temperate systems, and that the understanding that extreme wet season flooding has a significant impact on benthic infauna (Ecoutin et al. 2005), it would be expected that the extreme seasonality of tropical estuarine transition zones would result in very dynamic faunal patterns. Despite freshwater inflow being one of the most influential processes affecting benthic invertebrates in estuaries (Sklar & Browder 1998), there is no understanding of exactly what components survive the impacts of extreme seasonal change, how resilient tropical transitional benthic fauna are, what the pattern of recovery of assemblages is in these transitional zones, or how these changes influence the food webs and functioning of estuaries. Gaining this understanding has far-reaching implications. For example, many fish that reside in transitional zones rely on benthic infauna as their primary food source; however, when floods occur, benthic infauna abundances decline or disappear, thereby forcing the fish to move downstream to find food (Russell & Garrett 1983, Baker & Sheaves 2005). However, while this seems like a simple solution the situation is actually much more complex. Piscivorous species such as barramundi (*Lates calcarifer*) undergo obligate seasonal migrations through transition zones to upstream freshwater nursery habitats (Davis et al. 2014a), and rely on the resilience of transition zone food webs for nutritional support during these migrations. Consequently, the speed and pattern of recovery of benthic assemblages may be critical to successful migration of these species.

As well as dynamic impacts on distributions and utilisation of transitional zones by higher trophic levels, spatial variations in the benthic fauna of transitional zones have substantial implications. In general, faunal distributions have been explained by physical factors such as temperature, pH, turbidity and salinity (Ysebaert et al. 2002, Gimenez et al. 2005a, Gimenez et al. 2005b). However, benthic assemblages may also

be influenced by a range of biological factors (e.g., primary productivity, competition, predation, acclimatisation). Natural seasonal and inter-annual changes in these variables can also modify recruitment success and mortalities of individual species, and consequently the community structure of the benthos. A recent study of fish distribution in a number of sites in a transitional wetland in north-eastern Australia (Davis et al. 2014a) sheds light on how the distribution of benthic invertebrates can influence the distribution of fish assemblages. Davis et al. (2014b) found that particular fish assemblages were associated with particular habitats. For example, high elevation sites had specialist fish assemblages, while low elevation sites had generalist fish assemblages. Although variables such tidal connection explained some of the differences in fish assemblage structure, a considerable proportion remained unexplained. When Davis et al. (2014b) examined the benthic assemblages at these sites they found that the patterns of distribution of invertebrates mirrored fish distributions, with assemblages of higher-elevation sites differing from those of lower-elevation sites. This study illustrated the intimate connection between benthic invertebrate assemblages and fish assemblages and that the relationship between the two trophic levels influenced the spatial distribution of fish assemblages.

Implications

Clearly, faunal assemblages in transitional wetland systems are structured by multiscale local and regional environmental and biological processes. While there is information about fish and invertebrates in these areas, very few studies have highlighted the various ways these habitats are utilised and their importance. For example, many species, including prawns (Collocott et al. 2014) and barramundi (Russell & Garrett 1985), utilise transitional zones for part of their life cycle, then as adults move downstream, while other species pass through transitional zones on their way upstream to freshwater nursery grounds. Without transitional zones none of the above would happen and the functioning of estuaries as we know it would be very different. Consequently, benthic infaunas are a crucial link in upper estuarine food webs, and underpin key processes occurring there. In particular, they are important in supporting fish moving into and through transition zones as necessary components of seasonal and life-history migrations. Consequently, while an understanding of fish ability to

utilise particular habitats is important, understanding cannot be complete without knowledge of infauna because fish recolonization and the connectivity processes require resilient, predictable and appropriate benthic-based food webs.

The lack of understanding of the ecology of transitional waterways has far-reaching implications in the human-modified landscape. Estuaries are often the focus of human activities, which have caused modifications to the physical characteristics of estuaries through dredging, land reclamation, industrial development, recreational and tourist development (Borja et al. 2011), dams and bund walls (Sheaves et al. 2007) as well as anthropogenically mediated changes such as climate change, pollution, blackwater events and estuary repair.

Natural phenomena, such as floods and blackwater events (large quantities of organic material washed into estuaries generally during floods), cause significant impacts on benthic assemblages in transitional zones, although, in an unmodified environment, their impact generally lasts for a short period of time and assemblages are able to recover (Magalhaes Neto et al. 2010). Anthropogenic activities produce additional complicating factors that introduce great changes into benthic assemblages in transitional zones. For example, the construction of dams or bund walls changes the natural flow, connectedness and functioning of the estuary, thereby creating a permanent impact on assemblages (Magalhaes Neto et al. 2010). In addition, increased frequency and severity of rainfall events resulting from climate change could lead to prolonged flooding periods, with insufficient time for assemblages to recover (Magalhaes Neto et al. 2010). The pressure from normal seasonal climatic events is alleviated shortly after the phenomenon occurs, in contrast to anthropogenic disturbances that are continuously exerted over benthic communities.

Objectives

Despite the obvious ecological importance of estuarine transitional zones and the wide range of human pressures on them there is an almost complete absence of knowledge about their benthic invertebrate assemblages and how they respond to, and recover from, flooding events. Consequently, the overall objective of this project was *to understand the consequences of the interplay of fresh and marine influences on benthic*

infauna of estuarine tropical transition zone environments, in particular to investigate the *patterns and processes of loss and recovery and how these intersect with anthropogenically mediated change*. Understanding the dynamics of the benthic infauna of transition zones will help in explaining the drivers of broader faunal change in transitional zones, and identifying the challenges faced by components of the fauna that utilise transition zones and rely on the nutritional support of benthos-based food webs.

To address this objective, this thesis addresses four specific aims:

- 1: To develop a detailed understanding of habitat-specific relationships of macrobenthic assemblage of a tropical estuary (Chapter 2). The results of this study underpin the sampling design in subsequent studies.
- 2: To establish the nature of the macrobenthic invertebrate assemblage of transitional wetlands and the extent to which they differ from the fauna of other parts of tropical estuaries (Chapter 3).
- 3: To develop a detailed comparative understanding of the spatial and temporal changes in the structure of estuarine macrobenthic assemblages along upstream gradients in tropical and sub-tropical estuaries across climatic regions (Chapter 2).
- 4: To determine how the asymmetric annual alternation between marine and freshwater conditions shapes macrobenthic assemblages of transitional wetlands and, in particular, to understand the nature and pattern of response to and recovery from freshwater flood events (Chapter 4).

Chapter 5 synthesises the results of the foregoing chapters – to draw together main findings of this thesis

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Chapter 2: Benthic invertebrate habitat preferences; differentiation at high taxonomic levels

Abstract

Estuaries consist of a mosaic of different habitat types (e.g. sand, mud and seagrass) that are often utilized by different taxa in different ways. However, many studies of estuarine benthic invertebrates fail to account for these habitat differences and produce a picture of the faunal assemblage that is homogeneous across a range of habitats, which is rarely the case. In this study I examined the influence of different habitat types on macrobenthic invertebrate assemblages. Five samples were collected (using a van Veen grab) from eight different habitat types (e.g. sand, mud, algal and seagrass beds) in the mouth region of Deluge Inlet, a pristine estuary on the north-east coast of Queensland, Australia. Habitat differences had a profound influence on faunal assemblage structure. Some taxa inhabited a wide range of habitats (e.g. fine and coarse sand) while others showed strong habitat preferences (only occurred in mud and *Halophila ovalis* site). For example, the two bivalves *Gari* sp1 and sp4, were almost completely confined to sand habitats without organic matter (algae or seagrass), whereas another bivalve, *Dosina alta*, preferred habitats containing substantial amounts of organic matter. Although it would be optimal to sample all habitat types in estuaries, this is not always possible as not all tropical estuaries have all the various habitat types. Therefore, for my broad scale and fine scale study sand habitats were sampled as they were the dominant habitat type found in all the estuaries. This allows for valid comparisons of the structure and functioning of the estuarine benthic assemblage in these habitats.

Introduction

Macrobenthic invertebrates are key contributors to estuarine ecosystem functions. For instance, their bioturbation activities, (e.g. feeding, tube-building, burrowing, locomotion and excretion), substantially influence the exchange of materials between the sediment and the overlying water column (Aller & Aller 1986, Hansen & Kristensen 1997). Macrobenthic invertebrates also comprise a major component of food webs

within estuarine ecosystems; they integrate detrital material and other primary food sources into food webs (Riisgard 1991), and are the major food source for many fish (Hyndes & Potter 1997, Chuwen et al. 2007) and birds (Moreira 1997, Lourenco et al. 2008).

Estuaries comprise a wide range of benthic habitat types including seagrass and algae beds, mud flats and sandy shores (Olsen et al. 2013). In this study, sites are defined as a location in an estuary with a particular sediment types (e.g. sand) and at a particular location within the estuary (e.g. mouth sites, within 100m of the mouth of the estuary). The strong association between the macrobenthic assemblages and the habitats they inhabit is a well-known phenomenon (Gray 2002, Thrush et al. 2003, Anderson 2008). These strong habitat associations lead to extremely patchy distributions, both among major habitat types (e.g. vegetated vs. non-vegetated soft sediments) and within habitat types (Barry & Dayton 1991, McIntosh 1991). For example, the oyster *Crassostrea virginica* requires a hard substrate on which to settle and grow, therefore can only inhabit areas where suitable substrates (e.g. rocks) are available (Swannack et al. 2014). Macrobenthic invertebrates are a diverse group of animals with wide variation in habitat requirements and feeding strategies, and the extent of the specificity of requirements is highly variable; some species have a strong relationship with a particular habitat type while others show little affinity with any one particular sediment type, and the taxa within different sediment/habitat types invariably show some degree of overlap (Snelgrove and Butman, 1994).

There have been few studies of the relationships between macrobenthic invertebrates and the range of sub-tidal habitats available in tropical estuaries, and few previous tropical estuary studies have accounted for such differences. Where habitat differences have been investigated (Dittmann 2002), they have usually been confounded with position along the intertidal gradient. This paucity of information on tropical macrobenthic assemblages (that are central to ecosystem functioning) presents a substantial problem for understanding and interpreting the ecology of tropical estuaries. This study begins to address this problem by examining the variability of benthic assemblages among the range of habitats occurring in one reach of a pristine

tropical estuary. In this study I examine the variability of benthic assemblages in a range of habitats in the mouth region of Deluge Inlet.

Materials and Methods

Sampling and habitat types

Deluge Inlet is a small (~8km long) pristine tidal estuary located on the landward side of Hinchinbrook Island (Sheaves et al. 2014). The mouth of Deluge Inlet is mangrove-lined, has a semi-diurnal tidal range of approximately 3.6m and consists of a variety of benthic habitat types (Sheaves 2009, Sheaves et al. 2014) including fine and coarse sand, sand/algae, mud/seagrass and sand/seagrass all within the mouth area. To minimise the effect of upstream gradient, samples were collected from a variety of habitats within the mouth area (Figure 2.1).

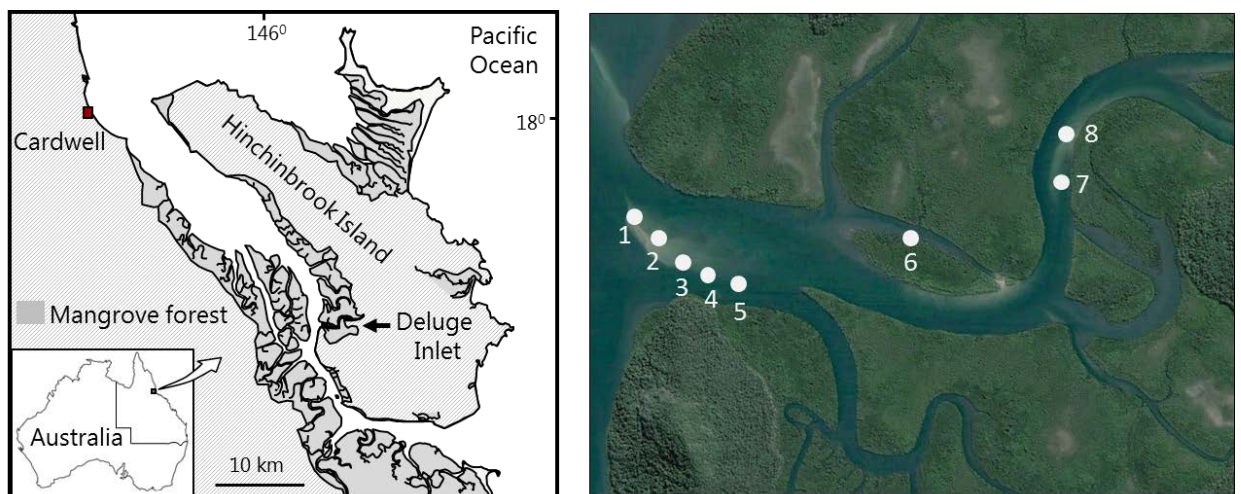


Figure 2.1. Locations of the eight sampling sites at Deluge Inlet on Hinchinbrook Island. For descriptions of sites see Table 1.

Eight sites were established in the downstream 2km (mouth region) of Deluge Inlet (Figure 2.1). The sites represented the range of soft sediment intertidal habitats occurring at Deluge Inlet. At each site, five replicate samples were collected within a 10m² radius from the intertidal/sub-tidal interface using a van Veen grab with a sampling area of 0.1m². Validation trials indicated that the grab collected sediment to an approximate depth of 40mm. The contents of the grab were then wet-sieved in the field using a 1mm sieve and the retained animals, plants and sediment were transferred

to plastic bags and fixed with 10% buffered formalin. Samples were sorted in the laboratory and all invertebrates identified to the lowest possible taxonomic level and enumerated.

Sediment size analysis

Sediment samples were collected from each site and taken back to the laboratory for grain size analysis. 100g of sediment was placed on the top sieve, with the use of a squirt bottle of distilled water the sieves were agitated mechanically and each size class was trapped on the mesh that is too small for it to pass through, therefore, separating the sediment sample into groups of grains that range in size between the larger sieve (2mm) through to the smallest mesh size (0.064mm). These samples were then placed into individual Petrie dishes and then dried in an oven. Once dried, the samples were then weighted and then classified according to the Wentworth scale (Wentworth 1922). Sites were categorized by the dominant grain size as well as the flora present at each site (Table 2.1).

Table 2.1. Sediment types, flora present and grain size of sampling sites at Deluge Inlet.

Sites	Sediment type	Average grain size (mm)	Seagrass/algae/organic matter
Site 1	Medium sand	0.5	No plant
Site 2	Medium sand	0.5	Filamentous algae
Site 3	Coarse sand and mud	1	No plant
Site 4	Coarse sand	1	No plant
Site 5	Fine sand	0.25	Mangrove detritus
Site 6	Mud	< 0.063	<i>Halodule uninervis</i>
Site 7	Fine sand	0.25	<i>Halophila ovalis</i>
Site 8	Mud	<0.063	<i>Halophila ovalis</i>

Data analysis

Patterns of similarity in faunal composition over the eight sites were analysed using multivariate classification and regression trees (mCARTs) (De'ath & Fabricius 2000, De'ath 2002) based on Bray-Curtis similarities, with multidimensional scaling (MDS)

using abundance data and the Bray-Curtis similarity measure, to display the patterns graphically (MDS's were produced using Primer) mCARTs are a statistical technique used to explore, describe and predict relationships between multispecies data and explanatory variables (e.g. site, sediment size, site description and plant material present). mCARTs were produced using TreesPlus. Unstandardised data were used to emphasise differences in faunal assemblages between the various habitats. Only taxa occurring in >5 % of the sites were included in statistical analyses, to reduce variability caused by rare taxa (Tausch et al. 1995). Data were 4th-root transformed before analysis to down-weight the influence of dominant taxa.

Results

All taxa

Analysis using all taxa showed substantial differences in faunal assemblages among sites, with the first split of the mCART showing a clear separation of faunal assemblages of seagrass sites from non-seagrass sites (Figures 2.2a & b). Some taxa were recorded in all sites sampled (e.g. *Nereis* sp 2, *Circe* sp 1 and *Polinices* sp 2); however, these taxa occurred in low abundances. In the non-seagrass sites, the bivalves *Gari* sp 1 and *Parvilucina crenella* were the most abundant taxa. In the seagrass sites, the polychaete *Owenia* sp 1 and the amphipod *Gammarus* sp 3 were the most abundant taxa (Figure 2.2a)

MDS also indicated some clear differences in assemblage composition between the seagrass and non-seagrass sites (Figure 2.2b). At seagrass sites, the most abundant species were gammarid amphipods and the polychaetes *Owenia* sp 1, *Maldane* sp 3, *Isolda* sp 1 & 3, and the bivalve *Gari* sp 5. There was a slight separation of non-seagrass sites, with sites 1 and 4 separating from sites 2, 3 and 5. At sites 1 and 4 *Nereis* sp 2 and *Gari* sp 1 were most abundant, whereas at sites 2, 3 and 5 *Nereis* sp 1 and the bivalves *Circe* sp 1 and *Parvilucina crenella* were predominant (Figure 2.2b).

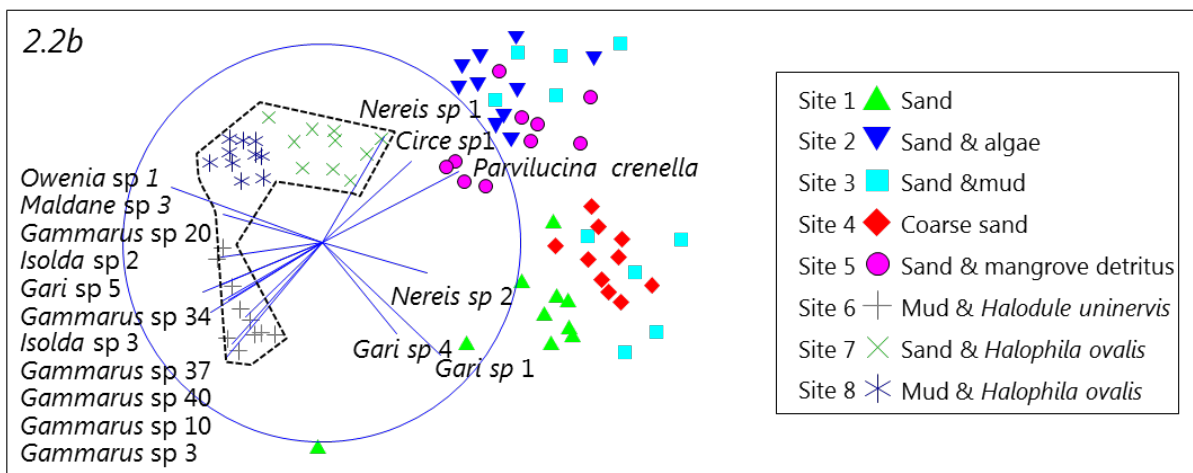
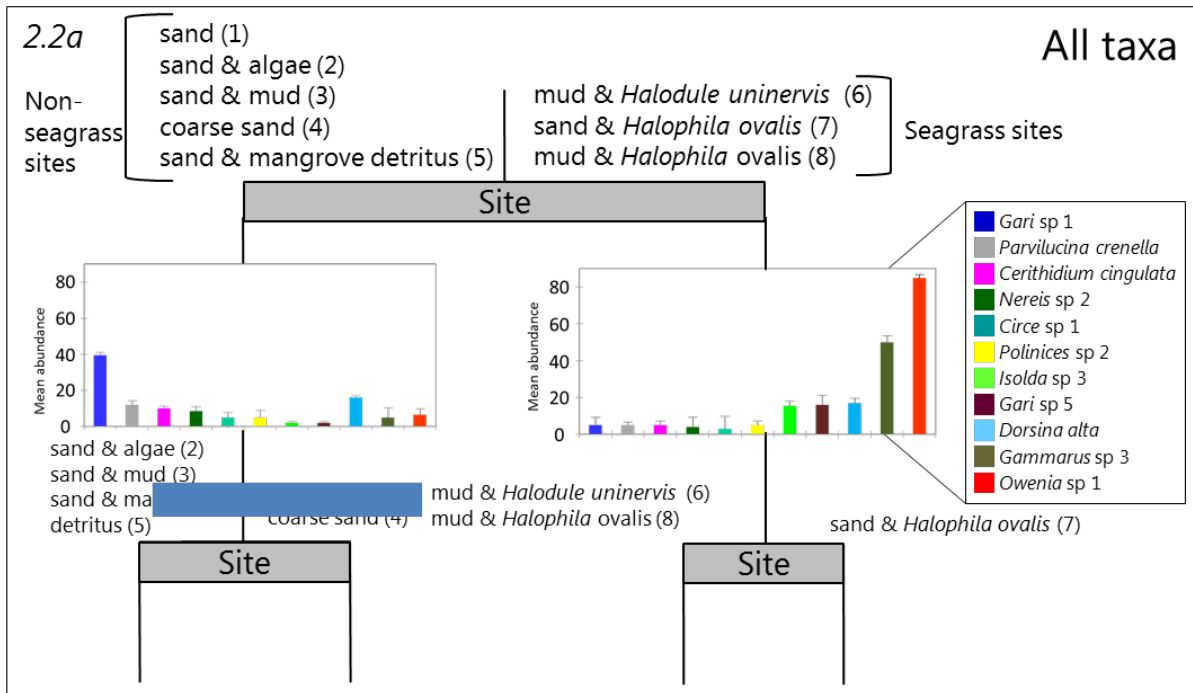


Figure 2.2. (a) Multivariate classification and regression tree for site and sediment factors using all taxa occurring in >5% of samples. Abundance data were 4th root transformed. (b) Two-dimensional multidimensional scaling solution (MDS) (stress = 0.15), Bray Curtis similarity. Vectors indicate the direction of greatest increase in abundance of the species most highly correlated with the ordination space. Vector lengths are proportional to the R^2 for each species. Key: ▲ Site 1 (sand), ▼ Site 2 (sand and algae), ■ Site 3 (sand and mud), ◆ Site 4 (coarse sand), ● Site 5 (sand and mangrove detritus), † Site 6 (Mud & *Halodule uninervis*), × Site 7, (sand and *Halophila ovalis*), * Site 8 (mud and *Halophila ovalis*)

Individual analysis

The data were separated into four taxonomic groups (bivalves, crustaceans, gastropods and polychaetes) and each analysed separately to examine the patterns of habitat specialisation of each group.

For both bivalves and crustaceans the mCART reflected the same results as the 'all taxa' analysis with the first split of the mCART showing a clear separation of faunal assemblages of seagrass sites from non-seagrass sites (Figures. 2.3a & 2.4a). The MDS of the bivalves showed some interesting spatial patterns. Replicates of most sites grouped together, indicating similarity in faunal assemblages, for example sites 1 and 4 (both sand sites) grouped together and were characterised by high densities of *Gari* sp 1 and 4, whereas sites 6, 7 and 8 (the mud/seagrass and sand/seagrass sites) grouped together and were characterised (high densities) by *Dosinia alta* and *Gari* sp 5 (Figure 2.3b).

The MDS of the crustaceans differed from the bivalves in that while some of the replicates of particular sites (e.g. site 4, 6, 7 and 8) grouped together, the replicates of the other sites were more broadly spread. Gammarid amphipods were the most abundant crustaceans recorded with different species predominating at particular sites. For example, Site 4 (coarse sand) was dominated by *Gammarus* spp 6 and 12. Whereas site 6 (mud and *Halodule univervis*) was dominated by *Gammarus* spp, 3, 9, 10, 34, 37 and 40 (Figure 2.4b).

Analyses of gastropods and polychaetes did not show a simple seagrass versus non-seagrass pattern. For both gastropods and polychaetes, the first split on the tree separated the two mud/seagrass sites (sites 6 and 8) from all other sites (Figures. 2.5a & 2.6a).

The MDS of the gastropods grouped some replicates of particular sites (e.g. sites 4 and 5) while the replicates of the other sites were broadly spread (Fig 2.5a). Unlike the crustaceans, where there were many species abundant in particular habitats, the only abundant species in particular habitats was *Haminoe* sp 1 at sites 1 and 7 (Fig 2.5a)

In contrast, the MDS of the polychaetes showed strong habitat associations for a number of taxa. For example, *Owenia* sp 1 was most abundant at sites 6, 7 and 8 (mud/seagrass and sand/seagrass sites) and *Nereis* sp 1, *Eunice* sp 2, *Isolda* sp 1 were most abundant in the assemblages at site 2 (sand and algae) and *Nereis* sp 2 was most abundant in sites 1 and 4 (Figure 2.6b).

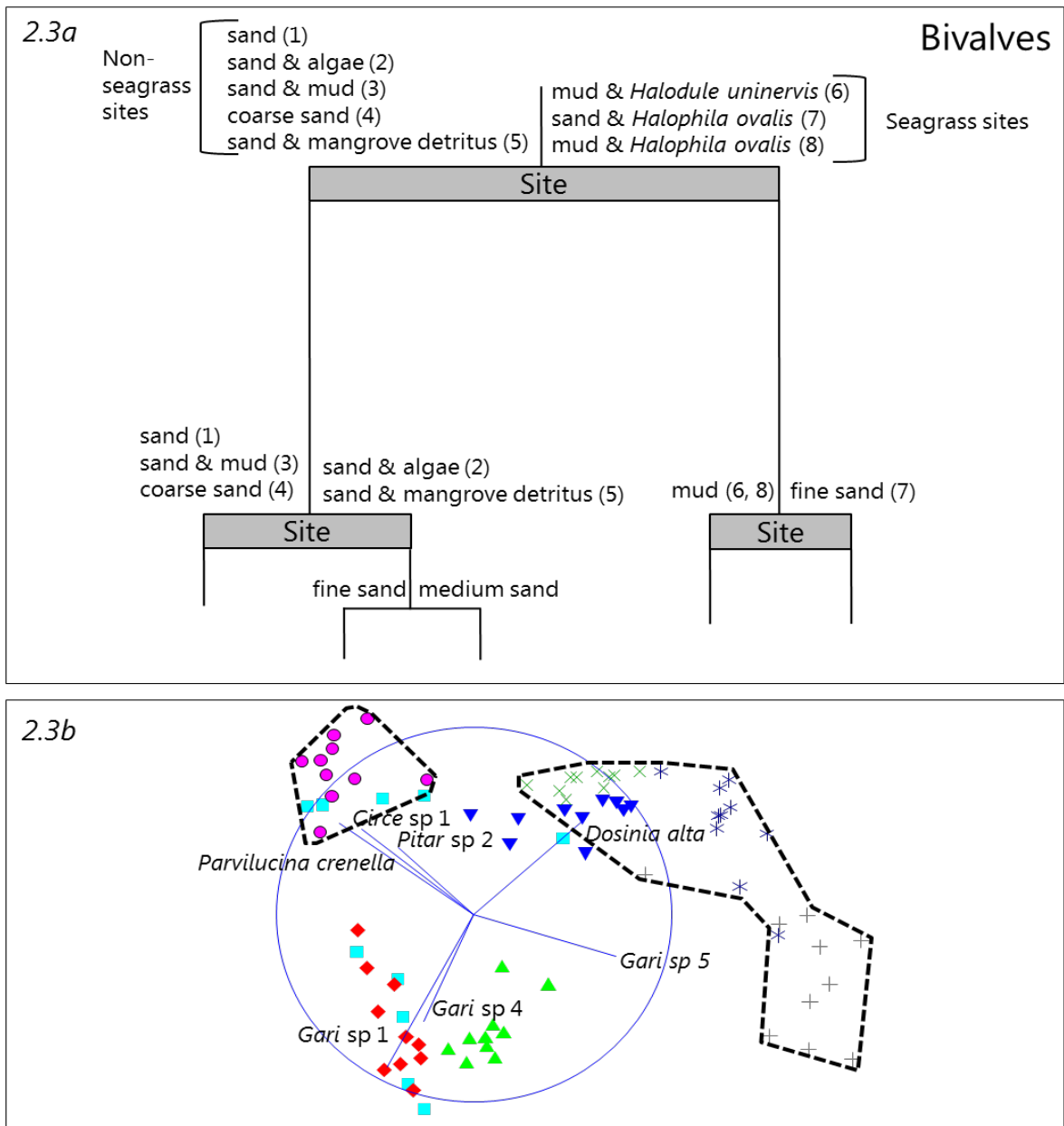


Figure 2.3 (a) Multivariate classification and regression tree for site and sediment factors using bivalves occurring in >5% of samples. Abundance data were 4th root transformed. (b) Two-dimensional multidimensional scaling (MDS) (stress = 0.14), Bray Curtis similarity. Vectors indicate the direction of greatest increase in abundance of the species most highly correlated with the ordination space. Vector lengths are proportional to the R^2 for each species. For key to sites see Figure 2.2.

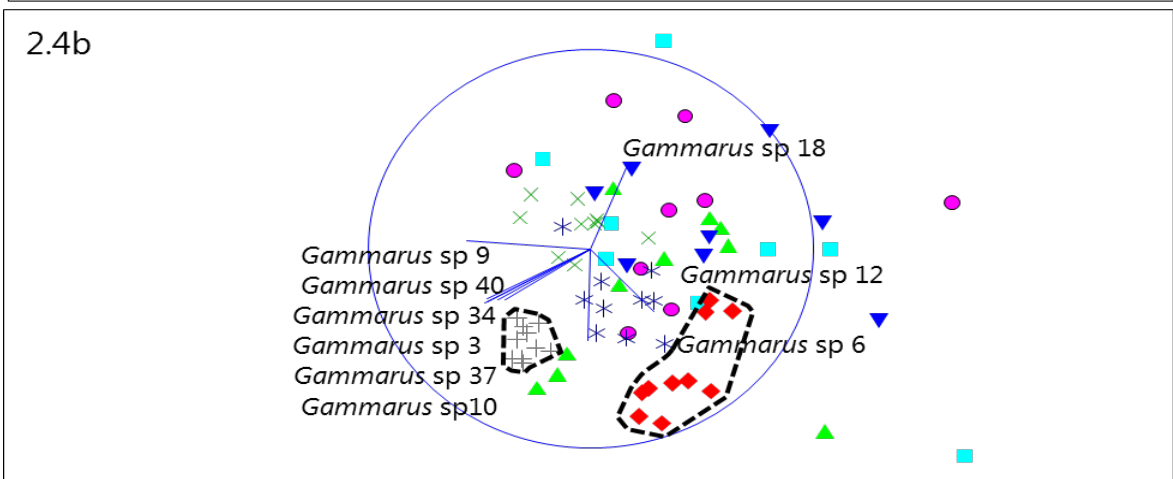
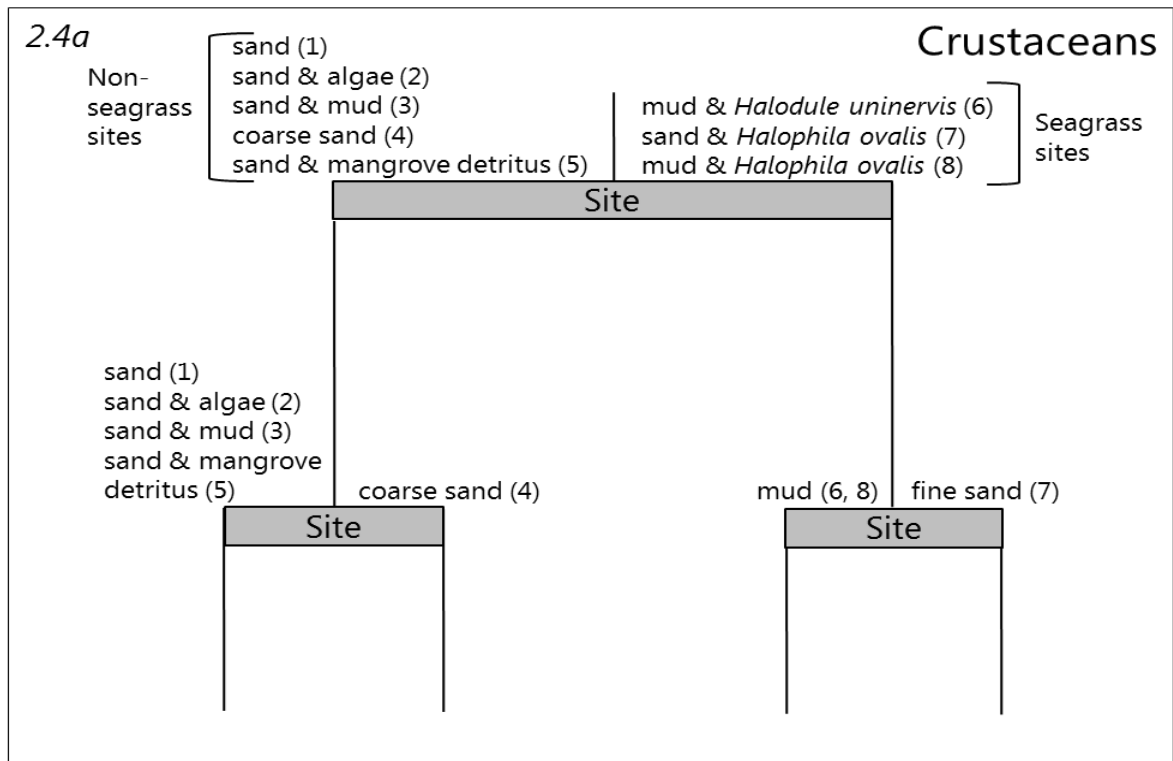


Figure 2.4. (a) Multivariate classification and regression tree for site and sediment factors using crustaceans occurring in >5% of samples. Abundance data were 4th root transformed. (b) Two-dimensional multidimensional scaling (MDS) (stress = 0.15), Bray Curtis similarity. Vectors indicate the direction of greatest increase in abundance of the species most highly correlated with the ordination space. Vector lengths are proportional to the R^2 for each species. For key to sites see Figure 2.2.

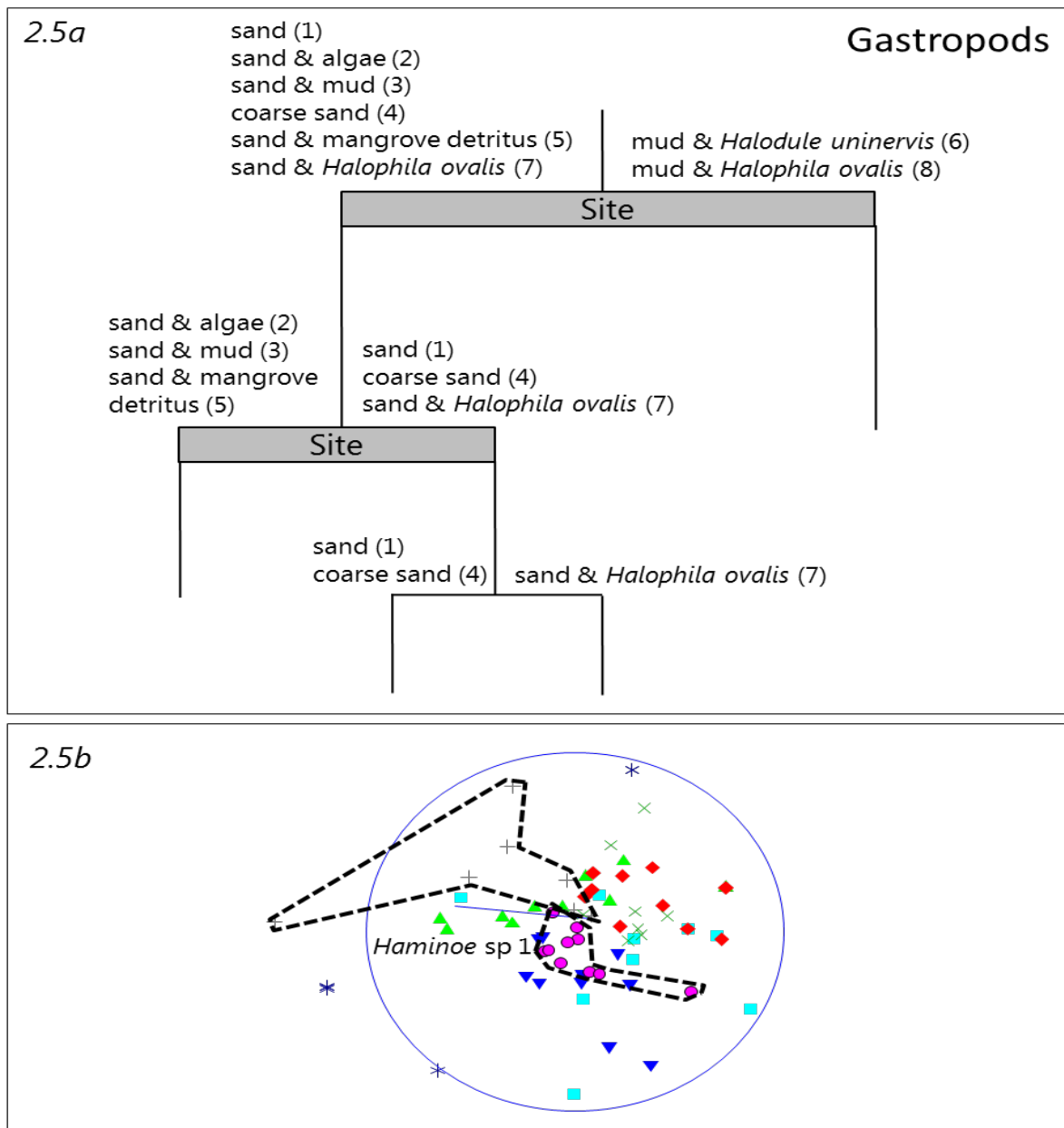


Figure 2.5. (a) Multivariate classification and regression tree for site and sediment factors using gastropods occurring in >5% of samples. Abundance data were 4th root transformed. (b) Two-dimensional multidimensional scaling (MDS) (stress = 0.17), Bray Curtis similarity. Vectors indicate the direction of greatest increase in abundance of the species most highly correlated with the ordination space. Vector lengths are proportional to the R^2 for each species. For key to sites see Figure 2.2.

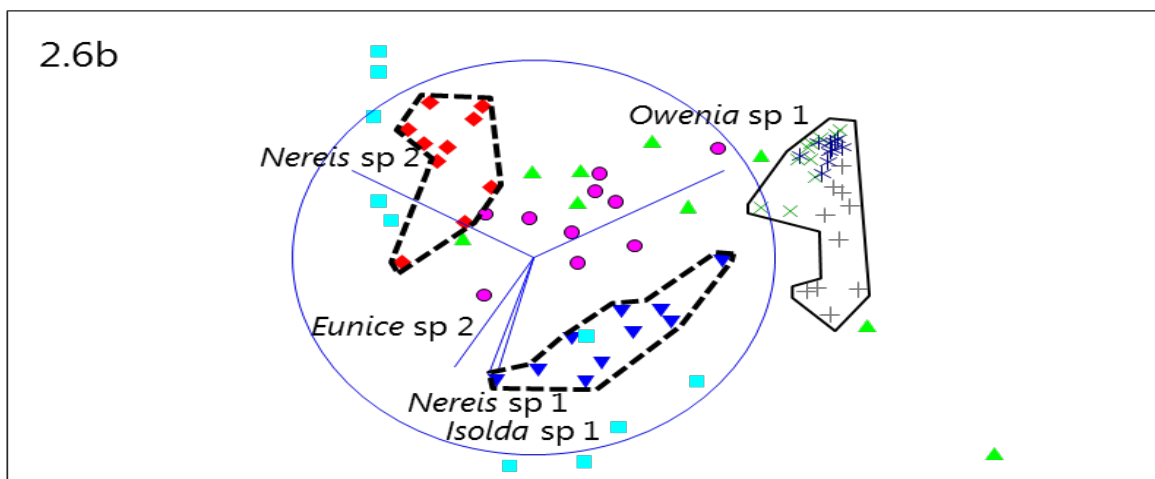
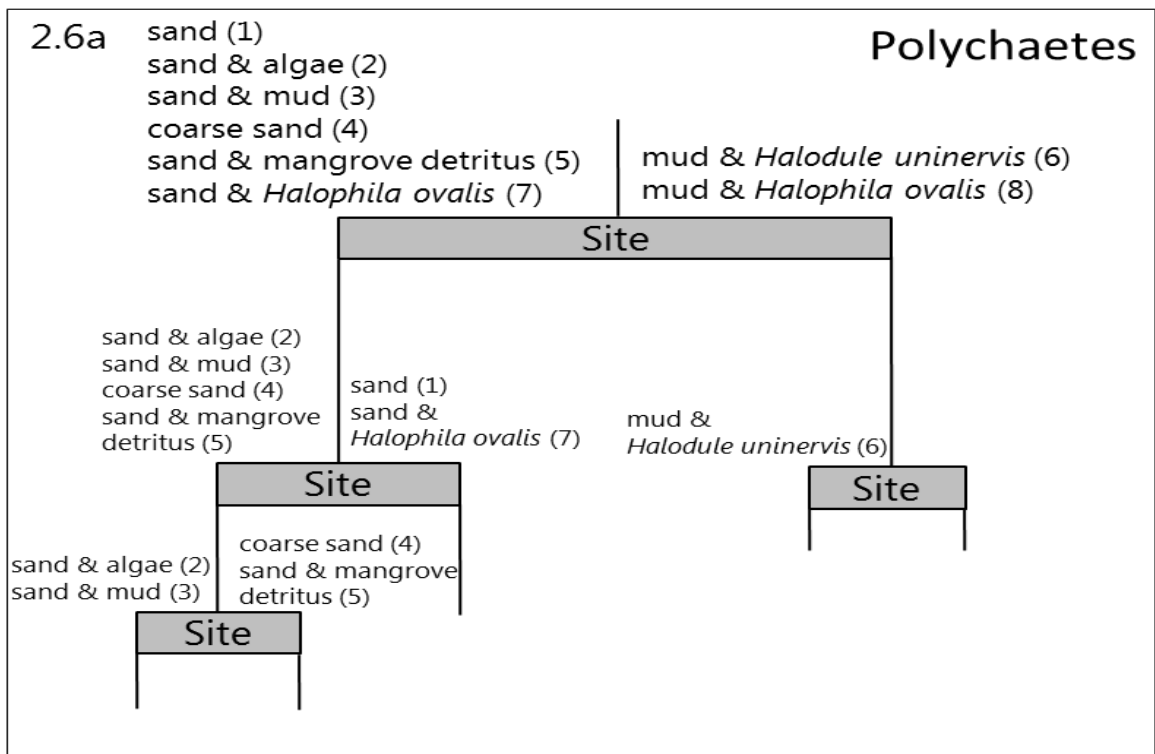


Figure 2.6. (a) Multivariate classification and regression tree for site and sediment factors using polychaetes occurring in >5% of samples. Abundance data were 4th root transformed. (b) Two-dimensional multidimensional scaling (MDS) (stress = 0.14), Bray Curtis similarity. Vectors indicate the direction of greatest increase in abundance of the species most highly correlated with the ordination space. Vector lengths are proportional to the R^2 for each species. For key to sites see Figure 2.2.

Discussion

Like many other estuaries (Duan et al. 2009, Chung et al. 2012, Demars et al. 2012, Gamito et al. 2012, Schröder et al. 2013, Washburn & Sanger 2013), Deluge Inlet has a mosaic of different habitat types (e.g. sand, sand with seagrass, mud, mud with seagrass etc.). Analysis of the data indicated that a number of taxa showed distinct preferences for a particular habitat type. This was particularly evident in the differences in faunal assemblages between the seagrass and non-seagrass sites, where gammarid amphipods dominated the faunal assemblages in the seagrass sites and bivalves and some species polychaetes were the dominant taxa in non-seagrass sites. Preference for particular habitat type is common in macrobenthic assemblages (Barry & Dayton 1991, Morrisey et al. 2003) and has been attributed a wide variety of factors such as flow conditions (Melo & Froehlich 2001) and local physical and chemical characteristics (Thrush et al. 2003); however, substrate type (e.g. sand, mud) is often the most influential factor determining overall benthic assemblage structure (Anderson 2008, Duan et al. 2009).

The distribution of benthic invertebrates in estuaries can be highly variable: some invertebrates live in a range of different habitats, whereas other taxa are found in only one habitat type. For example, *Tellina* bivalves prefer habitats of bare sand, whereas the polychaete *Heteromastus filiformis* is generally only found in silt-clay habitats (Maurer et al. 1978, Demars et al. 2012). Although assemblages may differ between the various habitats, they form an integral part of the broader ecosystem or metacommunity. The mosaic of different habitats in the mouth region of Deluge Inlet illustrates how areas with different habitats may support different taxa and life stages and possibly perform different functions. Therefore, to understand the functioning of these areas, we need to understand how the assemblages in various habitats function, not only as separate entities, but within the ecosystem.

Thus, for example, estuaries are essential nursery grounds for a wide range of fish species (Hajisamae & Chou 2003, Le Pape et al. 2013) including juvenile flathead (*Platycephalus fuscus*, *P. arenarius*) (Baker & Sheaves 2005) which prey on gammarid amphipods, and therefore settle in habitats where amphipods are present. As they

grow larger, *Platycephalus* spp. switch to a diet of fish such as *Acentrogobius viridipunctatus* (Baker & Sheaves 2005), which in turn largely rely on penaeid prawns for food. Consequently, *Platycephalus* spp. progress to habitats where the densities of penaeids are high. Therefore, a range of habitats are required in an ecosystem to fulfil the needs of a diverse biota and their various life history stages.

Consequences for understanding benthic assemblages

The comparative habitat-by-habitat study of Deluge Inlet benthic fauna highlighted that the patterns of similarity and difference among habitats detected was influenced substantially by the taxonomic yardstick used. The picture varied, often substantially, depending on whether all taxa were analysed together or if analysis focussed on a particular taxonomic group (e.g. crustaceans – see figure 2.4 and gastropods – see fig. 2.5). This has two implications. Firstly, it provides a basis for using particular taxa to investigate specific habitat differences – for instance, where specific taxa distinguish among habitats that are not well differentiated when the full data set is analysed. For example, analyses of all data, bivalves and crustaceans grouped all seagrass sites together and differentiated them from other habitats. In contrast, both gastropods and polychaetes clearly separated sandy seagrass sites from the other seagrass sites. Secondly, it clearly indicates that the results of habitat comparisons are highly dependent on the efficiency of the sampling approach used, with different gear sampling to different depths, sampling epifauna versus infauna with different efficiencies, or having upper or lower limits on the size of animals collected (Anderson 2008, Zajac 2008). This not only complicates comparisons among studies but also means that descriptions or animal-habitat relationships are not absolute but should be viewed as estimates relative to the various aspects of gear efficiency.

Implications for further sampling

While many factors influence the distribution of macrobenthic invertebrates in estuaries, for example, the organic content of bottom sediments (Snelgrove and Butman, 1995), pollution (Gray et al, 1990) the presence of polychaete tubes and seagrass (Eckman and Nowell 1984), the microbial community (Grossmann and Reichardt 1991) and predation (Dauvin and Gillet 1991), substratum type is one of the

major factors influencing benthic assemblages (Gray 2002, Thrush et al. 2003, Anderson 2008). Consequently, it was not surprising that different assemblages were associated with the wide variety of habitat types occurring in Deluge Inlet. The substantial differences in assemblages associated with those habitats make it clear that it is critical to minimize differences in habitat types among samples, and therefore essential to choose a single habitat type that is common in the majority of estuaries. From the analysis in this study and a pilot study of 30 North Queensland estuaries there was only one habitat type (sand) that was available in all estuaries from the mouth to their upstream reaches, therefore in subsequent studies for this thesis sand habitats will be the habitat type sampled. There are trade-offs inherent in this approach as it does not allow a holistic view of the benthos of all the estuaries but it is a pragmatic approach to comparing patterns and processes across and within estuaries with limited resources.

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Chapter 3: Spatial and temporal variation in benthic invertebrate assemblages in tropical and sub-tropical estuaries

Abstract

In this study the benthic invertebrate assemblages in ten estuaries, located over 1000km of Australia's eastern tropical coast, were examined to develop a detailed comparative understanding of the spatial and temporal changes in the structure of estuarine benthic invertebrate assemblages in tropical and sub-tropical estuaries incorporating both wet and dry climatic regions. More specifically, the study aimed to investigate: (i) the influence of climatic region (wet tropics vs. dry tropics vs. dry sub tropics) and latitudinal change on the diversity, density and community structure of the benthos, and (ii) the distribution of benthic organisms along upstream-downstream gradients of wet and dry tropics estuaries to determine how patterns of within-estuary change are modified by climate and latitude. While there were some taxa that occurred in all three climatic regions (e.g. the bivalves *Soletellina petalina* and *Cerithidium cinclulata*) other taxa (e.g. *Nereis sp 16* and *Paraonis sp 2*) were only recorded in wet tropics and dry tropic estuaries. In general, the faunal assemblages in tropical zones differed from assemblages in sub-tropical zones. There was also a distinct difference between assemblages in mouth and upstream transitional zones. Differences in benthic invertebrate assemblages between the wet tropics and dry sub-tropics correlated with differences in salinity regimes, which are driven by differences in rainfall, with wet tropic estuaries receiving substantially more rainfall than dry sub-tropical estuaries. The differences between transitional and mouth assemblages appear to be driven by difference in salinity and salinity dynamics, with little temporal change in salinities at mouth sites in comparison to transitional zones where salinities are often dramatically reduced during rainfall events. These results emphasise the importance of understanding spatial variations and climatic regimes and location of assemblages within an estuary when examining and comparing estuarine assemblages.

Introduction

Although a number of studies have investigated benthic diversity in tropical estuaries (Wu & Richards 1981, Warwick & Ruswahyuni 1987, Arasaki et al. 2004), most of the studies considered only a single or small number of estuaries (e.g. Dittmann 2000, 2002). As a result, these studies failed to investigate the effects of even the most likely sources of difference, such as the influence of wet versus dry tropical conditions on estuarine assemblages, or latitudinal effects. Although these studies provide valuable information, they are restricted in their general usefulness, as the patterns observed only relate to that particular estuary or group of estuaries (Edgar & Barrett 2002) and in general, do not examine estuary-to-estuary and region-to-region.

Sixty-eight percent of Australian estuaries are found in the tropics (Bucher & Saenger 1991). Australian tropical estuaries are dynamic and feature short-lived episodic freshwater flow during the wet season and very little freshwater flow over the dry season (Hamilton & Gehrke 2005, Webster et al. 2005). Although Australia's tropical estuaries share similar patterns of seasonal change (i.e. wet and dry season), they include areas of both high rainfall (wet tropics) and low rainfall (dry tropics). During periods of high rainfall the freshwater inflow into the estuaries reduces salinities, particularly in the upper reaches, and has a major impact on the abundance and distribution of estuarine invertebrates (Nanami et al. 2005, McLeod & Wing 2008, Prado et al. 2013). It is therefore expected that the faunal assemblages in estuaries with similar rainfall regimes (e.g. wet tropics) would be more similar to each other than faunal assemblages in estuaries with a different rainfall regime (e.g. dry tropics). There are currently no published data comparing estuarine faunal assemblages in Australia's various tropical climatic regimes.

All estuaries are inherently different (Harris & Heathwaite 2005) and consist of a mosaic of habitats that vary along the upstream-downstream gradient (Davis et al. 2014). In addition, the competing influences of marine and freshwater inputs vary along estuaries thereby providing a range of physical environments. In general, estuaries can be broadly divided into two sections: a lower mouth area, which is in free connection with the ocean and under consistent tidal influence, and an upstream transitional zone

that is subjected to daily tidal action, but also characterized by substantial fresh water influences, particularly during the wet season (Fairbridge & Finkl 1980, Hutchings 1999). During freshwater flow events, freshwater from the land flows into the upper reaches of the estuary, reducing salinities quite often for extended periods of time, particularly in the transition areas (Montagna & Kalke 1992, Attrill & Rundle 2002). The long-term reduction in salinities in transitional zones potentially has a harmful effect on the relatively sedentary benthic communities (Ecoutin et al. 2005), thereby creating an upstream–downstream faunal gradient (Barros et al. 2012).

In this study the benthic invertebrate assemblages in ten estuaries, located over 1000km of Australia's eastern tropical coast, were examined to develop a detailed comparative understanding of the spatial and temporal changes in the structure of estuarine benthic invertebrate assemblages in tropical and sub-tropical estuaries incorporating both wet and dry climatic regions. More specifically, the study aimed to investigate: (i) the influence of climatic region (wet tropics vs. dry tropics vs. dry sub tropics) and latitudinal change on the diversity, density and community structure of the benthos, and (ii) the distribution of benthic organisms along upstream-downstream gradients of wet and dry tropics estuaries to determine how patterns of within-estuary change are modified by climate and latitude.

Materials and Methods

The study area and sampling design

Queensland's climate varies considerably north to south, from the wet tropics, with high summer temperatures and high summer rainfall (coastally 2300-4000 mm per year), to the dry tropics with warm summer temperatures and moderate rainfall (~1200mm) to the dry sub-tropics, with warm summers and lower rainfall (~850mm per year) (Bureau of Meteorology, 2014) (Figure 3.1). The difference in rainfall determines the different flow regimes and freshwater input in the estuaries in these regions.

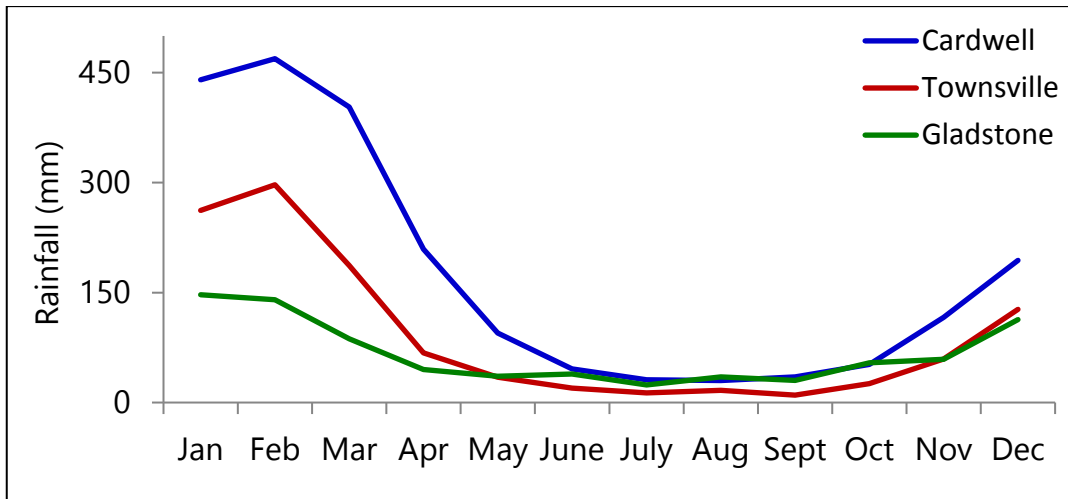


Figure 3.1. Average rainfall recorded for Cardwell (wet tropics), Townsville (dry tropics) and Gladstone (dry sub-tropics) [Data obtained from Bureau of Meteorology].

Samples were collected from ten estuaries from three climatic regions along the north-east coast of Australia (Figure. 3.2): The length of the estuaries varied from 2.3km (Meunga Creek) to 78km (Fitzroy River); some had permanent freshwater in the upper reaches and catchment size varied from 56km² to 142km² (Table 3.1).

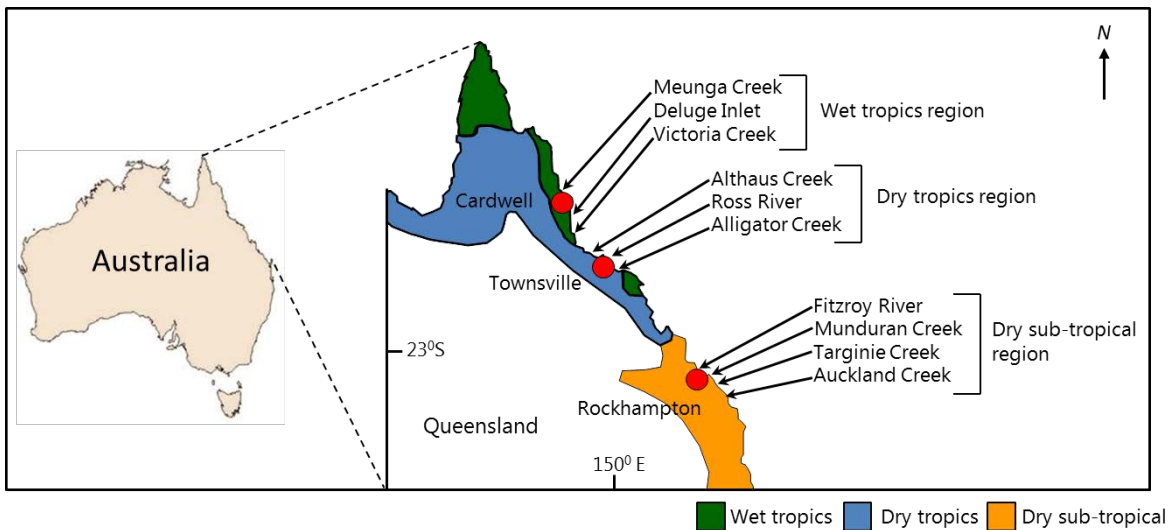


Figure 3.2. Map showing location of three climatic regions and the locations of the ten estuaries studied.

Table 3.1. The location (latitude and longitude), length, tidal range and catchment areas of the estuaries sampled.

Region	Estuary	Latitude	Longitude	Length of estuary (km)	Tidal range [from nearest tide gauge] (m)	Catchment area (km ²)
Wet tropics	Meunga	146°00'42.27"E	18°14'01.09"S	2.3	2.3	226
	Deluge	146°12'40.55"E	18°25'03.66"S	7.6	2.3	58
	Victoria	146°19'22.30"E	18°38'39.62"S	12.8	2.2	78
Dry tropics	Althaus	146°28'16.63"E	19°05'20.53"S	2.7	2.5	81
	Ross	146°49'50.57"E	19°16'36.71"S	21.9	2.3	881
	Alligator	146°56'33.78"E	19°19'28.39"S	8.2	2.3	149
Dry sub-tropical	Fitzroy	150°46'34.76"E	23°30'47.18"S	78.0	4	142
	Mundurran	151°04'36.84"E	23°38'41.69"S	8.2	3.2	89
	Targinie	151°08'14.51"E	23°43'05.64"S	4.6	3.2	35
	Auckland	151°14'06.85"E	23°50'28.72"S	7.0	3.2	56

In each estuary, two areas were sampled – an upstream transitional and a mouth area. The transitional areas were located in upstream regions that are penetrated by tides over 3m and get flooded by only half of the high tides per year and where salinities transition between marine and fresh seasonally. The salinity changes in these transitional zones is asymmetrical, as there is often a rapid transition from marine to freshwater conditions following flood events, followed by a gradual return to marine conditions (Davis et al. 2012). The mouth areas were located within 100 metres of the mouth of the estuary.

To reduce the influence of different sediment types (e.g. sand, mud, silt) on faunal assemblage structure, only sand habitats were sampled. Samples were collected on four separate occasions: April 2002 and 2003 (post-wet season), June 2002 (dry season) and December 2002 (wet season). At each area, five replicate intertidal samples were collected (within a 10m² radius) using a van Veen grab, which sampled an area of 0.1m² and collected the top 40mm of the substrate. The contents of the grab were wet-sieved

using a 1mm sieve and all animals were transferred to plastic bags and fixed with 10% buffered formalin. Samples were sorted and identified to the lowest possible taxonomic level in the laboratory.

Information on environmental variables was recorded at each site on each sampling occasion. Salinity and water temperature were measured using a TPA-WP-84 conductivity/salinity/temperature meter, and pH using a TPS-WP-80. Sediment samples were also collected from each site for sediment size analysis. Sediment samples were dried and weighed and placed in a Fritsch Vibrating Sieve shaker, water was added and samples were sieved for 10 minutes through a series of sieves (2mm, 1mm, 500 μ m, 250 μ m, 125 μ m and 63 μ m). The sediment remaining on each sieve was then removed and weighed to provide the size structure of the sediment.

Data analysis

Patterns of similarity in faunal composition over the 10 estuaries and four sampling trips were analysed using multivariate classification and regression trees (mCARTs) (De'ath & Fabricius 2000) using Treesplus (De'ath, 2002). Row-standardised data were used to emphasise faunal composition. mCARTs are computer-intensive statistical techniques used to explore, describe and predict relationships between multi-species data and explanatory variables (De'ath & Fabricius 2000). Clusters of samples are formed by repeated splitting of the data, with each split chosen to minimize the dissimilarity (variability) of samples within clusters. At each split, data are partitioned into two groups that are mutually exclusive and as homogeneous as possible. mCARTs were fitted using 10-fold cross-validation and the "best" tree sizes selected under the 1-SE criterion (i.e., the smallest tree within 1 standard error of the tree with the minimum cross-validation error), an approach that produces valid, interpretable trees (De'ath & Fabricius 2000). Only taxa occurring in >4% of the sites were included in statistical analyses to reduce variability caused by rare species (Tausch et al. 1995). Data were 4th-root transformed before analysis to down-weight the influence of dominant species. To illustrate relationships, non-metric multidimensional scaling (nMDS) (Clarke & Ainsworth 1993) was performed on 4th-root-transformed abundance data using Bray-Curtis dissimilarities.

Results

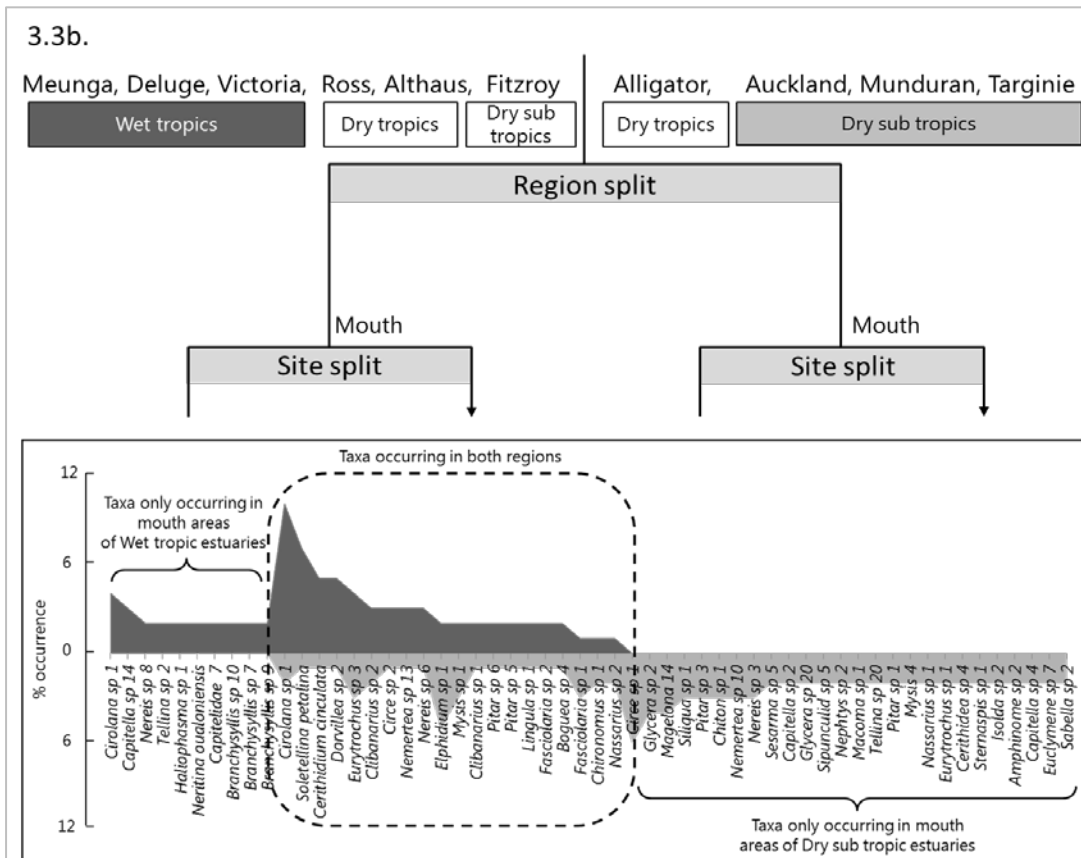
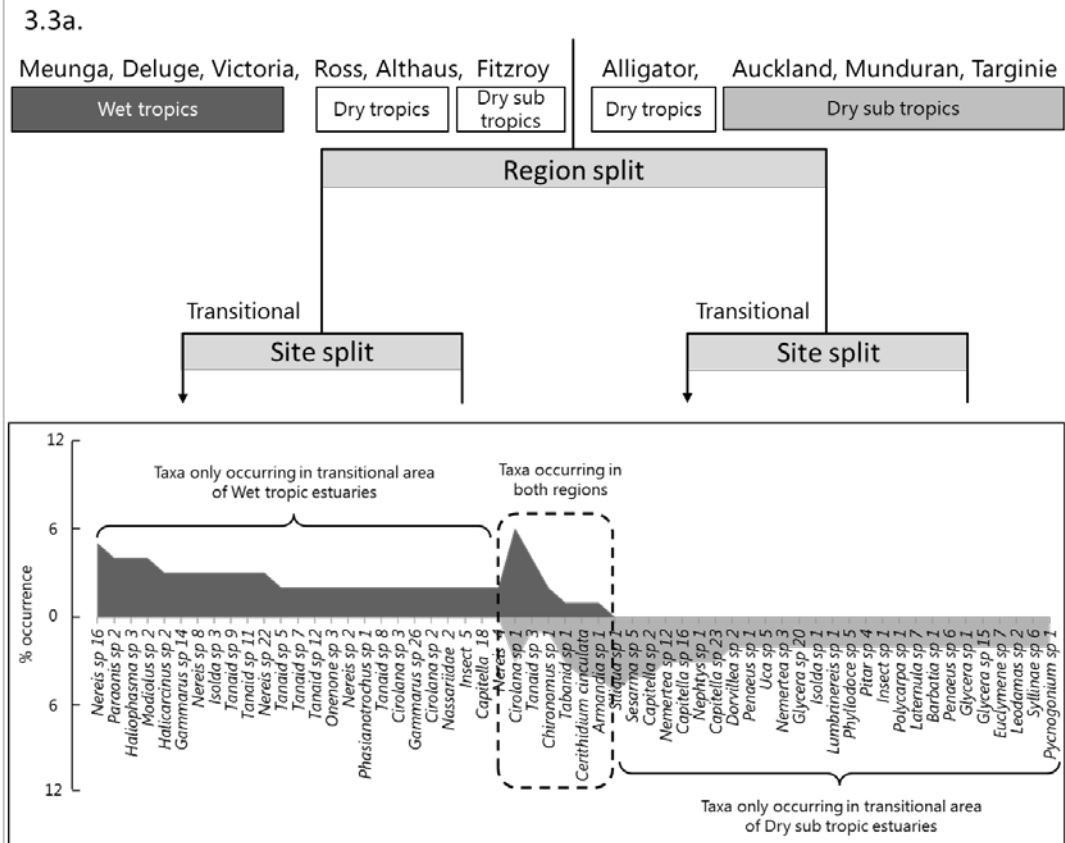


Figure 3.3a and figure 3.3b are the same tree. Figure 3.3a shows the taxa occurring in the transitional areas of wet and dry tropic estuaries. Figure 3.3b shows the taxa occurring in the mouth sites of wet and dry tropic estuaries. The multivariate classification and regression tree for faunal composition is based on >4% occurrence of taxa from wet tropic and dry sub tropic estuaries. Multivariate CARTs for spatial (climatic region, estuary, site), temporal (trip) and physical (salinity, temperature, sediment size, pH) properties. Figures below terminal branches of the tree indicate % occurrence of taxa occurring in >8% of samples and superimposed onto the tree structure.

The first two splits on the Classification and regression tree

The first split on the mCART shows that faunal assemblages in the wet tropical estuaries (Deluge Inlet, Meunga Creek and Victoria Creek) were distinct from those of the dry sub-tropical estuaries (Auckland Creek, Munduran Creek and Targinie Creek) with the exception of Fitzroy River, which grouped with the wet tropic estuaries, and Alligator Creek, which grouped with the dry sub-tropical estuaries (Figures 3.3a and 3.3b).

The second split on the tree shows that all estuaries, regardless of climatic regime, had clear differences between taxa recorded at mouths sites and taxa recorded in transitional sites (Figures 3.3a and 3.3b).

Species level analysis of transitional areas and mouth sites

Transitional sites – Wet tropics Vs Dry sub tropics

Analysis of the data at species level showed considerable regional endemism, with some taxa restricted to transitional areas in the wet tropics and other taxa restricted to transitional sites in dry sub tropics. However, there were some taxa (e.g. *Cirolana* sp 1, Tanaidacea sp 3 and *Cerithidium cinculata*) that were recorded in both wet tropical and dry sub-tropical transitional areas (Fig 3.3a).

Mouth sites – Wet tropics Vs Dry sub tropics

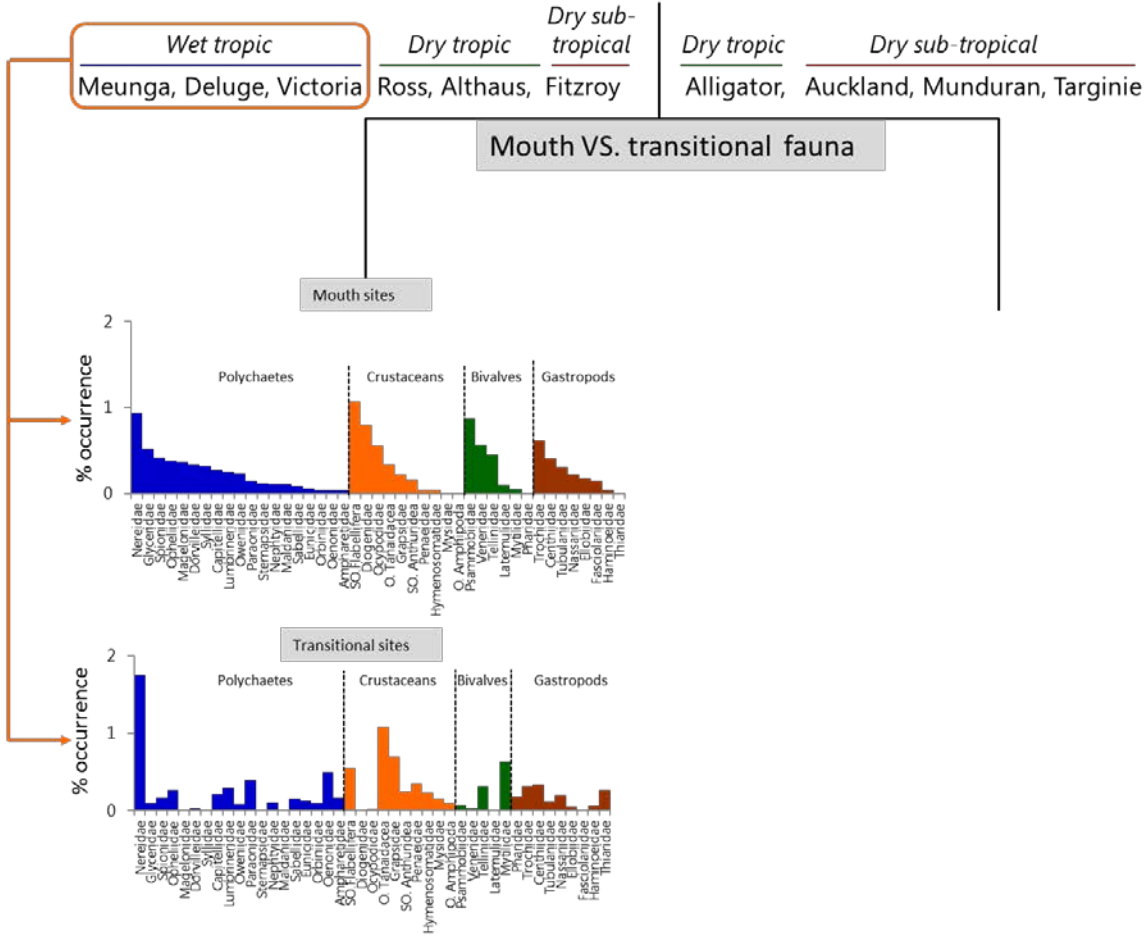
In the mouth sites of the dry sub tropics, 26 species showed clear regional endemism in comparison to 9 regional endemics in the wet tropics (Fig 3.3b). In comparison to the transitional areas, there were more species (21) that occurred in both the wet tropics and dry sub tropics mouth sites (Figures 3.3a and 3.3b). The predominance of taxa varied between transitional and mouth sites of wet tropics and dry sub-tropic estuaries.

For example, e.g. *Cirolana* sp 1, *Soletellina petalina*, *Cerithidium cinculata*) were most abundant in the mouth sites of wet tropic estuaries, while *Circe* sp 1 and *Glycera* sp 2 were most abundant in the mouths of dry sub-tropic estuaries (Figure 3.3b). In transitional areas, *Cirolana* sp 1 and Tanaid sp 3 most abundant while in dry sub-tropics *Armandia* sp 1 and *Siliqua* sp 1 predominated (Figure 3.3a).

Family level analysis

Analysis of data at the family level showed clear differences in assemblage structure between mouth and transitional areas for both wet tropics and dry sub-tropic estuaries (Figures 3.4a and 3.4b). For example, a number of families (e.g. Paraonidae, Eunicidae, Oeononidae, Anthuridae, Ellobiidae and Thiaridae) occurred in the mouth regions of wet tropic estuaries were not recorded in the mouths of dry sub-tropic estuaries (Figures 3.4a and 3.4b). These differences in faunal distributions maybe due to some environmental factors such as differences in rainfall (e.g. dry sub-tropic region receives ~850mm of rainfall per year and wet tropics receive 2300-400mm of rainfall per year) (Fig. 3.1) as well as tidal range (e.g. 3.2m in dry sub-tropics vs. 2.3m in wet tropics) (Table 3.1) which can influence sediment stability and larval settlement. In addition to these absences, there were differences in the predominance of particular families at mouth sites: for example, Sphaeromatidea and Psammobiidae were most abundant in the mouth regions of wet tropic estuaries, while Veneridae and Pharidae were most abundant in dry sub-tropic estuaries (Figures 3.4a and 3.4b). Similar differences were also seen in the transitional areas. For example, Nereidae and Tanaidae were most abundant in the transitional areas of wet tropic estuaries whereas Capitellidae and Sphaeromatidea were most abundant in transitional areas of dry sub-tropic estuaries (Figures 3.4a and 3.4b).

3.4a



3.4b

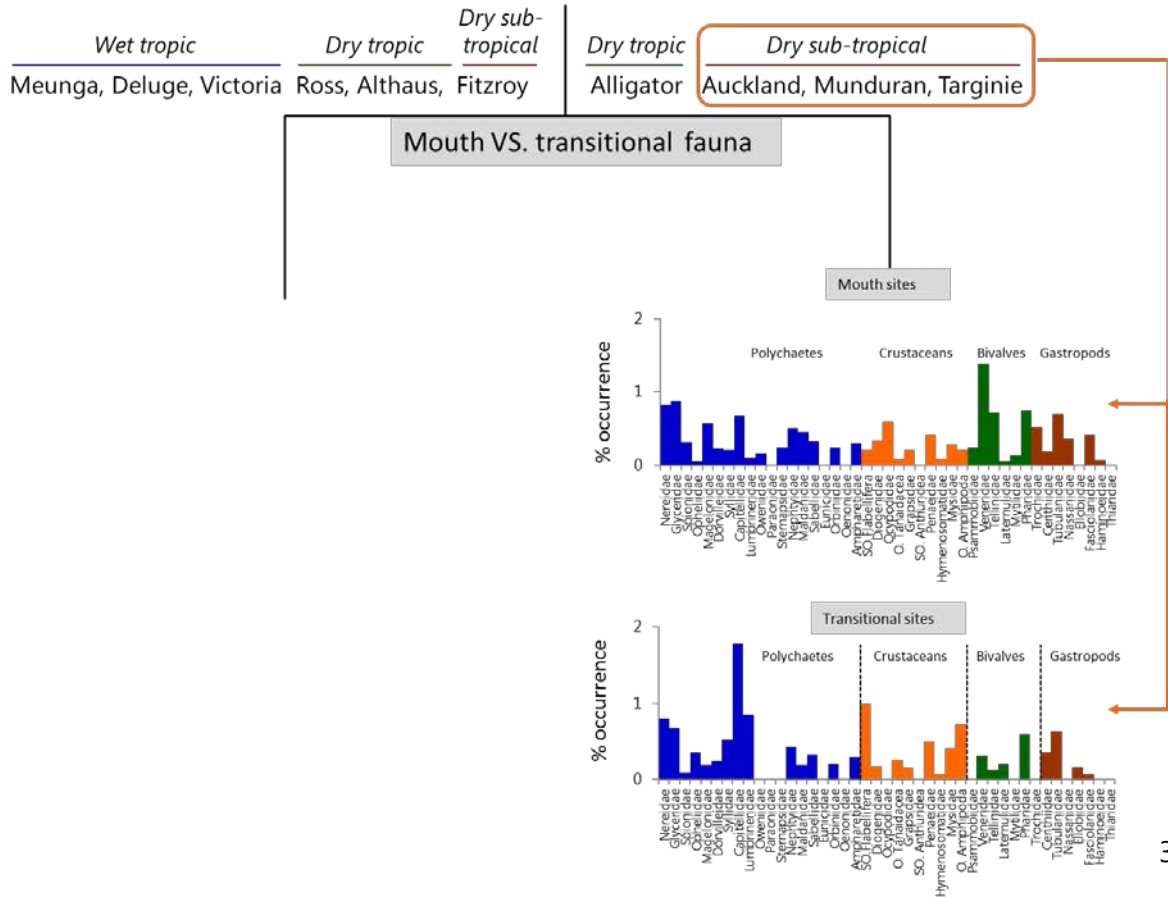


Figure 3.4. Multivariate classification and regression tree for faunal composition based on >4% occurrence for all estuaries. Multivariate CARTs for spatial (climatic region, estuary, site) and temporal (trip) and physical (salinity, temperature, sediment size, pH). Figures below terminal branches of the tree are taxa grouped into taxonomic groups (e.g. polychaetes, crustaceans, bivalves and gastropods). (a) Comparison of families occurring in mouth and transitional sites of wet tropic estuaries. b) Comparison of taxa occurring in mouth sites of dry sub-tropical estuaries.

Diversity and evenness

Analysis of data at species level showed that some streams from all climatic regions had high species diversity (e.g. Ross River, Auckland Creek, Munduran Creek and Deluge Inlet), while other streams had low diversity (e.g. Meunga Creek, Alligator Creek and Fitzroy River (Figure 3.5). All dry sub-tropic streams (Auckland Creek, Munduran Creek, Targinie Creek and Fitzroy River) had higher evenness, indicating that these streams had a number of species of similar abundance whereas streams such as Ross River, Meunga Creek and Victoria Creek and lower evenness, having a few species that predominated in the samples (Figure 3.5)

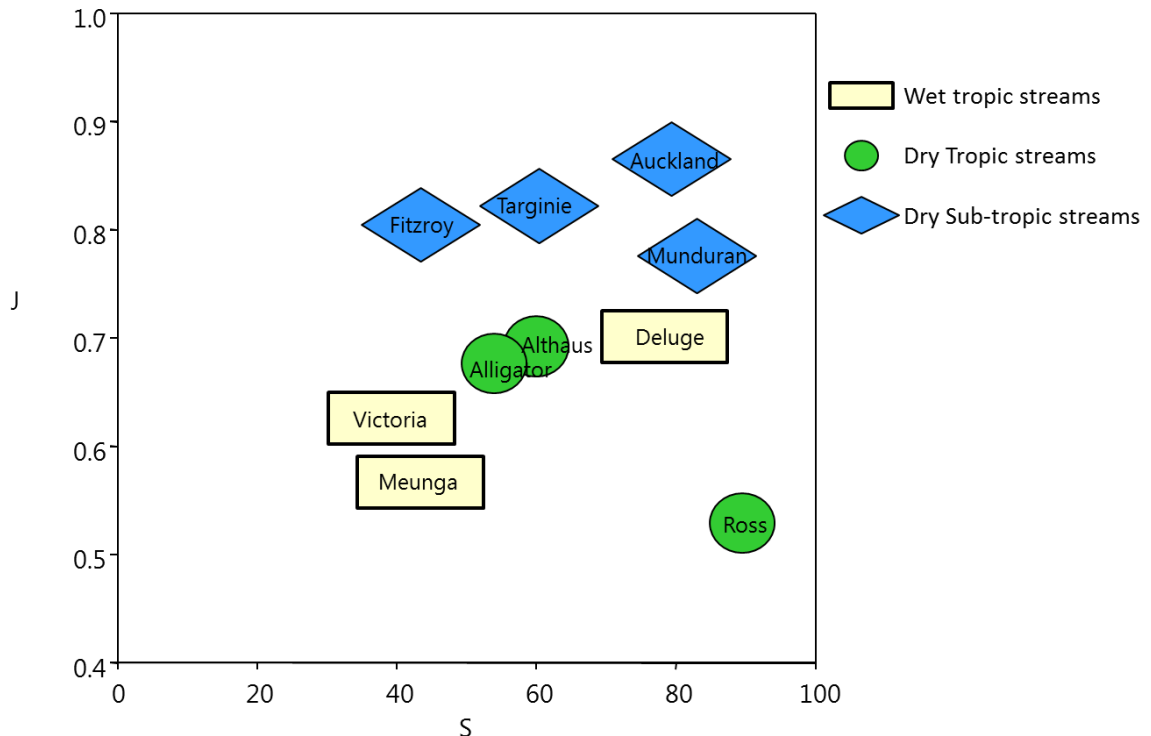


Figure 3.5. Diversity and evenness for all streams (mouth and transitional sites), based on >3% occurrence for all estuaries. S= number of species, J=evenness.

Discussion

Benthic faunal assemblages differed between northern wet tropic estuaries and southern dry sub-tropical estuaries. These differences in assemblages may reflect differences in rainfall regimes in the two climatic areas. The increased rainfall leads to a net increase in freshwater input into the wet tropics estuaries, resulting in reduced salinities, which usually lead to declines in the total number of individuals and in the number of taxa (Maurer et al. 1978, Snelgrove 1998, Hutchings 1999, Anderson 2008), both of which contributed to distinct differences in benthic faunal assemblages between the two regions. Given the differences in benthic assemblages between northern and southern estuaries it seems likely that the food webs and the functioning of these estuaries would differ as invertebrates provides the critical first consumer step in many estuarine food webs (Peterson 1991, Sarda et al. 1996, Sarda et al. 1998), and are a vital link in uploading nutrients into higher trophic levels, making it available for export (Virnstein 1977, Malmqvist 2002). The substantial differences at the species level may have far-reaching consequences for the functioning of local ecosystems and those ecosystems that rely on exported nutrients (Kneib 2000, Levin et al. 2001). For instance, the loss of key invertebrate species can lead to changes in assemblage structure that influence the recruitment of organisms that feed on those species (Levin et al. 2001). Although in the current study, there were differences between northern and southern estuaries at both family and species levels, there was little evidence that this represented functional change. Rather, a family absent in one region was usually replaced with another that was likely to be functionally similar. For instance, nereid deposit-feeding polychaetes (Beesley & Glasby 2000) were common in northern estuaries, but were replaced by capitellid deposit feeders (Maurer et al. 1999) in the south. This pattern was common across most other functional groups.

There was a clear change in faunal assemblages in all estuaries between the mouth and transitional areas. Mouth assemblages tended to have a high number of abundant taxa whereas, in the upstream transitional assemblages, a few taxa predominated, a pattern repeated at family level. Some were taxa confined to transitional areas and others to mouth habitats, suggesting that particular suites of species were adapted to the different environments. The typical configuration of an upstream transitional area,

where marine and fresh water intermixed, and an area at the mouth, where conditions were much more marine, changed rapidly during floods, when substantial freshwater flow causes significant decreases in salinities in transitional areas. In this study the typical temporal pattern for faunal assemblages in transitional areas was for high diversity and abundances in the dry season and reduced diversity and abundance in the wet season, as reported in other studies (Mannino & Montagna 1997, Platt & Connell 2003, Montagna et al. 2013). In this study in most instances the natural disturbance (flood) was non-catastrophic in that some specialised resident transitional taxa survived, enabling recolonisation of sites after the flood. The presence of these specialised resilient transitional taxa in estuaries would be a useful indicator of normal transitional functioning (see Chapter 4. However, if there was an extended dry period (e.g. a sequence of years with no flooding), then it is likely that there would be a reduction or loss of these specialised transitional assemblages, and assemblage structure might shift to one that more closely resembles those at the mouth. This was the case for fish assemblages in Ross River during an extended dry period (1992 to 1997) when no freshwater entered the system and a formerly distinct upstream faunal gradient degraded leaving a transitional assemblage indistinguishable from that in the mouth (Sheaves et al. 2007). The opposite situation could occur if areas received substantially more rainfall as a result of climate change. With increased rainfall, salinities in estuaries may remain depressed, leading to the proliferation of freshwater species in areas that were previously marine. There was no extended dry period during this study, so I was unable to gain an understanding of the nature of such changes and faunal responses to them.

Salinity in the transitional areas tended to be much more variable than in mouth sites. During floods it is not uncommon for salinities in the transitional areas of estuaries to go as low as 0‰. These freshwater conditions pose major problems for the marine benthic invertebrates living in these areas (Berger et al. 1995, Qiu & Qian 1997, Gimenez et al. 2005) because benthic invertebrates cannot readily move downstream to find better conditions. Consequently, if reduced salinities persist, the numbers of individuals and taxa are likely to decline (Gillanders & Kingsford 2002, McLeod & Wing 2008, Barros et al. 2012). This would have a flow-on effect through food webs, because

fish that feed on benthic invertebrates would need to move to forage further downstream. In essence, there are likely to be two distinct food webs: a dry season food web where abundant invertebrates are preyed upon by benthivorous fish; and a wet season food web with limited invertebrate abundance and a depauperate fish assemblage, or one that features quite different trophic links.

Most benthic taxa in the transitional areas are intermittently exposed to salinity reductions that greatly reduce diversity and abundances (Mannino & Montagna 1997, Edgar et al. 1999, Engle & Summers 1999). Recolonization and succession by taxa following flooding can vary considerably over space and time, owing to complex and variable mixtures of factors shaping the recovery (Zajac & Whitlatch 2003). Recolonization and succession in these areas is reflected in assemblage change over time (Chesson 2000a, b, Thrush et al. 2003) and driven by a series of natural environmental conditions (e.g. floods). It may be that there is some ecological succession (Zajac 2008), but it is highly unlikely that the assemblages reach a climax community (Ayling 1981, Hughes 1984, Ritter et al. 2005). This seems to be the case in the current study, because assemblages of most transitional areas had still not recovered to pre-flooding conditions at the beginning of the subsequent wet seasons. There was little evidence in the current study of directional species replacement (i.e. recolonising sequentially from downstream areas); instead it appeared that there was colonisation of sites by opportunistic species, something previously reported from Long Island Sound (Zajac et al. 2003, Zajac 2008). In fact, rather than being colonised by fast-growing, opportunistic taxa (*r*-selected) followed by proliferation of *k*-selected species (Sousa 1984, Burt et al. 2011), the species that colonised first remained dominant. Many studies cite connectivity between habitats as a major driver of recolonisation of sites after a flood (Zajac 2008 Ayata et al. 2010), and while this is important, other factors such as the recolonisation of sites from local reservoirs (taxa that survived the flood) are crucial to recolonisation after floods. Although this has not explicitly been mentioned in the literature, in all probability this occurs elsewhere.

While the mouth fauna did not differ substantially among southern to northern estuaries, the fauna occupying transitional zones was very different, to the extent that

there were very few species in common between the most distant locations (wet tropics vs dry south). Differences in assemblages could be due to a number of factors. Differences in rainfall regimes (2300-4000mm in the wet tropics and ~850mm in the dry sub tropics) may influence assemblage structure because many invertebrates are intolerant of low salinities (Moverley et al, 1986). As well as physiological responses to reduced salinities, increased rainfall and stream inflow may influence the amount of food available, thereby leading to changes in faunal composition (Richardson, 1991; Dobson & Hildrew, 1992; Wallace et al., 1997, Wallace et al. 1999). For instance, Abrantes et al. (2010) found distinct differences in the contribution of aquatic and terrestrial carbon sources between dry and wet tropical estuarine food webs. Other factors that might influence differences between the wet tropical and dry sub-tropical assemblages include differences in the physical heterogeneity of the streams, such as current velocity (Hynes, 1970), nutrient dynamics (Pringle et al, 1988), the retention and distribution of organic matter (Speaker et al, 1984) and presence or absence of refugia during disturbance (flooding) (Pringle et al, 1988). Not only are there a large number of possible reasons for differences in wet versus dry tropical assemblages, but the factors responsible are likely to interact in complex ways. Therefore, determining the factors influencing assemblage structure will require more extensive study incorporating a diversity of physical and biological factors.

The taxa in upstream transitional zones are specialists and are generally absent in mouth sites. This is significant because it implies that in order to understand the ecology or composition of transitional faunal assemblages it is necessary to conduct studies region by region. This is particularly important as transitional zones are the areas most at risk because of their proximity to anthropogenic development and to the greatest seasonal variation. If transitional taxa are lost from upstream reaches, many of the downstream taxa will be able to survive in the transitional areas, resulting in depauperate invertebrate assemblages, which would have significant impacts on food webs in these areas. It implies that there is substantial risk in making decisions about development (e.g. where to place dams, weirs etc.) without first gaining an understanding the strongly endemic benthic fauna of these transitional areas and

assessing the particular characteristics of proposed development location. It is likely that different decisions will be needed in different areas.

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Chapter 4: Response and recovery of tropical estuarine benthic invertebrates affected by floods

Abstract

Flooding is a natural occurrence in tropical estuaries and can have a profound effect on macrobenthic invertebrate assemblages by greatly reducing and/or eliminating taxa, particularly in the upstream reaches at times of low salinity. This study examined the effect of flooding and the subsequent recovery of the fauna at mouth and upstream sites of three North Queensland estuaries. Following the seasonal flood, upstream assemblages underwent radical restructuring ranging from the total loss of taxa from some sites to significant decreases in diversity and abundances at other sites. The recovery of faunal assemblages after the flood varied between sites and appeared to be mainly a function of the location of the site in relation to freshwater input (i.e. sites closest to freshwater input were more adversely affected than sites further away from the source of the freshwater input). This study provides insight into how assemblages respond and recover after a flood. Understanding this process is essential in order to understand the ecological functioning of the system

Introduction

Sixty-five percent of Australian estuaries are located in the dry tropic region, which is characterised by high summer temperatures and seasonal monsoonal rainfall. For example, in Townsville, approximately 80% of the annual rainfall occurs during December to February (Australian Bureau of Meteorology). During years of high rainfall, salinity levels in estuaries in this region can change from ~35 ‰ to freshwater conditions within a few hours (Sheaves 1998), meaning that estuarine organisms are faced with the physiological demands of dealing with rapidly changing salinity regimes. When the effects of extreme weather events, such as cyclones, are added to this picture, it is clear that rather than facing a benign, stable environment, tropical estuarine organisms must deal with a highly variable one.

Freshwater inflow is one of the most influential factors affecting benthic invertebrate assemblages (Sklar & Browder 1998). Flooding creates upstream/downstream salinity gradients within estuaries, with low salinities in the upstream region (Wetzel et al. 2012). Reduced salinity levels lead to distinct differences in faunal assemblages between the upstream and downstream regions (Sheaves 1996a, Attrill & Rundle 2002, Chapter 3). These salinity gradients can develop over very short distances leading to massive changes in faunal assemblages in upstream region but little seasonal shift in downstream assemblages (Sheaves et al. 2007).

Although many studies have examined changes in benthic invertebrate assemblages along downstream gradients in estuaries (e.g. Attrill & Rundle 2002, Prado et al. 2013), there has been little focus on tropical invertebrate assemblages in the estuary/freshwater transitional zone (upstream region where salinity levels transition between marine and fresh seasonally). The salinity changes in these transitional zones are typically highly asymmetrical, with a rapid transition from marine to freshwater conditions following floods, followed by a gradual return to marine conditions (Davis et al. 2012b). Floods in upstream transitional areas can be categorised as pulse events (with rapid but not sustained change) (Gillanders & Kingsford 2002). Associated changes in salinity can have major impacts on invertebrates in the transitional areas, including mortality, changes in community structure and movement of organisms (Gillanders & Kingsford 2002). While the effect of pulse events on benthic taxa in transitional areas is well known (Gillanders & Kingsford 2002, Telesh & Khlebovich 2010), how these assemblages recover after a flood is poorly understood. For example, how quickly do assemblages recover after a flood event, and, during recovery, do the surviving taxa from downstream sites move upstream to colonise the disturbed sites? Are assemblages in early succession dominated by fast-growing, well-dispersed taxa (opportunistic, fugitive, or r-selected life-histories) and as succession proceeds, are these taxa replaced by more competitive (k-selected) taxa. More research is required to answer these questions.

These transitional areas are ecologically important, providing short-term habitats and critical migration pathways between the estuary and freshwater nursery environments

for high value fisheries species like barramundi, *Lates calcarifer* (Davis et al. 2012b). The availability of benthic prey is critical for successful nursery occupation (Davis et al. 2014b). However, the availability of benthos in transitional wetlands is likely to be very variable, with extreme and rapid fluctuations in salinity meaning macro benthos assemblages are likely to undergo more dynamic change than in any other part of the estuary. Despite the understanding of the importance of benthos to ecological functioning, there is little understanding of the response and subsequent recovery of macrobenthic assemblages of transitional wetlands to seasonal flooding. To make the first steps towards such an understanding, I examined faunal assemblages in a series of transitional areas with increasing distance downstream from sources of freshwater input. The aim was to (i) determine the nature of the macrobenthic invertebrate assemblages that occupy transitional wetlands, and (ii) examine how the asymmetric annual alternation between marine and freshwater conditions shapes macrobenthic assemblages of transitional wetlands; in particular, to understand the nature and pattern of response to freshwater floods, including the subsequent recovery.

Materials and methods

Sampling design

Sampling was conducted between October 2003 and October 2004 in Ross River, Saltwater Creek and Althaus Creek (Figure 4.1). These dry tropic estuaries were selected as they all have similar rainfall regimes and pools in their upper reaches (Table 5.1). The pools in Ross River are located in an adjacent wetland area (Annandale wetlands) and are connected to Ross River by channels (Figure 4.1). There is a different arrangement of pools in Saltwater and Althaus Creeks. Their pools are located within the estuary bed, but are separated from the main estuary by sandbars (Figure 4.2, Table 4.1). These pools differ in their tidal connection with the main estuary. The downstream pools in Saltwater and Althaus Creeks are connected to the main estuary during a high tide >2.6m whereas the upstream pools require a >3.23m tide to connect with the main estuary.

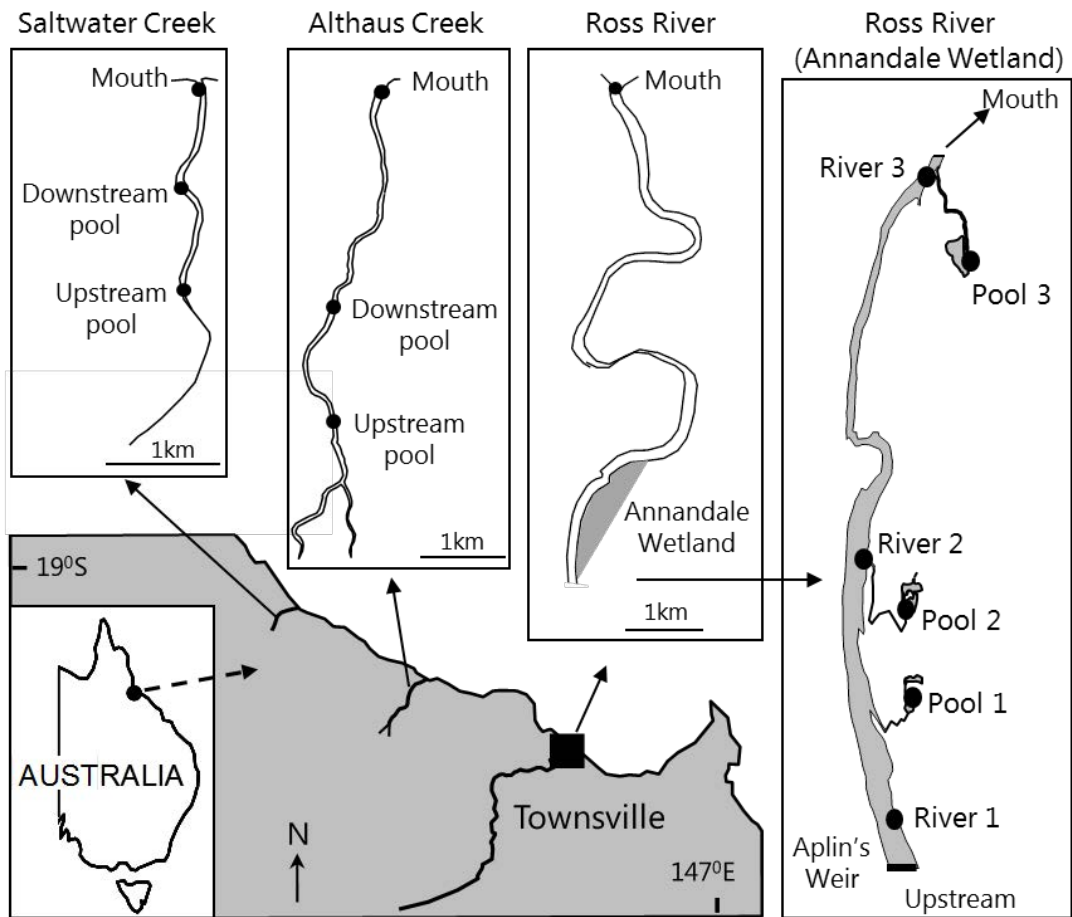


Figure 4.1. Map showing the locations of Saltwater Creek, Althaus Creek and Ross River sampling sites in North Queensland, Australia

Table 4.1. Description, sediment type and salinity range of sampling sites.

Estuary	Site	Sediment type	Site description	Salinity range ‰
Ross River	Mouth	Sand	Area 50m x 50m, located 100 metres from mouth entrance	27 to 39
	Pool 1	Sand	20m x 30m x 1.2m deep	13 to 40
	Pool 2	Sand	40m x 50m x 2m deep	13 to 37
	Pool 3	Sand	60m x 50m x 2.5m deep	21 to 37
	River 1	Sand	150m downstream from Aplin's Weir	2 to 38
	River 2	Sand	1km downstream from Aplin's Weir	8 to 37
	River 3	Sand	2km downstream from Aplin's Weir	15 to 37
Althaus Creek	Mouth	Sand	Area 50m x 50m, located 100 metres from mouth entrance	27 to 35
	Downstream pool	Sand	18m x 5m x .8m deep	0 to 39
	Upstream pool	Sand	12m x 8m x 2.5m deep	0 to 45
Saltwater Creek	Mouth	Sand	Area 50m x 50m, located 100 metres from mouth entrance	16 to 38
	Downstream pool	Sand	20m x 18m x 2.5m deep	5 to 39
	Upstream pool	Sand	40m x 15m x 2.5m deep	2 to 36

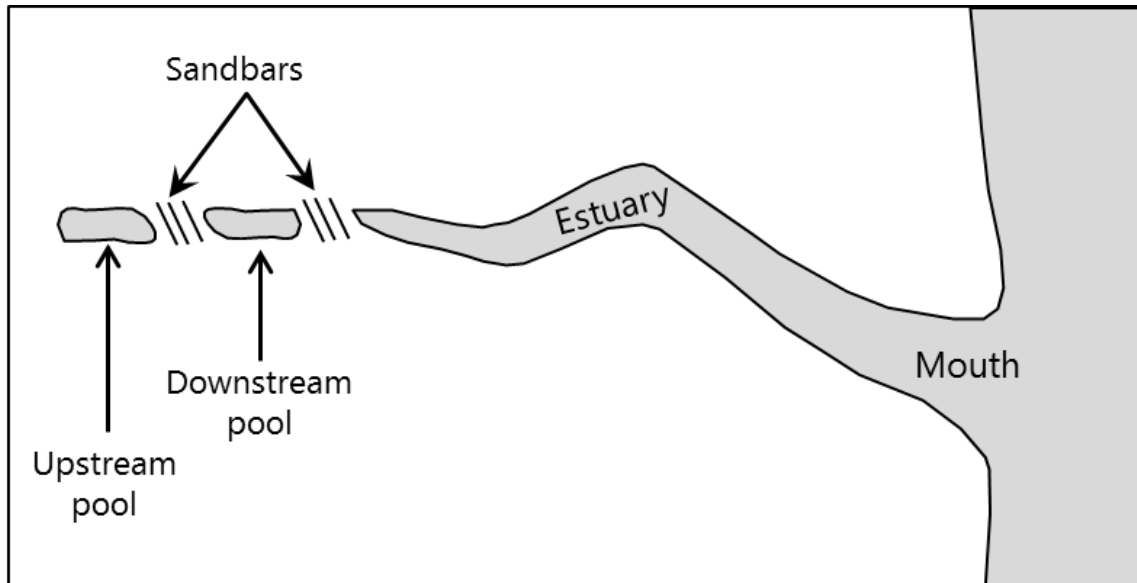


Figure 4.2: Diagrammatic representation of an estuary and associated in-stream pools (similar arrangement to the downstream and upstream pools of Saltwater and Althaus Creeks).

In Ross River, samples were collected from three pool sites (in wetland area adjacent to Ross River) and three estuary sites as well as the mouth site (Figure 4.1). In Saltwater and Althaus Creeks, samples were collected from upstream and downstream pools and mouth sites (Figure 4.1). Sampling was conducted at three-monthly intervals – October 2003, and January, April, July and October 2004 – to coincide with the major seasonal periods (wet, post-wet, dry and pre-wet seasons). To reduce the influence of differences in faunal assemblages due to sediment type, only sand habitats were sampled.

At each site six samples were collected using a van Veen grab. Samples were wet-sieved in the field using a 1mm sieve. In the laboratory all animals were identified to the lowest possible taxonomic level. Individuals that could be clearly differentiated were counted separately and recorded as identifiable morpho-types, although a lack of relevant keys and descriptions meant species names could not always be assigned. Raw counts were converted to densities per 10 litres of substratum. Salinity levels, pH, water temperature and sediment samples were collected from each site, on each sampling occasion, as described in Chapter 2.

Data analysis

Patterns of similarity in faunal composition over the 13 sites and five sampling trips were analysed using multivariate classification and regression trees (mCARTs) using Treesplus. Two mCARTs were constructed. The first employed row-standardised data to emphasise faunal composition, as sites with the same proportional representation by each taxon were considered to have similar composition. The other was based on unstandardised data so that it emphasised differences in faunal abundances. mCARTs are computer-intensive statistical techniques used to explore, describe and predict relationships between multi-species data and explanatory variables (De'ath & Fabricius 2000). In mCARTs clusters of samples are formed by repeated splitting of the data, with each split chosen to minimize the dissimilarity (variability) of samples within clusters. At each split data are partitioned into two groups that are mutually exclusive and as homogeneous as possible. mCARTs were fitted using 10-fold cross-validation and the "best" tree sizes selected under the 1-SE criterion (i.e. the smallest tree within 1 standard error of the tree with the minimum cross-validation error), an approach that produces valid, interpretable trees (De'ath & Fabricius 2000). Only taxa occurring in >10% of the sites were included in statistical analyses to reduce variability caused by rare taxa (Tausch et al. 1995). Data were 4th-root transformed before analysis to down-weight the influence of dominant taxa. Non-metric multidimensional scaling (nMDS) (Clarke & Ainsworth 1993) using Bray-Curtis similarities was used to illustrate relationships. All data were 4th-root-transformed to minimise the impact of species that occur in large numbers as these tend to swamp the effect of other species.

Results

A total of 109,048 invertebrates were collected from the three estuaries over the five sampling trips. The assemblage structure of the fauna varied between sites in all streams and was mainly influenced by spatial factors (assemblages in one estuary were different from assemblages in another estuary), with temporal factors having only minor influences (Figure 4.3a). In the final mCART model for row-standardised data (emphasising assemblage composition), differences among sites accounted for 63% of the explained variability and were responsible for the first five tree splits on the classification and regression tree (Figure 4.3a).

There were four major features on the mCART tree:

- (1) The Ross River and Althaus mouth sites were very different from all other sites. Ross and Althaus mouth sites had low species richness, and, unlike other sites, were dominated by bivalves and gastropods (Figure 4.3a and b);
- (2) Althaus and Saltwater pool sites also had low species richness and were depauperate in comparison to Ross River pool and river sites (Figures 4.3b and 4.4);
- (3) Ross River pools and river sites were taxonomically rich in comparison to Saltwater and Althaus pools (Figures 4.3b, 4.4, 4.5 and 4.6);
- (4) The final splits on the tree were largely based on differences between sampling trips. In general the months with the reduced salinity levels split from the other trips where salinity was higher (Figures 4.3a, 4.5 and 4.6).

A commonality among the pool and river sites of all three streams was the occurrence of 'resident' taxa (*Nereis* sp 16, *Lumbrineris* sp 9, *Cerithidea cingulata* and *Pasithea* sp 1 (Figure 4.3b), which occurred in >80% of all samples collected and were often the most abundant species recorded.

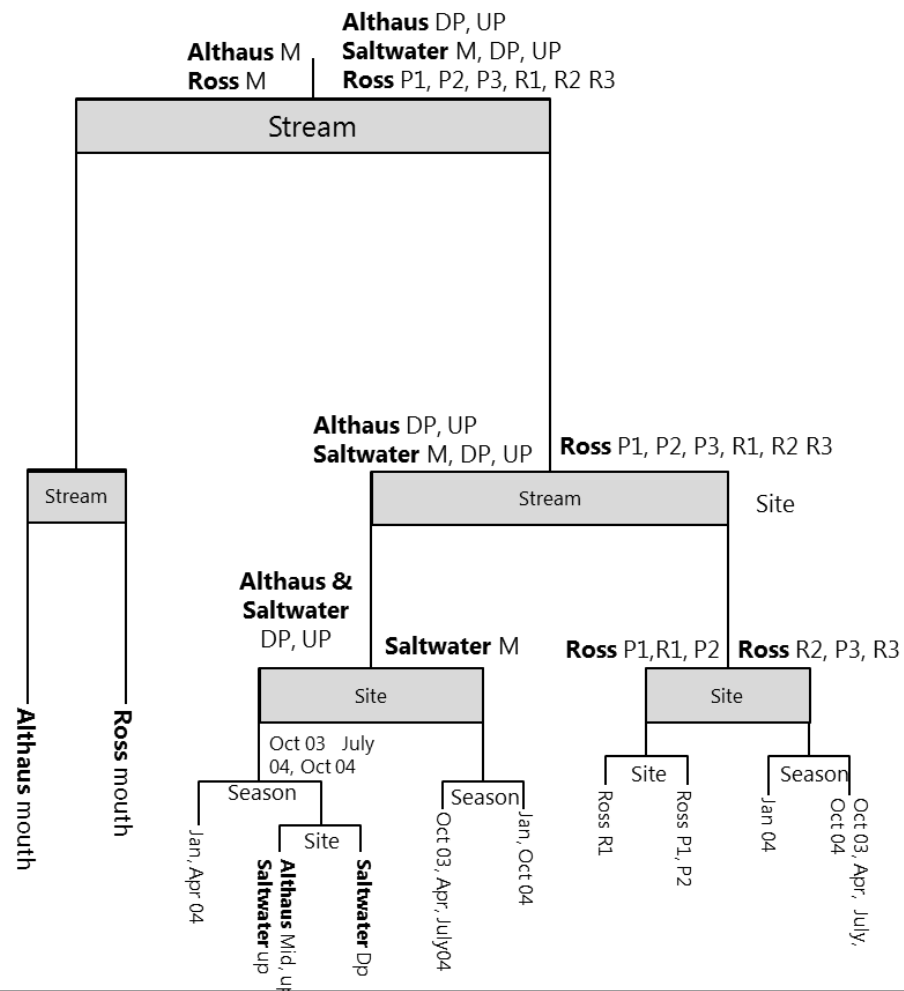
Multivariate CART (based on abundances) showed considerable temporal variability in the faunal assemblages (Figure 4.4). Sites on the left hand side of the tree were taxon-poor with very few organisms occurring in high abundances in comparison to sites on the right hand side of the tree which were taxonomically rich, with many taxa occurring in high abundances (Figure 4.4). The second feature was a general reduction in

abundances in January and April 2004, which coincided with extensive rainfall and depressed salinities (Figures 4.4, 4.5 and 4.6). Salinities at mouth sites did not drop below 18 ‰ and they recovered quickly in the following months (Figs 4.5 and 4.5). There were fluctuations in the number and density of taxa recorded at the mouth sites (see Ross River, Fig 4.5). At the Althaus mouth site, very few taxa were recorded and they occurred in very low abundances (Fig 4.6). This was a very unstable site with very strong water currents and the sand in constant motion, presumably making it difficult for benthic invertebrates to colonise.

Reduced salinity levels in January reduced the taxonomic richness and abundances of taxa at all sites, but sites closest to the source of freshwater input (i.e. Pool 1 and River site 1 in Ross River) took longer to recover than the downstream Ross River sites (River 3 and Pool 3) (Figure 4.5). This pattern was similar in Althaus and Saltwater Creeks, where faunal assemblages in the upstream pools recovered slowly in comparison to their downstream counterparts (Figure 4.6). Salinity levels in both Althaus and Saltwater upstream pools remained low from January to July due to limited tidal connection (the tide could only reach these sites about three times per month) and, as a consequence of this limited connection, taxonomic richness and abundance remained low for the remaining sampling trips (Figure 4.6).

There was a distinct change in taxonomic richness along the downstream gradient in Ross River, with sites closest to the freshwater input (Pool 1 and River 1) having low richness (a total of 24 taxa recorded) in comparison to the downstream sites (downstream Pool 3 and River 3) which had a total of 47 and 48 taxa recorded (Figure 4.5).

(4.3 a)



(4.3b)

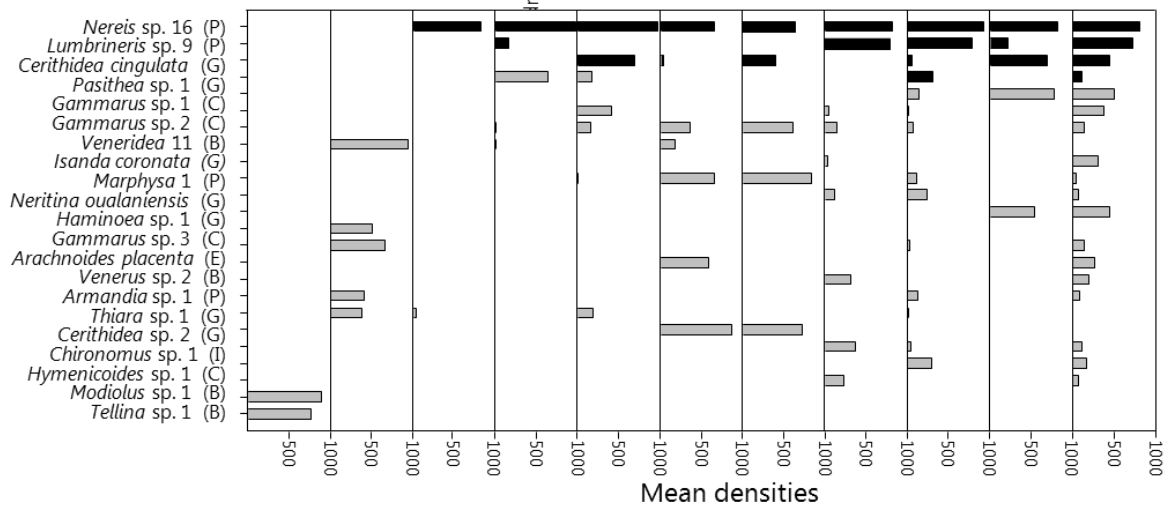


Figure 4.3: (a) Multivariate classification and regression tree (mCART) for spatial and temporal factors using species occurring (emphasising faunal composition at sites) in >10% of samples. Abundance data were row standardised (Error: 0.367 CV Error (pick): 0.667 SE: 0.0481).

Key to Codes in tree: M=mouth, P1=Pool 1, P2=Pool 2, P3 =Pool 3, R1=River 1, R2=River 2, R3=River 3, DP=downstream pool, UP=upstream pool. (b) Histogram of species (mean densities) occurring in at >10% of samples. Letters in brackets after taxon names in the histogram: B=bivalve, C=crustacean, E=echinoderm, G=gastropod, I=insect, P=polychaete.

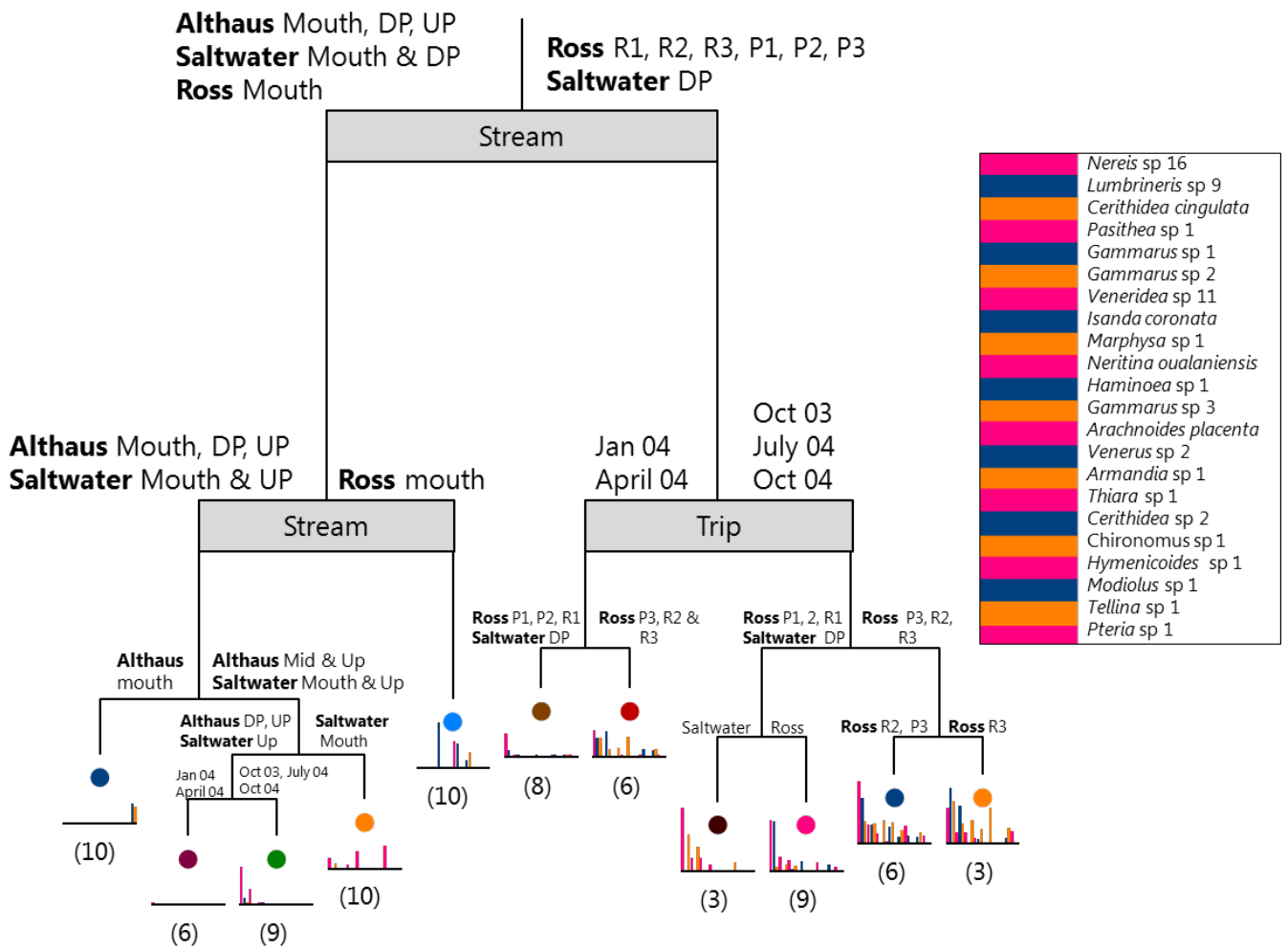


Figure 4.4: Multivariate classification and regression tree for spatial and temporal factors using species occurring in >10% of samples. Abundance data were 4th transformed (not row standardised). Error: 0.327 CV Error (pick) : 0.559 SE: 0.0563. Emphasizing abundances of species at sites. Key to codes; P1=Pool 1, P2=Pool 2, P3 =Pool 3, R1=River 1, R2=River 2, R3=River 3, DP=downstream pool, up=upstream pool. Numbers in brackets under histograms represent sample sizes.

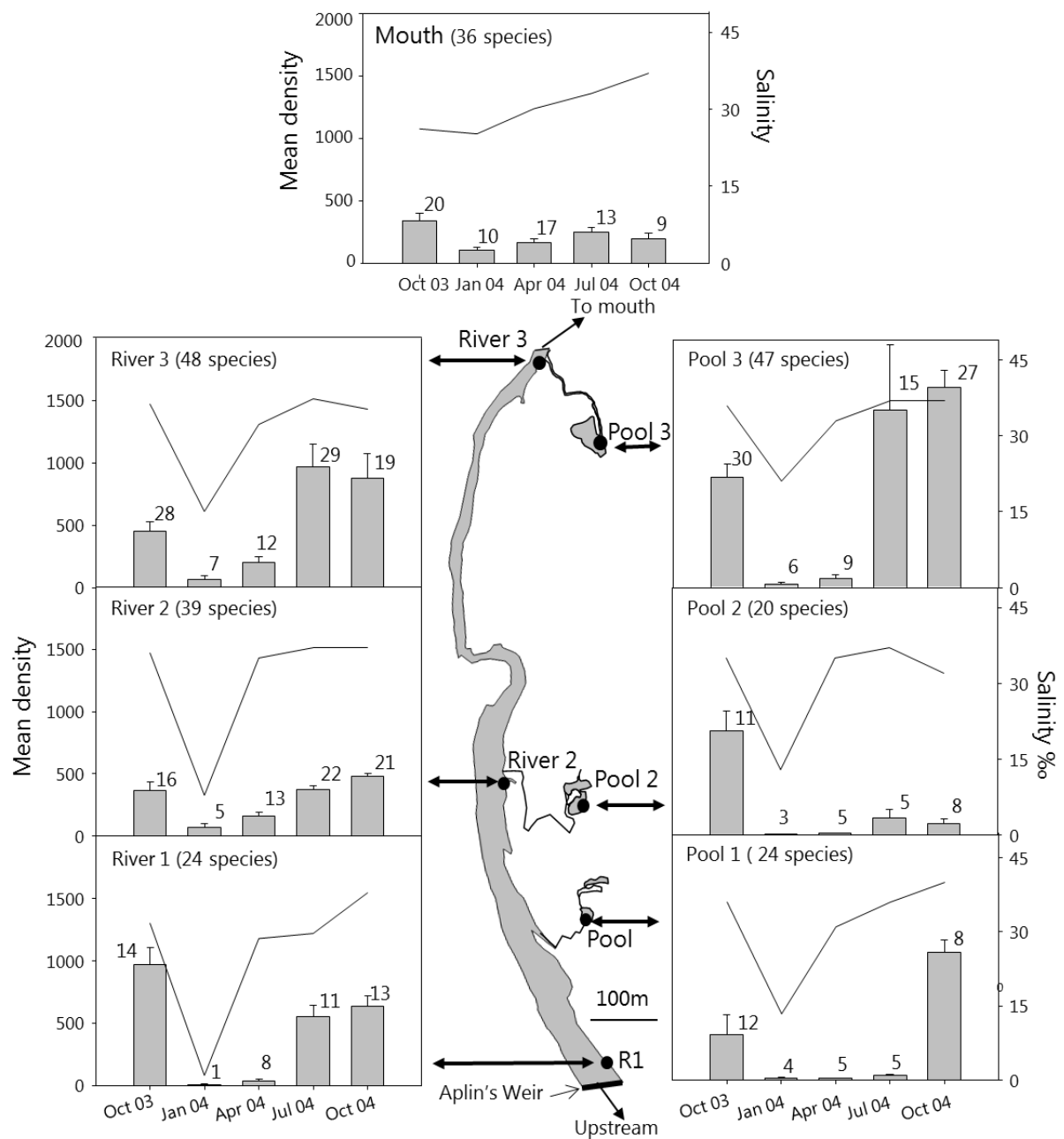


Figure 4.5: Detailed map of upstream estuary sites and off-stream pools in Ross River and histograms of the mean densities (per 10 litres) and salinities of all Ross River sites. Error bars are ± 1 s.e. Solid circles indicate position sampling sites. Numbers in brackets after the site name indicate the total number of species recorded at that site. The numbers above the bars in the histogram indicate the number of species recorded that trip. The lines represent the salinity levels for each trip.

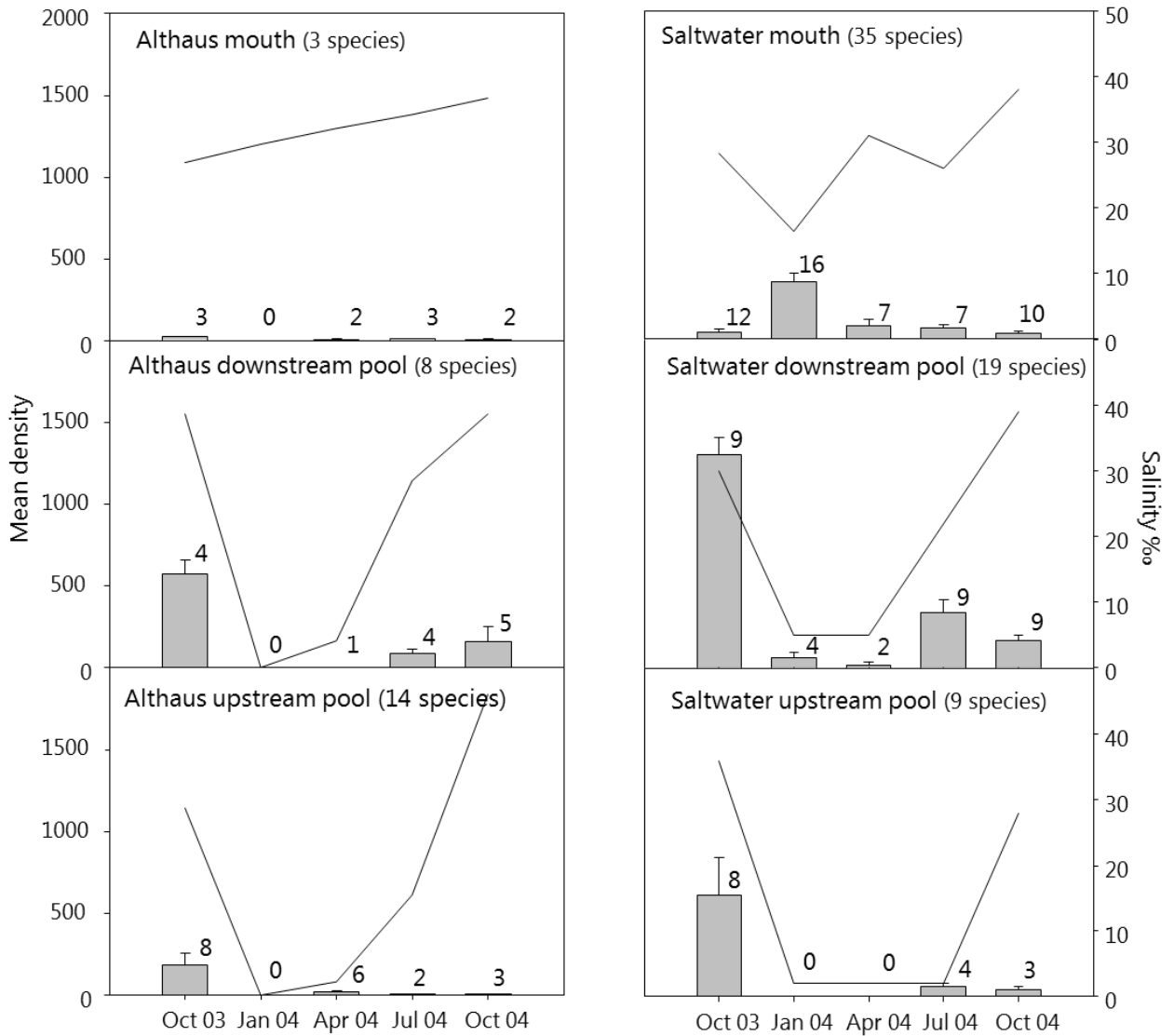


Figure 4.6: Patterns of change over time of benthic fauna and salinities for Saltwater and Althaus creeks. Histograms show the mean densities (per 10 litres) and salinities of Althaus and Saltwater Creeks sites. Error bars are ± 1 s.e. Numbers in brackets after the site names indicate the total number of species recorded at that site. The lines represent the salinity levels for each trip. The numbers above the bars in the histogram indicate the number of taxa recorded that trip.

Site-specific temporal trajectories

The four nMDS ordinations of Ross River and Pool and River sites 1 and 3 (Fig 4.7) all showed clear shifts in ordination space from October 2003 to January 2004, which is when the flood occurred. Subsequently the assemblages recovered, occupying similar ordination space in October 2004 to that of October 2003. In October 2003, the polychaetes, *Lumbrineris* sp 9 and *Marphaysa* sp 1 and the amphipods *Gammarus* spp 1 and 2 dominated the samples in terms of abundance. Most of these species were also recorded in January (during the flood) but their numbers had dropped significantly; over the ensuing months their abundances increased to similar levels to those recorded in October 2003 (Figure 4.7).

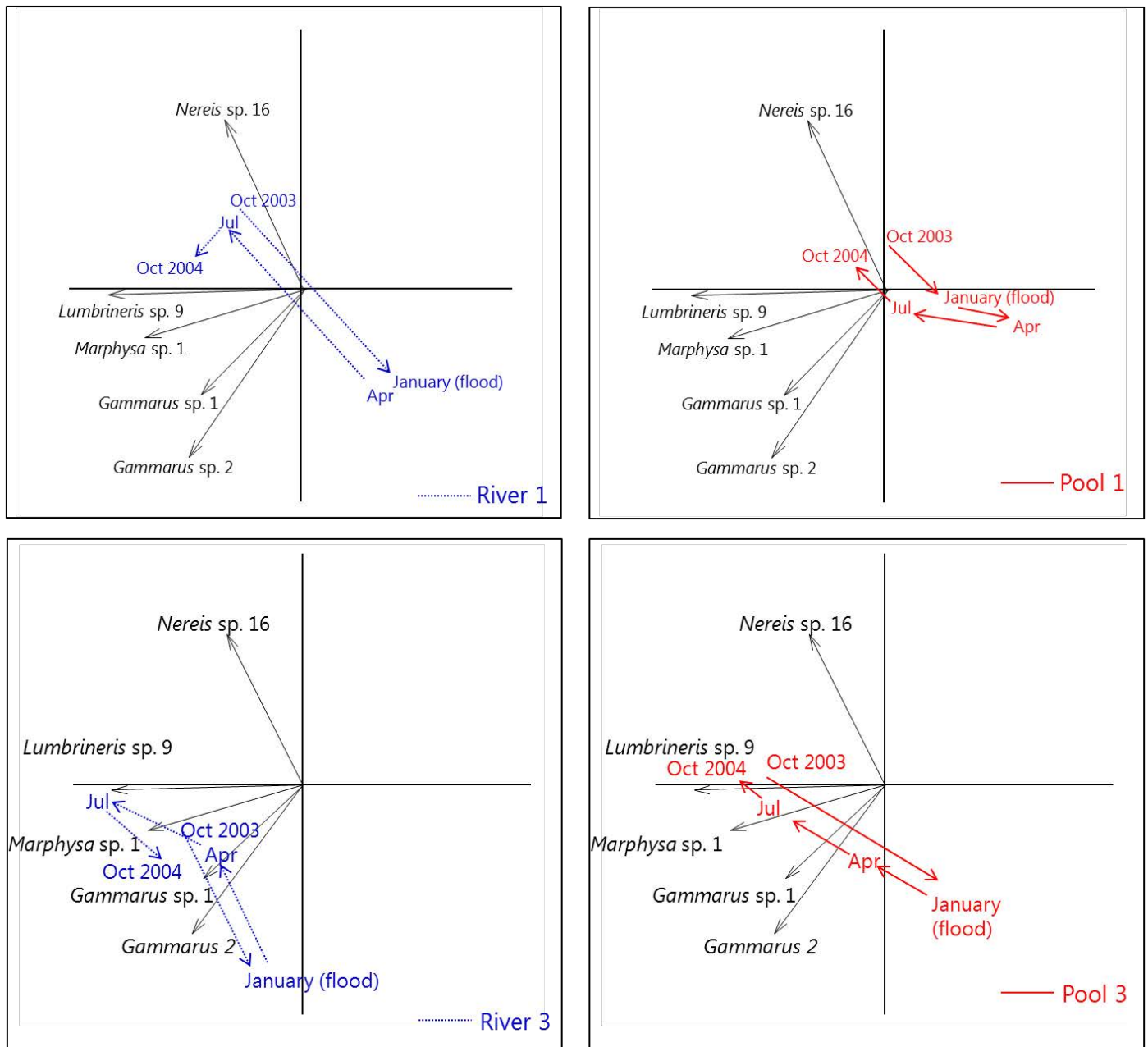


Figure 4.7: Four-dimensional solution (stress = 0.17) of multidimensional scaling of data for all five trips. Representing pre-flood (Oct 03), flood (Jan 04), then recovery of faunal assemblages (Oct 04). Arrow vectors indicate the direction of greatest increase in abundance of the species most highly correlated with the ordination space. Vector lengths are proportional to the R^2 for each species. Key; Numbers after the letters represent sampling trips 1=Oct 03, 2=Jan 04, 3=Apr 04, 4=Jul 04 and 5=Oct 04 (e.g. P4 = pool site sampled Jul 04)

Nature of the benthic invertebrate assemblage

The invertebrate assemblages in transitional areas of estuaries are dynamic and constantly changing. There are some different responses of taxa over the seasons. Some taxa remain at the same site over the seasons, although abundances decrease during times of low salinities, while some other taxa disappear for the site when salinity levels decrease. Some taxa colonise sites only when salinity levels are low while other are only recorded at sites after the flood (Figure 4.8).

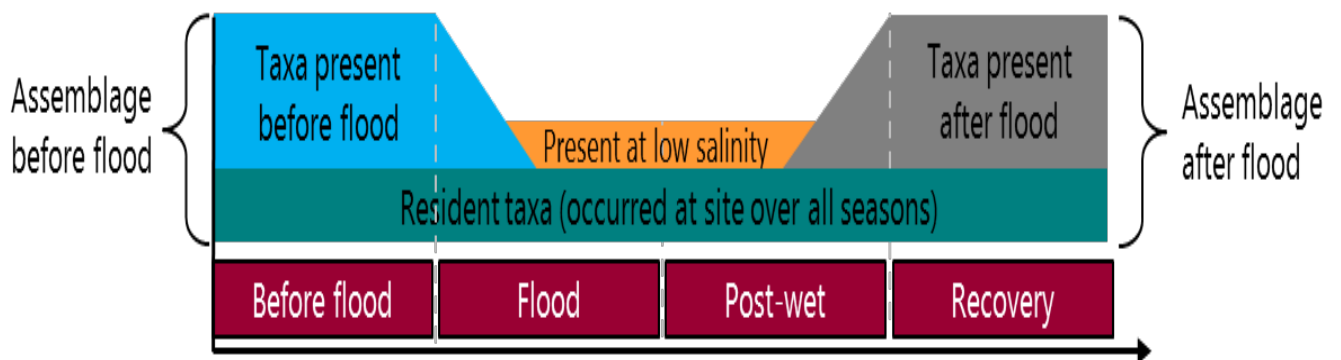


Figure 4.8: Conceptual model of changing assemblage structure over various seasons

Discussion

The distribution and abundance of macrobenthic invertebrate fauna underwent large temporal and spatial fluctuations, which, in large part, reflected fluctuations in the physical environment. The flood in January 2004 significantly altered conditions in all three estuaries, producing strong salinity gradients ranging from freshwater in the upstream areas to marine at the mouths. Reduced salinity levels had a negative impact on the macrobenthic invertebrate assemblages, triggering large shifts in faunal assemblages, with significant reductions in taxonomic richness and abundances along the downstream gradients. Faunal assemblages in sites adjacent to freshwater input (Saltwater and Althaus upstream pools) were the worst affected, with the total loss of all marine fauna in these sites. The pattern of faunal loss along the downstream salinity

gradient was similar for all estuaries and reflected the salinity gradients created by the flood. The loss of benthic fauna during floods has obvious implications for estuarine food webs as a wide variety of animals feed on benthic invertebrates, forcing predators to either switch to an alternative food source or move to areas where food is available (Grosholz & Gallo 2006).

Faunal recovery is influenced by a number of factors such as the level of connectivity to other sites and to other faunal assemblages (Wenner & Beatty 1985), the availability of larvae to recolonise sites (Kondolf et al. 2006), and the extent of depression of salinity levels during flooding. The major mechanism of recovery in ecosystems is ecological succession (Gray, 1981). In this study, the macroinvertebrate assemblages experienced significant changes after the flood, followed by colonisation and succession of organisms. Typically pioneering taxa (*r* selected) are the first to inhabit the site, as colonisation proceeds, competitive ability becomes increasingly important as carrying capacity (*K*) is approached and so species at later successional stages, *K*-selected species move in (Gray, 1981). However, in this study this did not seem to be the case. In Ross River, faunal assemblages at downstream sites (River 3 & Pool 3) recovered more rapidly than at upstream sites (River 1 & Pool 1).

However, recolonisation and succession of upstream sites did not follow an ordered pattern of recovery with upstream sites (River 1 & Pool 1) being recolonised by taxa from downstream sites [Pool 3 and River 3]; instead, colonisation seemed to be haphazard – for example, some taxa from Pool 1 site colonised River 3 sites and vice versa. In contrast, the upstream sites at Saltwater and Althaus Creeks did not recover. These sites had limited tidal connections (~8 days per month), resulting in reduced salinity levels for an extended period of time and limited access to potential colonising fauna (Carvalho et al. 2010, Barros et al. 2012). In essence, they had become freshwater pools with very limited marine influence. This suggests that self-recruitment from local populations in these estuarine transition zones is more important than metapopulation processes, a notion that is supported by the lack of recovery of upstream fauna at Saltwater and Althaus Creeks, presumably because no remnant pockets of upstream specialist fauna survived.

The seasonal changes in salinities lead to noticeable variations in the abundance and number of invertebrate taxa between the dry and wet season (Carvalho et al. 2010). This poses a problem for estuarine organisms that rely on the invertebrates as a food source (Quammen 1984, Malmqvist 2002). When invertebrate numbers are low in the wet season, many fish migrate downstream in search of a more abundant food source (Grosholz & Gallo 2006). This has far-reaching implications on the estuarine food web, as the trophic dynamics of the system changes seasonally from the wet season to the dry season (Schwendel et al. 2012, Matich & Heithaus 2014). In essence, the food webs in these areas change from a wet season food web (low invertebrate numbers) to a dry season food web where invertebrate numbers are high (Figure 4.8). Floods not only affect food webs, they also alter the patterns of habitat use, decrease nursery ground values of the area and change predator prey dynamics (Matich & Heithaus 2014). These changes can cause the estuarine areas to operate quite differently during floods in comparison to dry periods. For example, in dry times, juvenile *Penaeus* prawns inhabit the mid and upper pools in Ross River (Sheaves et al. 2007) where they rely on phytoplankton, epiphytic and epilithic algae and green filamentous algae for their nutrition (Abrantes & Sheaves 2009a, b). During floods this food source would die out and if these prawns were to survive they would need to migrate downstream to find food.

Although floods can have a devastating impact on the benthic assemblage, they are relatively short-lived events from which assemblages can recover (Hamilton & Gehrke 2005). However, in the light of climate change predictions of increases in intense precipitation events and greater year-to-year variation in rainfall in the tropics (Lough 2007) the long-term effects on macrobenthic invertebrates could lead to dramatic permanent changes in assemblages, if marine fauna do not have sufficient time to recover between high magnitude flood events (Berger et al. 1995, Barros et al. 2012), with the situation seen in Saltwater and Althaus Creeks potentially repeated in larger systems such as Ross River. Conversely, the persistence of freshwater conditions would see an increase in the occurrence of freshwater organisms such as fish and larval stages of some insects in areas that were previously occupied by marine organisms. In

essence, in wet years, dry tropics streams could function as wet tropics streams. Conversely, if there is greater year-to-year variation the result is likely to be a more intense alternation of wet and dry phase fauna, with the potential for the complete loss of key fauna leading to a tipping point where the current assemblages are replaced by a unique faunal mix (Laurance et al. 2011) or where a depauperate fauna becomes the norm.

Tropical estuarine systems show substantial temporal and spatial variability on a number of scales. Understanding the interaction between freshwater and marine influences on faunal assemblages is important in determining faunal outcomes and temporal variability at the marine/freshwater interface, while knowing how faunas change, and recolonisation and recovery differ across a variety of situations is important in understanding spatial differences in impacts and the likely response to flow events of different magnitudes.

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Chapter 5: General discussion

Estuarine assemblages are in continual flux, with changes in assemblages driven by the pulsing of the tidal cycle modified by climatic events that range from local storms to major floods (Sheaves & Johnston 2009, Barros et al. 2012). While sediment type, food availability, larval supply, temperature and predation are all important in structuring benthic invertebrate assemblages (Sanilkumar et al. 1994, Berger & Naumov 1996, Nanami et al. 2005, Prado et al. 2013), it is the interplay of regular tidal pulsing and periodic freshwater events that is the major agent of change and is largely responsible for the distinct changes in benthic invertebrate assemblages along the upstream/downstream gradient (Ricklefs and Schluter, 1993, Hildrew and Giller, 1994). While the effects of floods and the subsequent recovery of estuarine fish and plant assemblages are well documented (Sheaves et al. 2007, Sheaves & Johnston 2008, Davis et al. 2012b) this is not the case for estuarine invertebrates. Many studies have emphasised the importance of salinity changes in shaping benthic invertebrate assemblages, however, most of these studies have been in temperate areas (Edgar et al. 1999, Engle & Summers 1999, Attrill & Rundle 2002, Andrei et al. 2008, Lautenschlager et al. 2014). Although estuarine ecologists are beginning to document the interplay of fresh and saltwater on benthic invertebrate assemblages and the relative influence of local and regional factors on them (Maurer et al. 1978, Kimmerer 2002, Gimenez et al. 2005, Power et al. 2013, Prado et al. 2013), very few studies have examined tropical invertebrate assemblages prior to a flood, how assemblages change during a floods or how assemblages recover over time after a flood.

This information is essential as transition zones in estuaries are often impacted by human activities (e.g. urban development, dams and weirs) (Wetzel et al. 2012, Prado et al. 2013), meaning that there is a continual need for managers to make decisions about urban development in these areas, implement remedial action, and to monitor the effects of those decisions and actions. This study shows what happens to benthic invertebrate assemblages when there is a reduction in salinities (sometimes from 35‰ to 0‰) and how assemblages recover. This helps managers in a number of ways. For example, for an environmental impact assessment conducted for a development along an estuary, timing is crucial – if the assessment was done after a flood, it would not

represent the 'true' assemblages of the estuary and may indicate that the estuary is species poor, which may not normally be the case. Without critical information on the natural patterns of change of transition-zone fauna there is no way to determine if impact or recovery have occurred or how far down the path of recovery an assemblage is.

The abundances of taxa and the composition of benthic invertebrate assemblages respond strongly to the alternation of marine and freshwater conditions (Nanami et al. 2005, van der Linden et al. 2012, Prado et al. 2013). By investigating estuaries across a tropical climatic gradient at a range of spatio-temporal scales, this study provides a new level of detail on the responses of assemblages to adverse conditions and their patterns of recovery. The study of the transitional faunal assemblages in Ross River, Althaus and Saltwater Creeks (Chapter 4) demonstrated the role of a disturbance (flood) in shaping the diversity and dynamics of invertebrate assemblages and shows different patterns of re-establishment of benthic assemblages. The basic pattern of change was unsurprising. The benthic assemblages were at a certain level prior to the flood, then the flood occurred and there was extensive loss of marine invertebrates followed by a period of recolonization and recovery during the dry season. This sequence matches reported changes in other parts of the world (Barrat-Segretain & Amoros 1996, Death 1996, Seburn et al. 1996). Recolonisation and recovery of fauna was varied and was dependent on the extent (minor or major) of the flood, and the location of the fauna in relation to freshwater input. However, not all estuaries are the same; while some assemblages recovered following to the flood, other assemblages did not – for example in the upstream pools of Althaus and Saltwater Creeks. Therefore, while some broad generalisations can be made, there is still the need to investigate each estuary individually. Recovery of upstream assemblages is complex. It involved not simply an upstream movement of downstream taxa, recolonising depauperate sites, but also more complex metapopulation dynamics, with some taxa that had persisted in upstream sites recolonising downstream sites and vice versa, thereby illustrating the importance of the survival of 'remnant' assemblages, which when conditions are suitable, supply other areas with colonising taxa.

Changes over time are often seen as progress towards a climax assemblage (Ritter et al. 2005); however, this is usually more of a null hypothesis than a reality, except in cases where disturbance is infrequent. It is probably better to think of progress over time as a move toward a quasi-stable assemblage state. The rate of progress towards a quasi-stable condition varies greatly among systems, with less frequently disturbed riverine assemblages recovering very slowly compared to those in areas with more frequent disturbance (Barrat-Segretain & Amoros 1996). In the present study, most assemblages reached a predictable quasi-climax state before the next seasonal freshwater event. This suggests assemblages are resilient to this normal seasonal change. While this is probably the normal situation under natural seasonality, these systems do go through periods of altered seasonality at multi-year scales (Covich et al. 1996) where there may be an extended dry season that lasts for as long as six years (Sheaves et al. 2007). In these cases, the fauna seems to continue to shift beyond the quasi-stable state such that transitional assemblages come to resemble downstream assemblages.

One of the major features of the small- and large-scale spatial studies was the collapse and subsequent recovery dynamics of the invertebrate assemblages, particularly in upstream areas. The collapses can be catastrophic (Figs. 5.1a, b & c), and the subsequent recovery variable and dependent on a range of factors. These sorts of dynamics have been investigated and modelled using the concept of tipping points (Ling et al. 2015), where an environmental change (e.g. flood) can cause a major shift in assemblage structure, but where the assemblage structure returns to a similar state in time (Laurance et al. 2011); and hysteresis, where there is a shift in assemblage structure and the assemblages do not return to a similar state (Ling et al. 2009, Ling et al. 2015). This happened in the upstream pools of Saltwater and Althaus Creeks: initially the pools operated as a marine system with a distinct marine food web, but after the flood, the pools essentially operated as a freshwater system with a freshwater food web.

The various patterns of change have a range of consequences depending on the pattern and extent of recovery, and on the details of the particular situation in which they occur. The important points about the dynamics of decline and recovery are:

- Major flooding leads to catastrophic decline in faunal density and richness, which have major implications for organisms that rely on invertebrates as food.
- Faunal recovery lags behind salinity recovery, because of the need for fauna to re-establish.
- The taxa that recover in upstream areas are transition-zone specialists that are generally absent or rare in downstream sites. These taxa can be used as indicators of the 'health' of the transition section of an estuary
- Where transition fauna did not recover, evidence indicates it was not because of poor connectivity because salinity levels returned in a predictable way.
- In contrast, in Ross River the eventual recovery was slow – the specialist taxa that dominated transition zones were able to recover, probably because of the more complex wetland systems in Ross River providing local refuges where these species were able to persist during low salinity events.
- The nature of the local environment is important – recruitment from outside the system is clearly limited, and persistent local sources are required to drive local-scale community dynamics. The survival of transitional fauna in remnant areas is very important in the recovery of upstream assemblages.

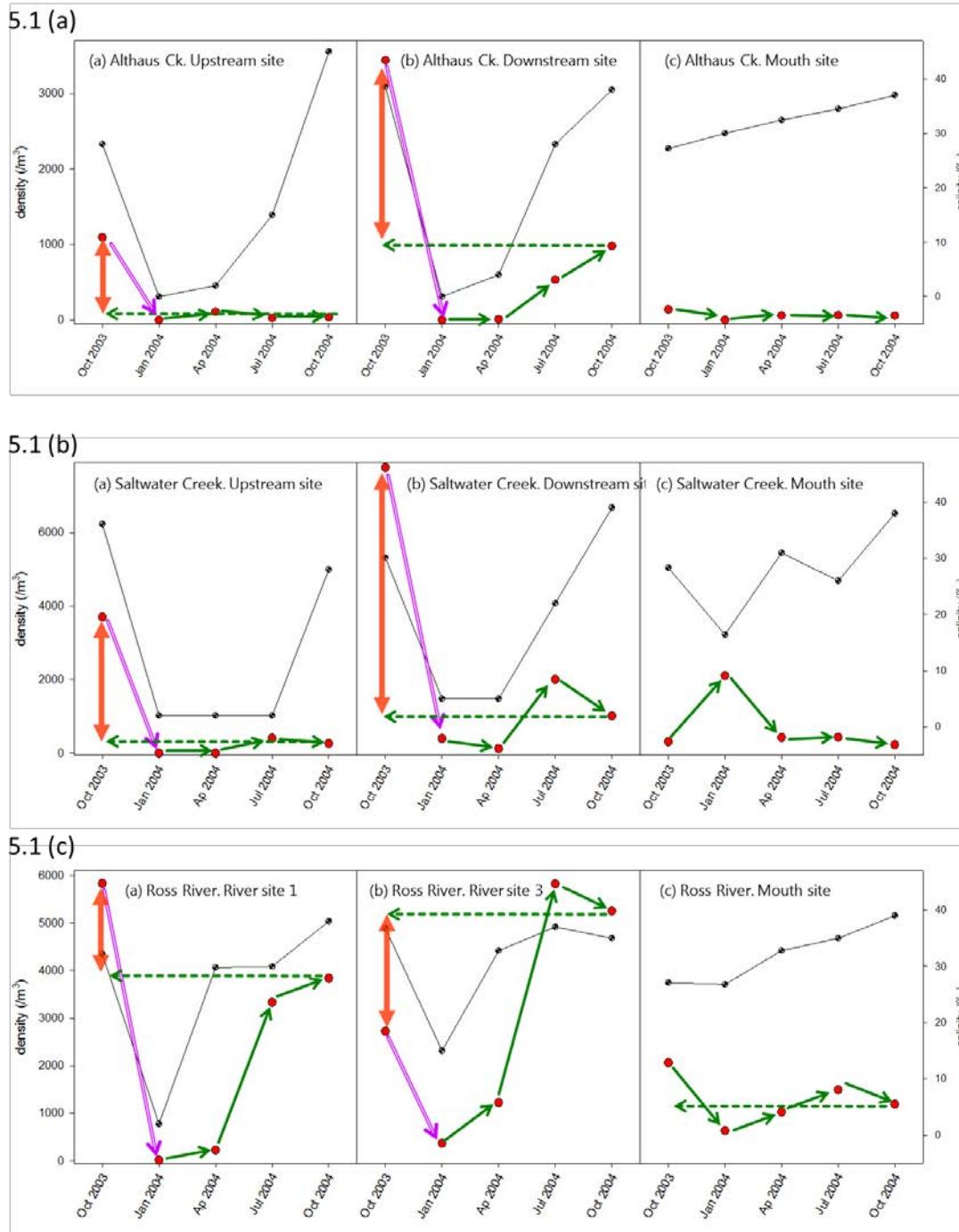


Figure 5.1. Changes in densities (m^3) and salinities over five sampling trips in Althaus Creek, Saltwater Creek and Ross River. Black circles and black line indicate salinities for each site. Red circles indicate densities (m^3) for each trip. Purple line indicates catastrophic decline in faunal density and richness. Green solid lines indicate direction of change in densities per trip. Green dotted line indicates the level of October 04 densities and distance from October 02 densities. Red solid line indicates differences between October 03 and October 04 densities. 5.1.a. Althaus upstream, downstream and mouth sites. 5.1.b. Saltwater upstream, downstream and mouth sites. 5.1.b. Ross River, River site 1, Ross River, River site 3 and mouth site.

These patterns of collapse and recovery have far-reaching implications in a regime of increasing climate variability. Slow rate and often incomplete recovery means that the reestablishment of the full faunal complement of many transition zones is likely to require more than a year. Therefore, when severe events reoccur at increased frequency, invertebrate assemblages are likely to undergo progressive change with the eventual loss of endemic transitional taxa and perhaps a shift to a fauna with a greater and more persistent freshwater component. Even with a return to a more 'natural' periodicity of extreme events, recovery will be slow because these endemic taxa are uncommon in downstream areas. Consequently, streams with reservoir areas for the endemic taxa will recover more rapidly and more predictably. This clearly indicates the importance of maintaining the overall spatial complexity of transition zone habitats – something that is the first thing to go when humans begin to modify these environments (e.g. by restricting the estuary to particular channels by the imposition of training walls). Furthermore, the loss of specialist upstream taxa is likely to be amplified when long periods of sequential intense wet seasons are followed by extended low-rainfall years. In this case upstream areas are likely to be invaded and dominated by downstream species making recovery of the unique fauna more difficult.

In the study of invertebrates in estuaries of different climatic regimes (wet and dry tropics and dry south regions), faunal patterns were highly variable, with species richness, total abundances and assemblage structure varying among regions (wet tropics, dry tropics, dry south), among estuaries within the same region (e.g. Meunga Creek and Deluge Inlet) and among sites (mouth and transitional). The geographic extent and climatic range covered by this study can explain the differences in timing and extent of physical change that elicited differences in the faunal responses. However, despite differences in detail, substantial physical changes occurred in all transition zones and drove predictable and parallel patterns of biological responses. So, regardless of the geographic location of the estuary and differences in physical features, the patterns benthic invertebrate assemblages was the same; that is, the mouth fauna differed significantly from the upstream transitional fauna and there was a distinct upstream/downstream faunal gradient.

Wet season rainfall invariably produced substantial physical change in transition zones, with salinities declining from euhaline to fresh, in effect resetting the system, and causing substantial loss of invertebrate assemblages or reductions in the densities of most species. However, declines varied even over scales of hundreds of metres as shown in the sites downstream from Aplin's Weir in Ross River, where assemblages in more upstream transition zones were more affected than those in more downstream sites, where the extent and duration of salinity depression was less than at upstream sites. Importantly, some taxa were resilient, maintaining populations in all except the most extreme situations. This small group of species includes the two polychaetes *Nereis* sp. 16, *Lumbrineris* sp. 9 and the two gastropods *Cerithidea cingulate* and *Pasithea* sp. 1. The consistent occurrence of these taxa in transition zones, and their resilience to natural perturbations, suggest they could play an important role as indicators of normal transition-zone function, such that any extended absence is likely to point to severe dysfunction. Certainly in the estuaries studied, these 'resilient' taxa can be used to determine the 'health' of upstream transitional areas.

This study (chapter 4) has particular relevance for our understanding of how climate change might affect estuarine ecosystems. Under present climatic regimes, invertebrate assemblages are subjected to periods of low salinities followed by periods of normal oceanic salinities. The periodicity of these events drives the patterns of faunal change characteristic of wet and dry tropics. Climate change is expected to alter the periodicity of major flood events, with increasing climate variability seeming set to produce more extended and more intense wet and dry periods (Thrush et al. 2003, Harley et al. 2006, Bernhardt & Leslie 2013, Pecl et al. 2014). As a result, wet tropics areas may move more towards dry tropics conditions and/or dry tropics areas may become more like wet tropics systems. The results of this study provide a base-line enabling evaluation of biological responses to such changes. Similar changes have occurred due to human activities. For example, prior to sugar cane irrigation, Barratta Creek in north Queensland was a typical dry tropics estuary, with upstream transition zone reaches typically becoming hypersaline in the dry season and only impacted by freshwater flooding in years when heavy rainfall occurred (Sheaves 1996). Over recent years Barratta Creek has functioned as a tailwater conduit for excess fresh water from

irrigation, converting it into a permanent pseudo-wet-tropics system (Davis et al. 2008, Davis et al. 2012a). If baseline data, such as provided by the current work, had been available it would have been possible to definitively evaluate the biological impact of this human-induced change.

Evaluation of other anthropogenic pressures on benthic assemblages is hampered by the lack of baseline data. The Deepwater Horizon oil spill in the Gulf of Mexico in 2010 is an obvious example. It was the largest oil spill in history (Haney et al. 2014) affecting huge areas of critical coastal wetlands (Mendelssohn et al. 2012, Yin et al. 2015). While baseline information is available to assess the damage to wetland birds (Haney et al. 2014), dolphins and turtles (Follett et al. 2014) and some commercially important invertebrates (Mendelssohn et al. 2012), because of the lack of baseline information for benthic invertebrates, there is no meaningful information that can be obtained about the effect of the oil spill on this group. As these animals have vital roles in coastal wetlands, including biomass production, sediment bioturbation and stabilization, organic matter decomposition and nutrient regeneration, and secondary production and energy flow to higher trophic levels (Danovaro et al. 2008, Montagna et al. 2013) and are a major component of food webs (Snowden & Ekweozor 1990, deSzalay & Resh 1996, Chung et al. 2012, Montagna et al. 2013). However, given the lack of baseline information for benthic invertebrate assemblages there can be no real evaluation of the recovery of food webs in this area, as there are no details of benthic assemblages and the functioning of the food web prior to the oil spill. Information is even more sparse in developing countries: for example, a lack of information on estuary benthic invertebrates prevented identification of the full extent of impacts of the 2008 oil spill in Bodo, Nigeria (Zabbey & Malaquias 2013), the largest-ever oil spill (~260 000 barrels of oil were spilled) in a transitional mangrove wetland, which devastated the flora and fauna of this area (Pegg & Zabbey 2013). Clearly, definitive baseline information on assemblages and assemblage-supporting processes is critically important for determining on how organisms respond to catastrophic events, how they recover and, if they are lost from the system, how the loss impacts on other organisms and ecosystem processes.

Knowledge of the pattern of change and recovery of transitional zone benthic invertebrates is also important in relation to estuary repair (Sheaves et al. 2014, Creighton et al. 2015). For example, blackwater events are a natural part of the ecology of estuaries, and particularly impact transitional wetlands (King et al. 2012, McCarthy et al. 2014). These events occur when floods wash large amounts of organic material from the floodplain into the estuary, creating high concentrations of organic carbon (Kerr et al. 2013). They can be both beneficial and detrimental to estuarine organisms. Blackwater events bring large amounts of carbon into the estuarine system, providing food for aquatic organisms, increasing densities of phytoplankton, zooplankton and invertebrate, which in turn provide food for fish (Thorp et al. 2006). Blackwater events are intensified and extended by human activities such as flow management and wetland bunding and draining (Wong et al. 2010, Hladyz et al. 2011, King et al. 2012), which may exacerbate the downside of blackwater events: as microorganisms consume dissolved carbon they can use up oxygen in the water faster than the oxygen can be replenished, leading to the development of blackwater hypoxia, resulting in the asphyxiation and death of aquatic organisms (e.g., the 2010 blackwater event that devastated invertebrate and fish assemblages in the Murray River, New South Wales, Australia (King et al. 2012)). During blackwater events fish tend to move downstream where conditions are more favourable; however, these unfavourable conditions can often have drastic consequences for invertebrate assemblages because of their lack of mobility, (King et al. 2012). This has far-reaching consequences that go beyond the direct impacts to benthic fauna. When conditions improve, fish migrate back upstream, but if the invertebrate assemblages have not recovered there is no food available to the fish and they move back downstream to find food, thus causing dramatic changes to food webs as well as the functioning of the estuary. A baseline understanding of the dynamics of transitional macro-invertebrate assemblages and their patterns of recovery is a necessary underpinning for understanding anthropogenically enhanced blackwater events and for developing effective management plans.

Perhaps the most important use to which the new understanding of transitional-zone benthic assemblages can be applied is in developing management strategies for the banded transitional wetlands that are common throughout Australia's coastal zone

(Sheaves et al. 2014a, Creighton et al. 2015). Australian coastal and estuarine environments are under increasing pressure from urbanisation with ~85% of Australians living on or near the coast (Australian Bureau of Statistics). Many of the estuaries in this study (e.g. Ross River, Alligator Creek) have transitional wetlands that are isolated from normal estuary processes by bund walls, which separate upstream areas from the rest of the estuary, impeding hydrological and biological connectivity (Bednarek 2001, Sheaves et al. 2014b), reducing wetland productivity (Creighton et al. 2015) and changing the biological processes that would normally operate in these areas. To reduce these losses and return estuaries to a more natural state, there has been a substantial move to rehabilitate many estuaries by removing the bund walls. The new understanding of the dynamics of transitional wetland invertebrate assemblages provides the opportunity to monitor and assess changes, something that has not previously been possible. There are a number of river assessment schemes available that might be adapted for estuarine monitoring. For example, in Australia AUSRIVAS (Australian River Assessment System) is a prediction system used to assess the biological health of rivers (Hawkins et al. 2000, Simpson & Norris 2000). The presence or absence of macro-invertebrates in a stream is compared with regional reference models (based on biophysical characteristics similar to those of the test site) to determine the ecological health of the site in question. However, such systems would need to take into account normal functioning of estuaries: for example, they need to accommodate the effects of antecedent flows as well as the normal tidal dynamics of estuaries.

Estuarine invertebrate assemblages are highly dynamic and closely reflect the physical conditions of the estuary. They experience greater variability than either the upstream fresh waters or the downstream marine systems that they link. Nevertheless, understanding how they operate is clearly possible, as this study demonstrates. While variability within and among estuaries may be the norm, there are consistent patterns that are eminently available for modelling, for determining reference conditions, and for ecosystem health monitoring. Nevertheless, despite the broad scope of this study, including focus on a wide latitudinal range as well as on small-scale dynamics, further regional studies elsewhere in the tropics are required to enable the development of

general models of estuarine ecosystem dynamics. This study provides a suitable framework for a major component of such research.

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