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JAMES COOK UNIVERSITY
AUSTRALIA

Patterns and processes at multiple scales shape fish assemblage structure in tropical estuaries

Thesis submitted by

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Statement of contribution from others

Nature of assistance	Contribution
Intellectual support	**Statistical support**: My supervisor Assoc. Prof. Marcus Sheaves provided advice on appropriate statistical analyses through much of this thesis
	Data interpretation: Lab colleague Ross Johnston helped to interpret the time-series data in Ch. 3 Lab colleague Dr. Ronald Baker aided the interpretation of data in Ch. 4
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Images used in several figures throughout the thesis were sourced from IAN symbol library and Wikimedia Commons.

Abstract

A fundamental goal of ecology is to understand the mechanisms that regulate patterns of abundance, distribution, and richness of species' across landscapes. Achieving this will ultimately help to inform better designed ecological surveys, improve predictive capabilities, and enhance efficacy of management and conservation measures. Although coastal systems provide valuable nurseries for commercially and recreationally important nekton species around the world, conceptual frameworks to facilitate understandings of their faunal patterns are scant. However, it is clear that models of coastal ecosystem function are becoming increasingly sophisticated, progressing away from fine-scale, single-scale focuses to incorporate more of the processes that underpin patterns. In this thesis I use Australian tropical estuaries as model systems to further develop ideas of coastal ecosystem functioning, by demonstrating how a hierarchy of processes interact across a broad spectrum of scales to shape local faunal outcomes in a coastal system.

Some information on broader-scale processes shaping faunal pattern in Australian tropical estuaries already exists. Starting at the broadest scale, biogeographic factors regulate species pools, setting the limits on which species can potentially utilise estuaries in a region. At a finer scale, within a bioregion the supply of recruits into individual estuary systems is systematically modified by the location of coastal spawning grounds relative to estuary mouths, the existing population size of self-recruiting estuary resident species, and connectivity to permanent freshwater recruit sources.

To determine how recruits from the three different sources (coastal marine, within the estuary, and from permanent freshwater reaches) typically distribute at finer scales, within an estuary system, catch data were compared across three different reaches spanning the entire length of the river-estuary axis (lower estuary, transitional wetlands, freshwater reaches). Patterns of distribution were diverse within the assemblage, varying in a species- and life-history-specific manner, and emerging in 7 general 'modes of dispersal' along the estuary axis. Three of these modes describe varying levels of upstream dispersal by marine-spawned species, while an additional group of marine-spawned species were unexpectedly biased towards upstream reaches. The other 3 modes consisted of uniformly distributed estuary-residents, and two groups of freshwater species with varying levels of dispersal into the upper reaches of the estuary. The interfacing of these diverse 'modes of dispersal' means that habitats embedded in different reaches of the estuary will be subjected to very different species pools.

Species pools in estuary reaches are not static however, but shift and morph seasonally in response to physico-chemical shifts and life-history cycles of estuary use. The nature and severity of seasonal shifts in faunal patterns were subsequently examined in the transitional zone of an estuary system, where the lower estuary and freshwater reaches interface. These transitional wetlands are the focus for extreme monsoon-driven physical shifts, and also subject to colonisation from all three recruitment sources. Fish were sampled on a monthly-bimonthly basis over 3 annual cycles, and trajectories of species' abundance and modal size-class revealed a diversity of temporal cycles that could be split into 4 modes based on varying responses to physical shifts and the relevance of transitional wetlands in life-histories of species. This included: (1) classic nursery cycles of post-larval recruitment, growth, and emigration, (2) nursery cycles periodically interrupted by freshwater flows/floods, (3) recruitment delayed until after freshwater floods – presumably as the species initial recruit to ephemeral wetlands associated with floods, and (4) year-round wetland residence and self-recruitment. These diverse and complex patterns suggest that assemblages will vary markedly relative to time of year sampled, as well as occurrence, timing and extent of monsoonal floods.

Following floods, transitional wetlands fragment to a series of tidally connected pools, providing a tractable system to examine finer-scale processes shaping spatial structure of assemblages in a coastal wetland system. Twenty pools were sampled through two annual cycles, to assess the relative influence of local (i.e. environmental constraints) vs. regional drivers (i.e. dispersal processes) on assemblage structure. Faunal patterns suggested that assemblages were primarily structured according to the level of hydrological connectivity with the estuary channel, and secondarily by local environmental conditions in pools. The assemblage can be broken up into two components based on responses to connectivity: an estuary generalist component constrained by connectivity to better connected pools closer to the estuary channel, and a wetland specialist component that seemingly ascended gradients of elevation to access pools further from the channel, perhaps reflecting a drive to access a unique nursery habitat. Additionally, among lower elevation pools, where frequent connections facilitated redistribution, there was some evidence of species sorting relative to preferred conditions (e.g. depth, substrate type). These results illustrate how different patches of seemingly similar habitat may perform different functions for the assemblage due to their position in the landscape.

To evaluate the extent to which spatial patterns in the wetland system may have been influenced by interactions with other faunal groups (prey), during the pre-wet season month

of October in two consecutive years, benthic invertebrate and zooplankton assemblages were sampled in a subset of 13 pools, concurrently with fish surveys. Linkages between distribution of fish and invertebrate prey suggested that the major assemblage split across the wetland may have partially been a response to prey sources as well as a function of pool accessibility. Moreover, prey distributions explained some patterns among the better connected pools, exhibiting patterns consistent with hypotheses of bottom-up control. These results highlight the importance of biological interactions as a key component of the spatial ecology processes structuring fish assemblages in coastal wetlands.

It is clear that local faunal patterns in Australian tropical estuaries are ultimately a function of all of these levels of process working in concert - processes characteristic of broader scales inevitably constrain faunal pattern at finer scales. Thus, in its simplest form this hierarchy of processes can be perceived as a succession of spatio-temporally variable filters imposed at different scales that sequentially refine the assemblage as levels are descended. Placing traditional study sites (or focal patches) within the framework of a broader ecosystem, recognising the interaction of processes across multiple scales in time and space, will therefore allow us to better account for observed patterns, and enhance the efficacy of ecological studies in these systems. The general principle of this hierarchical framework is also applicable to other coastal and estuarine systems in other parts of the world, although the exact nature of processes and their relative influence on faunal outcome will vary from place to place.

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Chapter 1 – General Introduction

Understanding fish utilisation patterns in coastal and estuarine systems: history, progress, and future direction

Estuaries and adjacent inshore coastal wetlands have long been regarded as nurseries for a diversity of nekton, many of high commercial and recreational value. However, detailed understanding of the spatial ecology of fish in these systems has been slow to evolve. By extension, our knowledge of the functional utilisation of coastal and estuarine ecosystems is incomplete, and substantial levels of faunal complexity remain unresolved.

A combination of factors has contributed to this slow progress. Most evidently, the characteristic high turbidities of many estuaries has restricted the use of direct visual observations, which have been the mainstay of studies of pattern and process in freshwater streams (Hankin & Reeves 1988) and coral reef systems (Brock 1982). The resulting reliance on a mix of sampling gears, each suitable for sampling different estuarine environments, has limited direct comparison of catches within and among estuarine systems (Rozas & Minello 1997). Meanwhile, a bias of studies and theoretical development toward certain geographical and climatic zones (Rozas 1995) has limited assessment of generalities and global relevance of findings (Blaber 2002, Faunce & Serafy 2006). However, arguably the most profound impediment to our understanding has been the slow development of conceptual frameworks of ecosystem function in which to develop theories and direct further study.

1.1 Trajectory of conceptual development

Early studies of fish fauna in estuaries were largely descriptive, neglecting ecological drivers of pattern and effectively perceiving estuaries as homogenous entities (McErlean et al. 1973, Hardisty & Huggins 1975, Blaber 1980). Several fish ecologists then began to investigate responses to gradients of salinity and turbidity that characterise the physical environment of estuaries (Blaber & Blaber 1980, Whitfield et al. 1981, Cyrus & Blaber 1987b, 1992, Barletta et al. 2005, Barletta et al. 2008). These studies, largely based on correlations between species occurrences and physical readings, yielded some valuable information on varying physiological tolerances, but were ultimately predicated on over-simplistic concepts. Fish distributions are likely to be complicated by a range of factors at multiple spatial and temporal scales, beyond conditions at the immediate time and vicinity of capture (Pittman & McAlpine 2003).

Moreover, many species adapted to exploit estuaries are likely to possess broad physiological tolerances, enabling persistence in a habitat in spite of broadly variable physical conditions (Elliott et al. 2007).

As the spatial resolution of sampling increased, species affinities for different constituent habitats of the estuary and coastal system emerged, including mangrove forests, salt-marshes, open channel, nearshore coastal waters, seagrass meadows (Blaber et al. 1989, Rozas & Minello 1998, Guidetti 2000, Bloomfield & Gillanders 2005). Subsequent efforts to explain faunal pattern (e.g. abundance, diversity, species richness) within these habitat types were primarily based on correlations with micro-habitat variables measured within the scale of the focal patch (i.e. the studied unit of habitat), such as seagrass blade density and stem length (Bell & Westoby 1986, Attrill et al. 2000), mangrove root complexity (Rönnbäck et al. 1999), epiphyte biomass (Gratwicke & Speight 2005), sediment characteristics, and local geomorphology (Allen et al. 2007). While it is evident that these fine-scale variables exert some influence over fish distribution (Heck & Orth 1980, Orth et al. 1984, Bell & Westoby 1986), much faunal variability often remains unexplained (Harris & Heathwaite 2012), suggesting overlooked processes may significantly influence local assemblage patterns.

1.1.1 Incorporating a spatial element

When we consider the movements that coastal fishes make through daily routines, and through the trajectory of their lives, it is clear that sampling sites that have typically been the focus of ecological studies constitute small elements of a much bigger picture. Most coastal nekton species have a tri-phasic life-cycle (Fig 1.1), characterised by the ingress of eggs and larvae from offshore spawning grounds into inshore coastal waters and estuaries (Elliott et al. 2007, Cowen & Sponaugle 2009, Sheaves et al. 2013). This is followed by a period of growth, where routine shelter and foraging movements maintain a home-range in a certain area (McGrath & Austin 2009, Nagelkerken et al. 2013), the extent and shape of which is shaped by spatial patterns in benthic habitat structure (Pittman & McAlpine 2003, Hitt et al. 2011). During this period species make 'ontogenetic migrations', shifting and/or expanding their home range to incorporate different habitat types as their resource requirements change with growth and development (Cocheret de la Moriniere et al. 2002, Caddy 2008), and finally migrations from adult habitats back to spawning grounds close the cycle (Sheaves et al. 1999). This range of movements across the marine landscape means that local faunal patterns are partially driven by landscape patterns and processes operating at broader scales than previously studied. Based on this premise, a patch of high intrinsic habitat quality may be

depauperate of nekton, while a seemingly low quality site may teem with life as a consequence of surrounding landscape structure (Skilleter et al. 2005). To more reliably explain faunal distributions we therefore need to perceive focal sites as being embedded in a broader landscape. This perspective has long been embraced in the study of terrestrial systems, and forms the basis for the field of spatial ecology, which incorporates spatially-explicit information of landscape structure (i.e. the spatial configuration and composition of habitats across an expanse of interest) into ecological studies (Simberloff & Abele 1976, Forman & Godron 1986).

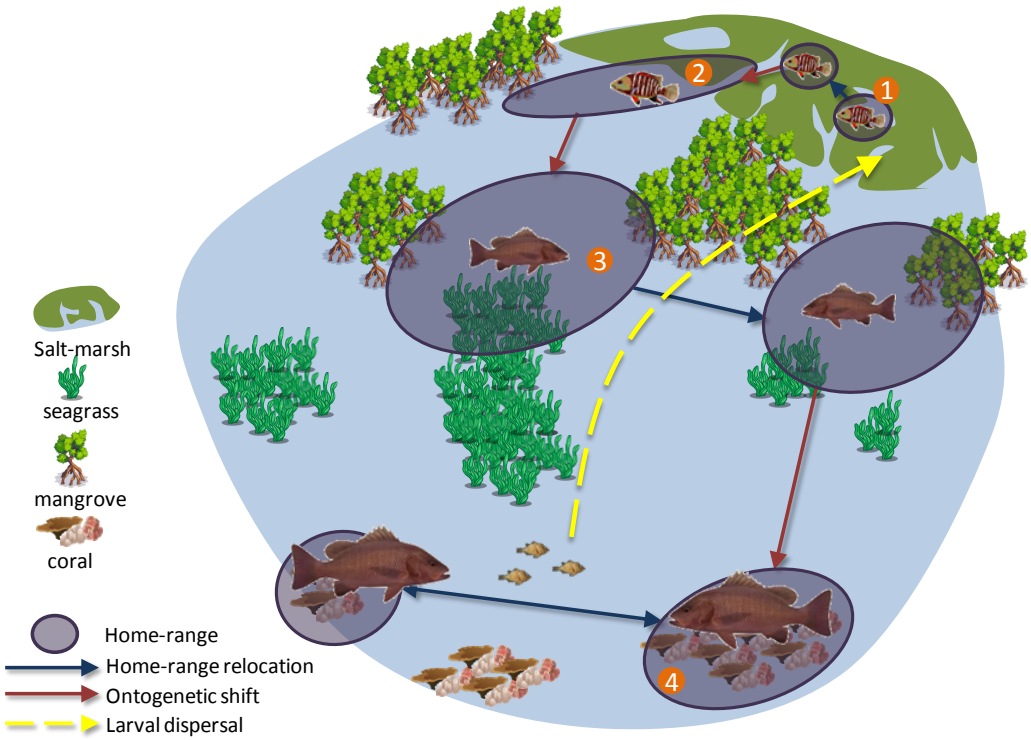

Figure 1.1: Conceptual illustration of the 4 main types of movement influencing distribution across a coastal seascape, using the mangrove jack *Lutjanus argentimaculatus* as an example. Numbers in orange illustrate the stage in a sequence of ontogenetic progressions.

Considering the influence of landscape structure on patterns and processes first means detecting and defining it. There are two main ways of conceptualising and analysing landscape structure, which have been developed in terrestrial systems, and subsequently applied to marine systems: the binary patch-matrix model, and the landscape mosaic model. These two models are each appropriate for tackling different ecological questions at different conceptual scales, although sometimes offer complementary ways of modelling animal-environment relationships (Haila 2002).

Binary landscapes

The most basic form of modelling and analysing spatial heterogeneity in the environment is to view the landscape as a binary system of usable habitat patches embedded in a less hospitable background habitat (called a matrix) (Forman & Godron 1981, Davies et al. 2001, Fahrig 2002). This perspective derives from the field of island biogeography, which recognises how the size of islands and their distance from a mainland stock of colonists affects their species richness and biodiversity (Simberloff & Abele 1976), by influencing colonisation and extinction rates (MacArthur & Wilson 1967). Most habitats, analogous to islands, exist as a fragmented complex of patches embedded in a hostile background matrix (e.g. forest patches in an agricultural setting). These patches harbour spatially separated populations and communities, connected by movements of individuals over a range of time scales (Hanski 1991), emphasising the importance of spatial context of patches as well as the internal characteristics (Forys & Humphrey 1999). In highly fragmented habitats the viability of a regional population is often dependant on dispersal between disparate sub-populations occupying patches (Hanski 1999). Ecologists have examined how spatial features of these 'metapopulations', including the size, number, and spatial arrangement of patches (e.g. relative patch isolation), influence the dispersal of individuals among sub-populations (Gustafson & Gardner 1996, Hein et al. 2004, Fahrig 2007). 'Landscape ecology' approaches have since developed these ideas, to link faunal patterns in terrestrial systems to a more realistic representation of spatial heterogeneity in the landscape. For instance, landscape ecology models have considered how detailed geometric features such as patch shape, isolation, inter-patch distance, clumping of patches, and edge characteristics (Turner 1989, Moilanen & Hanski 1998, McGarigal 2002), shape movement patterns of individuals across the landscape, and result in spatial variations in species abundance and community structure (Diffendorfer et al. 1995, Bender et al. 2003).

Many marine habitats can be viewed as submerged binary landscapes akin to those on land. However, only relatively recently have coastal ecologists started to break beyond a fine-scale, single-scale focus to explicitly incorporate the role of landscape structure into studies of faunal complexity. Such studies have largely been focussed around seagrass meadows, which naturally exist as a binary system of vegetational units embedded in a bare substrate matrix, lending themselves to spatially-explicit interrogation (Robbins & Bell 1994, Turner et al. 1999, Hovel et al. 2002, Bostrom et al. 2006, Jackson et al. 2006b). However, a range of

complications associated with working in open systems have meant that the influence of landscape-level features remain equivocal. A prominent issue in coastal spatial ecology is defining landscape structure at scales relevant to the patterns of species utilisation (Pittman & McAlpine 2003). Without information on movement patterns of individuals, or distribution data across a nested multiplicity of scales (Holland et al. 2004), study areas cannot be reliably scaled to match species' windows of spatial perception (Pittman & McAlpine 2003, Connolly & Hindell 2006, Grober-Dunsmore et al. 2009), which inevitably com promises meaningful ecological inference (Pittman & McAlpine 2003). Further obscuring ecological inference, factors related to sampling artefacts, the dynamic occurrence of fish in patches (Jackson et al. 2006b), and behaviours such as schooling, generate considerable noise in analyses (Connolly & Hindell 2006).

Parallel shifts in perspective, progressing beyond a fine-scale, single-scale focus, have also characterised recent conceptual developments in freshwater ecology. Community structure and dynamics in patches such as lakes, ponds, and stream pools, were traditionally examined in the context of local abiotic and biotic conditions (Leibold et al. 2004). Current models now incorporate movements among these patches by conceiving local communities as part of a broader 'meta-community', where patches are connected by a common regional species pool (Brown & Swan 2010). By simultaneously considering the influence of local processes (i.e. environmental constraints in patches) and regional processes (i.e. organism connectivity among patches), these studies offer new insights into faunal structure of wetland systems. In contrast to many coastal wetlands, fragmented freshwater systems consist of highly discrete patches that are inter-connected through easily defined pathways (e.g. channels), and embedded within an uninhabitable terrestrial matrix. Since fish are restricted to patches and the constrained pathways connecting them, there is high explanatory power in partitioning the relative influence of local and regional processes, providing a fertile ground for developing understandings in spatial ecology (De Meester et al. 2005). Several paradigms have emerged from metacommunity ecology, predicting how communities will be structured by varying levels of 'local' and 'regional' influence under different scenarios (Leibold et al. 2004, Winegardner et al. 2012) (Fig 1.2). For instance, the 'species-sorting' paradigm predicts that if hydrological/structural connectivity is sufficient to allow dispersal across a heterogeneous landscape, species will distribute according to niche processes. However, if dispersal rates are particularly high, regional effects may swamp local effects by enabling persistence of species in sub-optimal patches (i.e. a 'spill-over' effect), as predicted by the 'mass-effect' paradigm (Logue et al. 2011). If fragmented coastal wetlands similarly behave as a binary patch-matrix

system, then principles emerging from metacommunity ecology are equally applicable to coastal habitats, and can be useful in resolving the drivers of pattern.

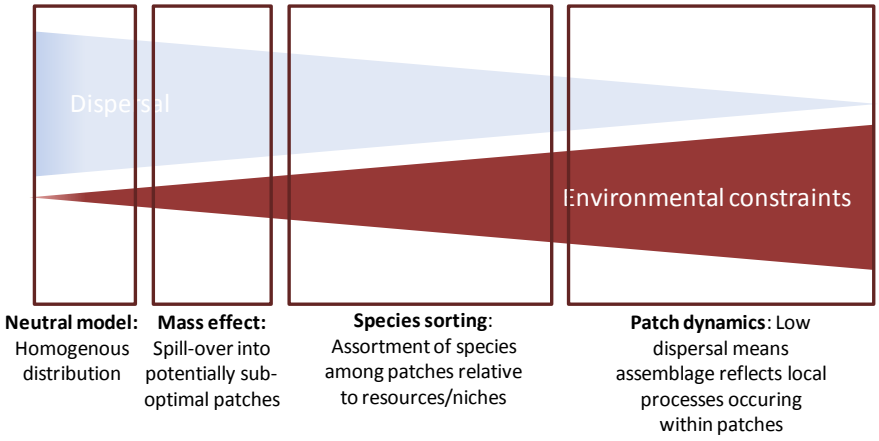

Figure 1.2: Conceptual model showing the predicted metacommunity dynamics given varying levels of dispersal and environmental heterogeneity/influence.

Landscape mosaics

In many scenarios limiting spatial ecology studies to a single habitat type only tells part of the story (Law & Dickman 1998, Pittman & McAlpine 2003), since organisms rely on a multitude of habitat types through routine daily functions (Hansson et al. 1995, Nagelkerken et al. 2013), and as they transition through ontogeny (Cocheret de la Moriniere et al. 2002, Caddy 2008, Snover 2008). Therefore, the composition (i.e. the abundance and richness of different habitat types) and configuration of disparate habitats within a landscape has strong implications for how a system operates for the faunal assemblage, by promoting or inhibiting functional connectivity (Wiens et al. 1993, Guerry & Hunter 2002, Grober-Dunsmore et al. 2009). To incorporate this ecological complexity into models of faunal pattern, landscape ecologists began viewing the landscape as a mosaic of functionally connected habitat components. In this model patches constitute units of multiple potentially interacting habitat types that provide complementary resources for animal assemblages (Dunning et al. 1992, Taylor et al. 1993, Wiens 1995). Recently, the mosaic approach has been applied to marine landscapes or 'seascapes' (Grober-Dunsmore et al. 2009, Bostrom et al. 2011), defined here as a heterogenous marine or intertidal environment, consisting of patches of multiple habitat types (e.g. mangrove, seagrass, sandy substrate, rocky reef). Like terrestrial animals, nekton perceive their environment as a mosaic of complementary resources, moving between different habitat types through routine tidal and diel movements (Kendall et al. 2003, Verweij & Nagelkerken 2007, Hitt et al. 2011), and also through longer-term ontogenetic migrations (Nagelkerken et al. 2001, Cocheret de la Moriniere et al. 2002, Unsworth et al. 2008) (Fig 1.1).

The influence of landscape mosaic patterns on faunal patterns in coastal systems is demonstrated by greater species richness and abundances in both mangroves (Pittman et al. 2004), and salt-marshes (Irlandi & Crawford 1997), adjacent to seagrass beds and vice-versa (Jelbart et al. 2007), than at sites where these habitats are far apart. Such 'seascape connectivity' often explains more site-to-site variability in assemblage structure than local habitat attributes (Skilleter et al. 2005, Olds et al. 2012), and is therefore a crucial consideration when explaining faunal pattern in coastal and estuarine systems.

1.2 Developing conceptual and operational frameworks in coastal systems

It is clear that models of coastal ecosystem functioning are becoming increasingly sophisticated. Ecological research in these systems was originally predicated on intuitive human-based perceptions of habitat, often focussing at scales markedly finer than routine daily movements. With developing knowledge and technical capabilities, these ideas are giving way to more holistic multi-scale approaches that more accurately reflect the manner in which fish use the landscape (Pittman et al. 2007a, Whaley et al. 2007, Green et al. 2012, Olds et al. 2012), recognising that local faunal patterns are the product of patterns and processes operating over a range of scales.

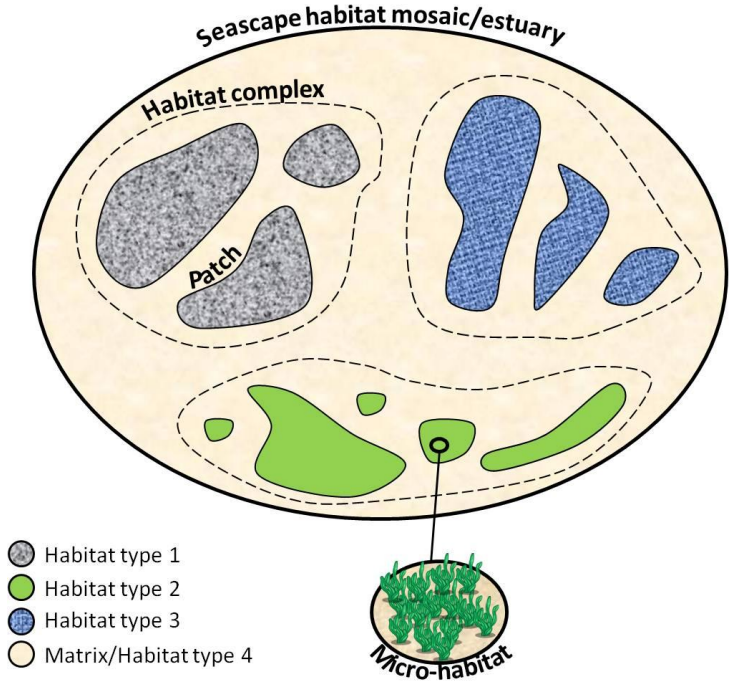

Figure 1.3: Diagram illustrating the nested organisational levels comprising a coastal seascape or estuary system. For simplicity, the patches of habitat have been presented as part of discrete habitat complexes (demarcated by dotted lines). However, patches of habitat types can also be interspersed among each other, such that habitat complexes overlap. In some models the matrix may be considered as an additional potentially important habitat type, although many models simply consider structural connectivities between habitat units embedded within the matrix.

Current seascape approaches factor in three main spatial and conceptual scales of focus: the mosaic of habitat types within a coastal system, the landscape attributes of a single habitat type (i.e. a habitat complex), and the micro-habitat attributes of a patch (Fig 1.3). This framework encompasses and accounts for processes associated with foraging movements, tidal excursions, home-range shifts, and some ontogenetic shifts (Fig 1.4). It is apparent however, that the scope of this framework is still

limited, as movement patterns of many coastal fishes extend beyond the boundaries of this spatio-temporal domain. We therefore need to further expand the realm of scales recognised in conceptual and operational frameworks, both in time and space. Spatial variation in recruitment from spawning grounds, and perhaps effects of broader-scale ontogenetic movements (e.g. cross-shelf migrations), will also engender substantial variability in faunal pattern. Meanwhile, gradients in physico-chemical conditions (i.e. salinity, temperature, and turbidity) of the water mass surrounding habitat mosaics may also constrain the distribution of species' across coastal wetlands and estuaries (Rakocinski & Fleeger 1992, Pittman et al. 2007a). While recruit supply and physico-chemical gradients are not necessarily overlooked, they are difficult to incorporate into seascape models as they typically do not relate to spatially-explicit features of the landscape, and have an apparent nebulous influence on faunal pattern.

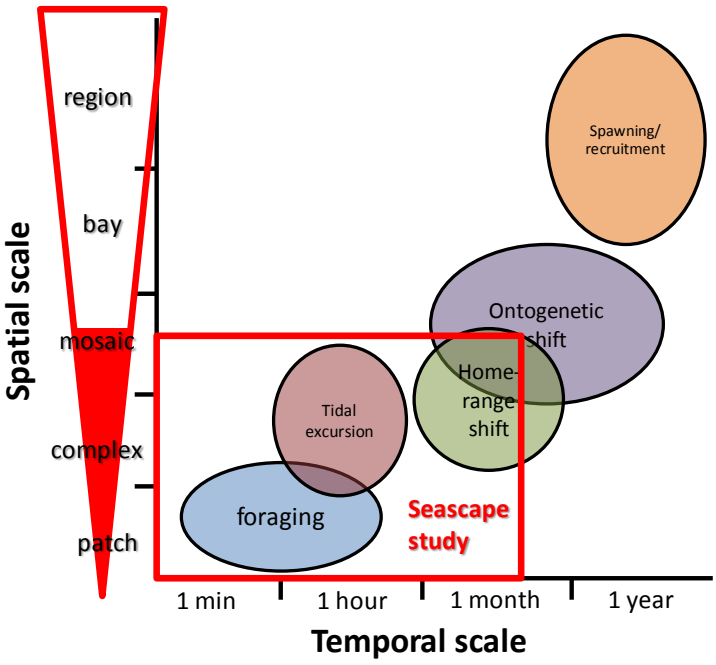

Figure 1.4: Spatio-temporal domains of movement made by a typical marine-spawned coastal or estuarine fish through its life-cycle. The red box represents the spatio-temporal domain accounted for in current seascape frameworks, and the filled section of the red arrow represents the organisational levels at which movements/processes are currently considered.

Due to the high labour demands of repeated sampling, seascape studies also rarely incorporate a temporal dimension (Bostrom et al. 2011). Patterns of recruitment in coastal systems are highly seasonal however (Yáñez-Arancibia et al. 1988, Barletta et al. 2008, Green et al. 2009), and as species pools and conditions change through the year, the influence of landscape features and environmental heterogeneity on assemblage structure are also likely to vary (Hovel & Fonseca 2005, Johnson & Heck 2006). Another notable limitation of seascape studies is the unilateral focus on a single faunal group (i.e. nekton) (Grober-Dunsmore et al. 2009, Bostrom et al. 2011), despite the likelihood that biological interactions with other faunal groups (e.g. benthic infauna, zooplankton, crabs) will play a substantial role in shaping distribution of species (Hovel & Regan 2008). Predator-prey interactions however,

are notoriously difficult to quantify in open coastal waters, as feeding grounds may only represent a small component of daily home-ranges (Sheaves 2009).

1.3 Dealing with scale multiplicity in complex systems

Faunal patterns can only be fully understood by an explicit consideration of phenomena at multiple scales, since different processes prevail and generate characteristic variability in animal assemblages across a range of spatial-temporal domains (Allen & Starr 1982, Levin 1992, MacKey & Lindenmayer 2001). The integration of ecological phenomena across a broad range of scales can be a difficult concept to grasp and implement however, and as we increasingly acknowledge the complexity of coastal ecosystems, we will need to develop models in which to frame and simplify multi-scale functioning.

Hierarchy theory provides a conceptual framework to deal with scale multiplicity in complex systems, and to facilitate a holistic approach to understanding biological patterns. Hierarchy theory recognises that complex systems can be broken down into discrete functional levels based on organisational scales and rates of process characteristic of these scales (Allen & Starr 1982, Urban et al. 1987, Wu & David 2002). Landscapes can be perceived to exist as multiple nested scales of discrete functional components that correspond to levels in the hierarchy (Kotliar & Wiens 1990). For example, forested landscapes can be broken down into a nested hierarchy of gaps (0.01-0.1 ha), forest stands (1s-10s ha), watersheds (100s-1000s ha), and physiographic provinces (10000 ha) (Urban et al. 1987). Meanwhile, in marine systems seagrass has similarly been described and analysed as a hierarchy of nested spatial structures, ranging from shoots at the finest scale (mm's), to clumps (cm's – m's), which aggregate to form patches (1-100 m), and at a greater scale meadows (km's), surrounded by a mosaic of disparate habitat types, such as mangroves and coral (Robbins & Bell 1994, Pittman & McAlpine 2003). In the hierarchy, higher levels typically correspond with broader spatial scales, where processes characteristically operate at slower rates. Meanwhile lower levels correspond with smaller spatial extents and finer scales, where processes characteristically operate relatively rapidly (O'Neill 1986). Due to the disparity in process rate between hierarchical levels, relationships between adjacent levels are asymmetric, with landscape patterns and ecological processes at higher levels appearing as constants and exerting constraints on the biological dynamics of lower levels (Urban et al. 1987). For instance, using the example of forested landscapes, broad-scale physiographic features such as mountain ranges may influence the local climate and dispersal of propagules between watersheds, in turn limiting the plant species capable of colonising and settling in a watershed. Conversely,

lower level dynamics can often provide a mechanistic understanding towards biological dynamics at the next higher level (Urban et al. 1987), e.g. photosynthetic activity at the level of individual trees will manifest in biomass at the level of a stand.

In aquatic systems, hierarchy theory has been interpreted and appropriated in different ways to inform conceptual and analytical models of faunal pattern. For instance, to examine how structural landscape patterns influence faunal pattern of nekton in inshore coastal wetlands, Pittman & McAlipne (2003) integrated a three-level hierarchy proposed by Allen & Starr (Allen & Starr 1982). In this model the intermediate (or focal scale) is anchored in time and space by the scales relevant to the phenomena of interest. For example, to examine distributions through daily routine functions, the focal level would be anchored at the scale of the home-range, which for many species may correlate with a mosaic of habitat patches in the seascape. At the lower level, finer-scale features of the landscape, such as seagrass leaf length, may influence distributions during portions of the home-rage and provide a mechanistic explanation for faunal patterns at the focal level. Meanwhile, at the higher level, broad-scale environmental features surrounding the home-range, such as gradients in wave action and salinity may lead to different faunal patterns over greater spatial extents or over time, but can be perceived as constants at the spatio-temporal domain of the study. Poff (1997) on the other hand advocated a top-down approach to modelling fish distributions in streams, conceptualising the riverine landscape as a nested sequence of filters, whereby environmental constraints acting at different organisational scales (from watersheds to valleys to stream reach to microhabitats) interact with species' functional traits to shape and progressively refine the assemblage as scales are descended. The mechanistic understanding that underpins this approach allows for greater generalisation in applying a predictive framework across different systems and regions (Levin 1992).

1.4 Australian tropical estuaries as a model system for developing frameworks

Tropical Australian estuaries provide an ideal model system in which to partition the influence of different levels of process spanning a broad spectrum of scales. They also present an opportunity to examine types of processes not typically considered in coastal seascape studies. Each estuary system naturally exists as a relatively discrete, semi-enclosed unit, as opposed to the diffuse, open nature of coastal seascape systems. Since recruits to estuaries primarily originate from external sources offshore (Sheaves et al. 2013), with little subsequent redistribution among estuaries, variable recruit supply can be indirectly assessed through estuary-to-estuary differences in assemblage composition (Sheaves et al. in review). Further,

the discrete bounds to individual estuary systems mean that the influence of broad-scale gradients in physical condition (e.g. salinity, turbidity, temperature) of the water mass can be more reliably separated from external influences (such as spatial patterning in larval supply and connectivity to adjacent un-sampled seascapes). In tropical estuaries these physical gradients are periodically accentuated, owing to episodic freshwater inflows, further facilitating assessment of physico-chemical influences on faunal distributions.

The effects of freshwater flows are most pronounced in transitional wetlands, where the upstream reaches of the estuary interface with freshwater reaches. The highly episodic nature of river flows in tropical Australia means conditions in transitional wetlands can shift from fully marine to fully freshwater in a matter of hours, before undergoing a gradual return to more marine salinities through the dry season. This provides a unique opportunity to examine the influence of extreme disturbances on faunal pattern, both spatially and temporally.

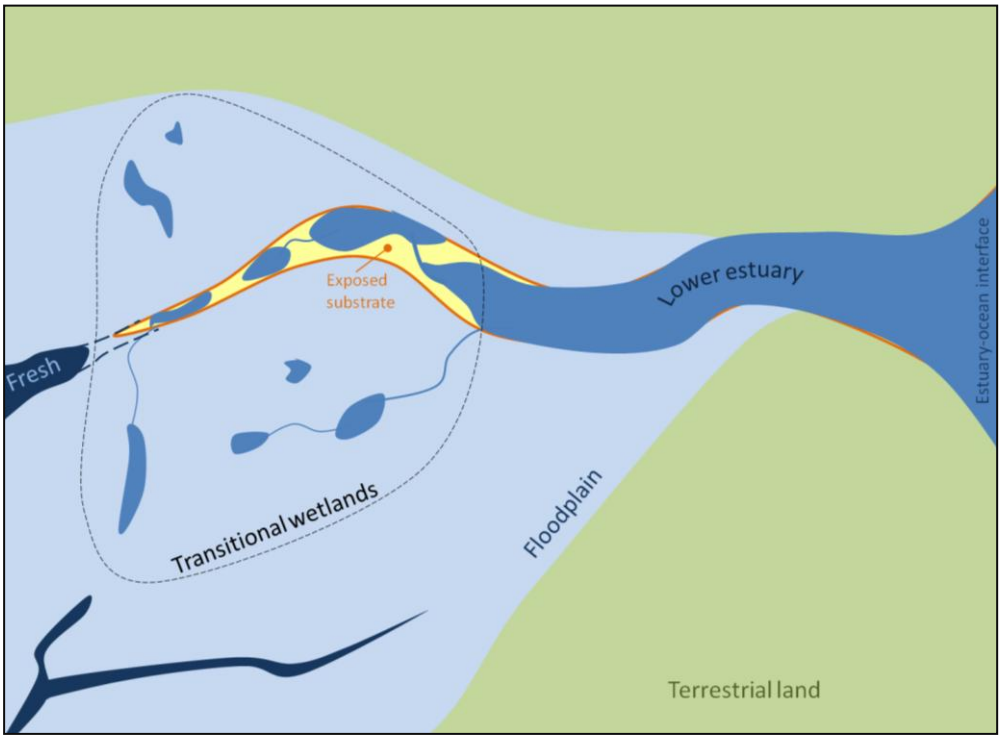

Figure 1.5: Diagram to illustrate the position of transitional wetlands within the sub/dry-tropical estuarine landscape. Transitional wetlands can be defined as portions of the estuary, upstream of continuous sub-tidal reaches (i.e. the lower estuary), that often fragment into a series of tidally-connected pools (generally during dry the season), and periodically connect to freshwater reaches during freshwater flows and floods (generally during the wet season). They can exist either longitudinally upstream of the lower estuary, or on adjacent floodplains.

Following seasonal floods, the upstream reaches of dry-tropical and sub-tropical Australian estuaries exist as a fragmented series of tidally-connected pools, both longitudinally upstream of subtidal channels and laterally across floodplains, (Fig 1.5), owing to the combined effect of shallow channels, low coastal reliefs and low average rainfalls (Sheaves & Johnston 2008). This provides a binary wetland system akin to the freshwater systems where metacommunity concepts have been developed. Tidal pools in transitional wetlands represent discrete patches embedded in a terrestrial or intertidal matrix (e.g. saltmarsh, saltpan, or pasture), that intermittently connect to each other and the subtidal estuary channel through constrained corridors (i.e. defined channels). These features are conducive to the examination of finer-scale spatial ecology processes that are more difficult to isolate in more open submerged habitat complexes (De Meester et al. 2005), with a high explanatory power in discerning between local and regional influences.

The objective of this thesis is to explore the range of drivers shaping fish assemblage structure across a hierarchy of spatial and temporal scales in Australian tropical estuaries. While some key processes influencing faunal pattern in these systems have been demonstrated in isolation, they have not been built into a holistic framework of interacting processes (Bostrom et al. 2006) that this study will endeavour to achieve. To accomplish this objective, a number of specific aims will be addressed (Fig 1.6):

(1) to determine how the fish assemblage is structured along the length of an Australian tropical river-estuary profile, and to assess the underlying processes regulating the patterns *(Chapter 2*).

(2) to monitor temporal changes in the assemblage of a transitional wetland through an annual cycle, and examine species' responses to extreme physical shifts imposed by episodic freshwater floods *(Chapter 3).*

(3) to investigate the finer-scale processes driving fish distributions across a coastal wetland habitat complex, by assessing the relative influence of local patch conditions vs. regional dispersal processes in structuring assemblages *(Chapter 4)*

(4) to assess the role of biological interactions (prey dynamics) in shaping fish distribution across a coastal wetland landscape *(Chapter 5)*

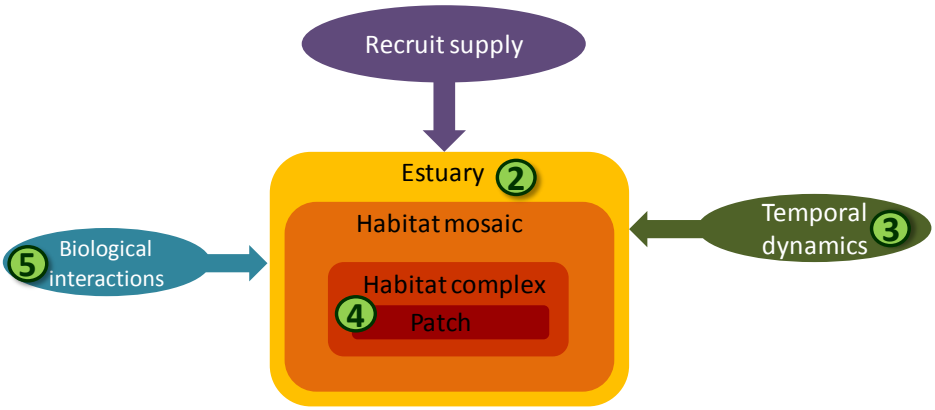

Figure 1.6: Thesis framework, showing the nested hierarchy of organisational scales that make up estuary landscape, and for which species-environment relationships are likely to influence assemblage structure. The bubbles around the 'nest' indicate additional levels of pattern and process that will further influence assemblage structure within estuaries, and which need to be investigated. Numbers in green circles signify where a level of process has been addressed in a data chapter.

When developing conceptual understandings based on empirical data it is important to properly demonstrate patterns before formulating explanatory theories or models about processes (Levin 1992, Underwood et al. 2000). Patterns in complex ecological systems are realistically driven by a 'causal thicket' of processes, including an unknown degree of stochasticity (Harris & Heathwaite 2012). Consequently, throughout this thesis, rather than simply analysing correlations between explanatory and response variables (which may lead to misinterpretation), key systematic processes were attributed to repeatable biological trends.

Chapter 2 *This chapter is being prepared for journal submission*

Varying patterns of fish distribution along Australian tropical estuaries

2.1 ABSTRACT

To reliably interpret fish-landscape relationships across coastal systems we must first understand how distributions are constrained by broader-scale influences that may lead to markedly different faunal characteristics in otherwise similar seascape settings. In this study I assessed broad-scale patterns of fish distribution along Australian tropical estuaries, by comparing assemblages and relative species abundances across three contiguous reaches spanning the length of the river-estuary profile, including the lower estuary, permanent freshwater reaches, and transitional wetlands wedged in-between these two reaches. By interpreting these data in the context of species life-histories, I was able to identify 7 'modes of dispersal', based on varying extents of estuary penetration from three different recruit sources (marine, estuary, and freshwater spawning grounds). The complex interfacing of these different dispersal modes means that habitat configurations in different parts of the estuary will be subjected to a range of species mixes, which may morph and shift both seasonally and inter-annually through direct and indirect responses to variable river flows. This broad-scale complexity needs to be built into models of ecosystem functioning along with information on spatio-temporal programs of nursery utilisation.

2.2 INTRODUCTION

Ecologists studying fish assemblage structure in coastal systems are moving away from a habitat-centric approach, and embracing broader-scale landscape concepts to help resolve complex faunal patterns. Many studies in coastal systems (commonly referred to as 'seascape' studies) now recognise how processes associated with landscape structure at 3 primary scales interact to drive assemblage patterns (Ch. 1): (from broadest to finest) seascape mosaic structure, habitat complex structure, and local patch structure. Despite this, considerable variability remains unexplained (Kendall et al. 2003), suggesting that a more holistic understanding of biological complexity requires the incorporation of additional levels of process.

Patterns and processes at spatial scales greater than habitat mosaics, including the effects of gradients in environmental conditions (e.g. salinity, turbidity, temperature, wave

exposure) across bays, inlets, and estuaries, and the supply of recruits from spawning grounds beyond the boundaries of coastal nurseries, inevitably cascade down to constrain the assemblage available to utilise finer-scale landscape structures. An understanding of how these processes influence faunal pattern is therefore necessary to fully account for differences between habitat mosaics occupying different positions in space. However, disentangling the effects of these broader-scale processes from one another, and from finer-scale processes has typically been challenging in open and diffuse coastal seascapes. As these seemingly nebulous influences are difficult to control for in coastal seascape studies they often manifest as unexplained variability (Hovel et al. 2002, Jackson et al. 2006). In estuaries however, influences of environmental condition and recruit supply are easier to separate due to the existence of each estuary system as a discrete unit in space. Recruits primarily move into estuaries from external sources (adjacent coastal waters) through a single point (the estuary mouth), and are subsequently subjected to environmental gradients once within estuaries.

In Australia's tropics, extensive surveys have revealed systematic estuary-to-estuary differences in assemblage composition (Sheaves & Johnston 2009), due to estuary-specific contributions of species from 3 recruitment sources: marine-spawned recruits, estuary residents, and freshwater migrants. Differences are primarily driven by spatial variation in the supply of marine-spawned larvae into estuaries (Sheaves et al. 2013, Sheaves in review). Young-of-year juveniles of these marine-spawned recruits numerically dominate estuary assemblages, moving to adjacent coastal waters as they mature (Deegan et al. 2002). Estuary-to-estuary differences are further exaggerated by contributions from an estuary resident component, the numbers of which are regulated by historical population dynamics within each specific estuary system (Sheaves in review). Additional estuary-specific differences are engendered by recruitment from permanent freshwater reaches into the upstream reaches of estuaries during seasonal freshwater flows (Davis et al. 2012). This broad-scale understanding of assemblage structuring provides a basis for exploring how recruits from these different sources are structured at finer scales, within estuary systems.

Faunal assemblages within estuaries are broadly structured along a longitudinal profile (also referred to as longitudinal axis or gradient) (Whitfield et al. 2012). Distribution patterns at this level are generally ascribed to varying responses to immediate physico-chemical conditions (Cyrus & Blaber 1992, Barletta et al. 2005, Whitfield et al. 2012). However, such inferences are often over-simplistic, failing to consider historical effects of physical regimes on fish distribution patterns (Sheaves 1998), food-web effects mediated by physical regimes

(Whitfield 1986), and alternative factors correlated with position along an estuary profile. In reality distribution patterns likely reflect interactions between multiple processes, including: (1) distance and connectivity to recruit sources (Bell et al. 1988, Faunce 2008)(2), response to gradients in physico-chemical condition (Thiel et al. 1995) (3) response to habitat types only occurring along certain parts of the river-estuary axis (Blaber et al. 1989, Adams & Blewett 2004), (4) life-history schedules/strategies (i.e. innate propensities to utilise certain estuary reaches independent of immediate conditions) (Moore 1982), and presumably (5) a response to gradients in prey availability. However, the relative influence of these different processes is difficult to separate, as some of these factors are spatially confounded and may interact in complex ways to shape patterns.

The aim of the present study was to resolve systematic spatial patterns of distribution along tropical Australian estuaries, and assess the likely drivers of these patterns. To achieve this, a spatially-resolved overview of species' distributions along a river-estuary profile was required. Fish assemblages in downstream reaches and permanent freshwater reaches are relatively well defined in tropical Australian coastal systems, providing an existing source of some of this information. However, the nature of the assemblage utilising wetlands in the transitional zone, between the lower estuary and permanent freshwater reaches, remains poorly understood. By resolving this intermediate 'transitional wetland' assemblage, species stratification across 3 different reaches (see Fig 1.5) of the river-estuary profile could be analysed. Outcomes of this analysis provide an overview of how assemblages are spatially organised at the estuary level, and how availability of fauna to utilise finer-scale landscape structure is constrained.

2.3 METHODS

Initially, the assemblage of a transitional wetland (Annandale Wetland) in a single tropical estuary (Ross River) was resolved in detail through multiple field surveys, and then substantiated with one-off samples from transitional wetland sites in other estuary systems (Fig 2.1). Transitional wetlands in this study are defined as portions of estuary above continuous subtidal reaches, which often fragment into a series of tidally connected pools, and periodically connect to freshwater reaches upstream during freshwater flows and floods. The 'transitional wetland assemblage' was compared to the assemblages of the lower estuary and permanent freshwater reaches, which were estimated from existing data.

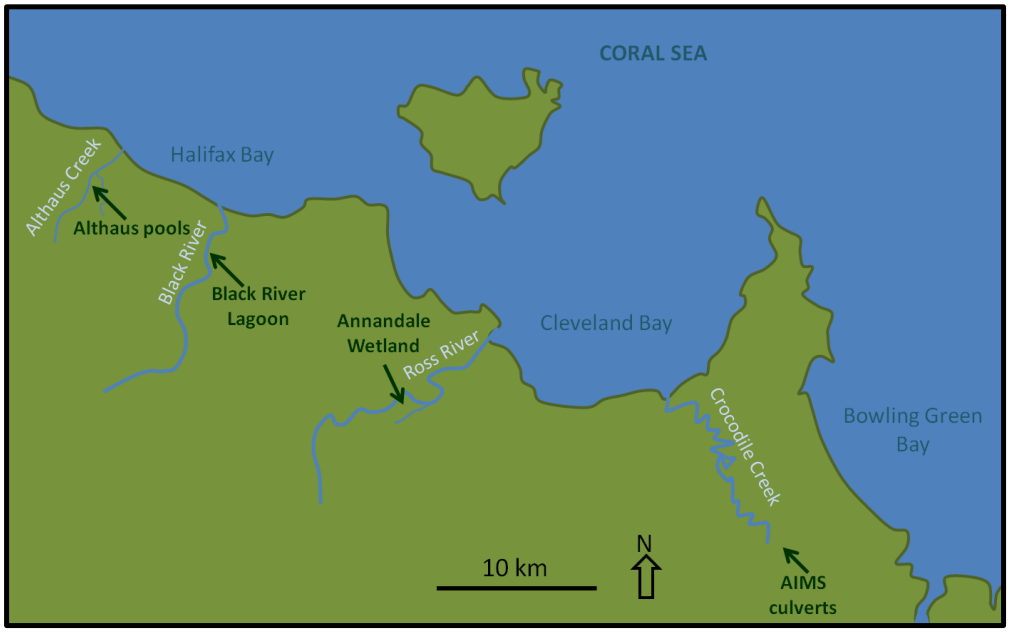

Figure 2.1: Geographic location of the transitional wetland sites

2.3.1 Data collection

Transitional wetland surveys

Annandale Wetland

The main study site was Annandale Wetland (19.19°S; 146.44°E)(Fig 2.2; see Appendix A for pictures), a 0.4 km^2 *Sporobolous virginicus* salt-marsh system situated on the Ross River floodplain, 8 km's upstream of the river mouth. Interspersed across the wetland are 20 discrete permanent pools, ranging in area from 80 m^2–2500 m^2, with maximum low-tide depths from 30 cm–130 cm. The pools generally lack aquatic vegetation or woody debris. They encompass a range of substrates, varying from fine mud to coarse rubble, and are variously skirted by narrow fringes of *Aegicerus corniculatum* mangrove from 1-5 shrubs thick, bordering 0-100% of pool perimeters. Pools connect to the Ross River tidally to varying extents, some connecting daily during most tidal cycles, while others may only connect during spring tides (i.e. only a few days/month). During wet season months (~January-March) the wetland also connects to freshwater sources when Aplins Weir (located ~0.9 km upstream of Annandale Wetland) overflows, blanketing the wetland in a sheet of freshwater. Salinity through the study period varied from 0 ‰ during floods to 34 ‰ during dry seasons.

All 20 pools in Annandale Wetland were sampled on a monthy-bimonthly basis over 3 annual cycles, between March 2010 and April 2012, with a hiatus during wet season months (January-February/March) when flooding prevented sampling. All samples were collected over the bottom quarter of the tidal cycle (i.e. around low tide) during the new moon phase to

ensure consistent tidal regimes throughout the study. Sampling was conducted using a beach seine net (12 m long, 2 m deep, 6 mm mesh) with an effective sampling width of 8 m. For each sample, the net was dragged for approximately 15 m, with one person operating each end, before being hauled onto the bank. Some pools could be comprehensively sampled in a single seine haul. However, in larger pools where one net haul covered <~75% of pool area, a single haul was less likely to provide an accurate representation of fish fauna. In such pools up to 3 hauls were taken to cover all within-pool micro-habitats which potentially harbour different taxa. Species were identified to the lowest possible taxonomic level and enumerated before being returned to the water alive, with the exception of the noxious pest species *Oreochromis mossambicus* which was euthanized on site in accordance with government regulation. To control for possible recaptures of the same individuals in pools requiring multiple hauls on a single sampling occasion, for each taxon only the maximum count across the 2-3 hauls was taken.

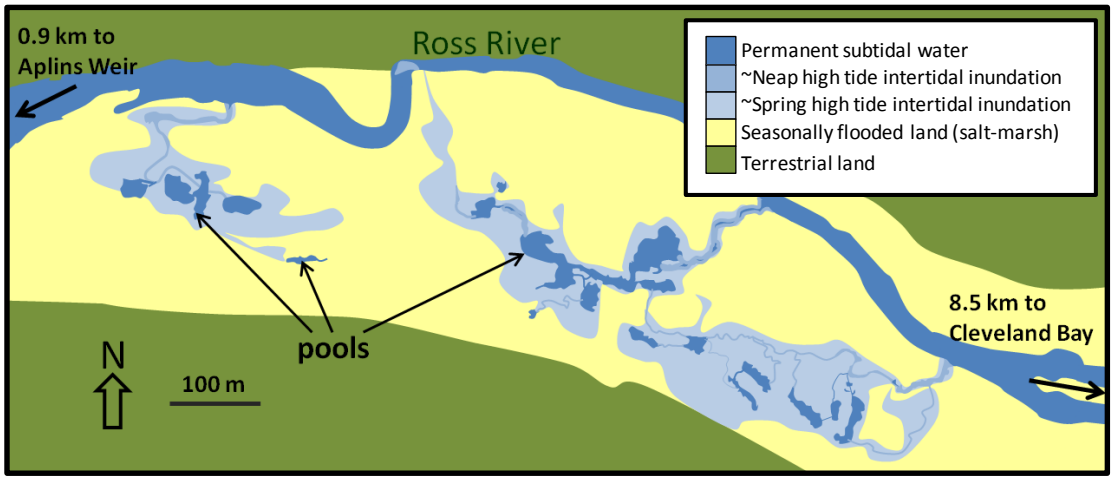

Figure 2.2: Site map of Annandale Wetland showing the 20 pools.

Seine netting was considered the most appropriate method of sampling fish and assemblages, as it was a time effective means of sampling entire areas of pools, with wide taxonomic and size representation. Cast netting was also considered, as multiple small samples are often considered to more reliably represent fish assemblages than fewer large samples (Johnston & Sheaves 2007). However, cast nets often under-represent larger, rarer species (Sheaves, 2010), and samples would have been limited to areas near the bank, as wading through the water to sample the centre of pools would have spooked fish.

Some issues associated with seine-netting were confronted through the study however, and an appraisal of these may be of value when designing future studies in similar systems. Fish species differed in their ability evade the net. Certain species, including *Lates*

calcarifer and *Lutjanus argentimaculatus* are highly agile, and capable of rapidly swimming away from, and around the path of the net. Meanwhile, *Megalops cyprinoids* and mugilid spp. are capable of leaping out of the net to avoid enclosure. The shape of the pools relative to the trajectory of haul is likely to have had an influence on the proportion of agile species represented in samples.

In some pools, a thick, mobile layer of silt sometimes collected in the back of the net, slowing down the haul, and likely compromising netting efficiency. Furthermore, some pools were fully skirted by mangroves, with narrow openings in which to haul the net onto land, and often up steep banks. To avoid losing fish in these hauls, the lead-line was pulled in part-way prior to landing, to purse the catch securely in the back of the net. Finally, the intensive labour requirements of hauling ~30 nets per day was physically exhausting, and necessitates the help of a capable volunteer to help drag the net.

Additional transitional wetlands

Three other transitional wetland sites were sampled (Fig 2.1; Fig 2.3) once during dry season months (June-August), also at low tide during new moon periods. These sites encompassed multiple wetland sub-types, including: in-channel pools (Althaus Creek; Fig 2.3a), an in-channel lagoon (Black River Lagoon; Fig 2.3b), and salt-pan pools (AIMS culverts; Fig 2.3c). Sampling of these wetlands was conducted from the bank using a cast net (20 mm mesh size) as the potential presence of crocodiles ruled out option of hauling seine nets. In each wetland a minimum of 35 casts were taken, stratifying for area to represent all parts of each wetland. Details of these wetland sites are provided below.

Althaus Creek (Fig 2.3a) consists of two linear series of pools occupying different branches of the upper tidal reaches of a small estuary channel. Pools range in area from ~150 m^2 – 2000 m^2, and maximum low tide depth from 30 cm -100 cm. Most pools connect to the downstream estuary during neap high tides, while those farther upstream only connect during spring high tides. During wet season flows, the pools are transformed into continuous freshwater streams. At the time of sampling Althaus Creek pools were disconnected at low tide, and varied in salinity from 15-25 ppt.

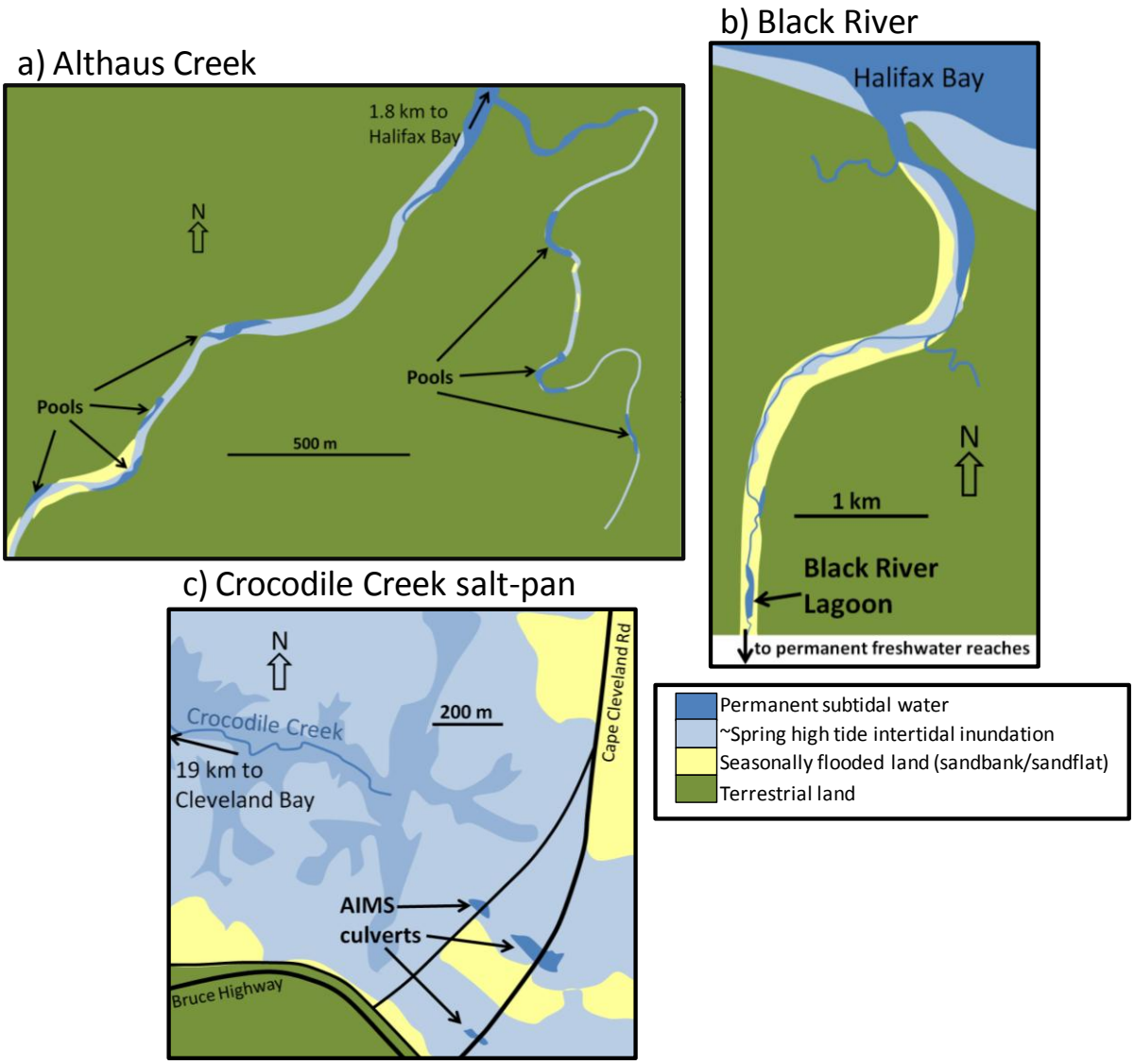

Figure 2.3: Site maps of transitional wetlands showing configurations of the sampled pools relative to permanent subtidal channels, and the approximate extent of tidal connections (based on satellite imaging). During a typical freshwater flood event all areas of the maps, apart from green areas, are completely inundated.

Black River Lagoon (Fig 2.3b) is a ~17,000 m^2, 150 cm deep, in-channel body of water 2.8 km upstream of the permanent subtidal channel of Black River. The lagoon is connected to subtidal reaches on the highest spring tides via a narrow channel that runs through an

extensive sandbar, and limits tidal connection to depths <15 cm. Like Althaus Creek, Black River transforms into a continuous stream during wet season months, becoming a conduit for freshwater flows. Trickle flows sometime persist through the dry season, maintaining some freshwater connection to Black River Lagoon. Salinity at the time of sampling was 5 ppt, with a residual trickle flow.

AIMS culverts (Fig 2.3c) comprise 3 pairs of pools either side of a road intersecting a salt-pan. Individual pools range in area from ~50 m^2 – 600 m^2, and in maximum low tide depth from 30-80 cm. The pools are connected to Crocodile Creek on spring tides which flood a vast area of saltpan surrounding the pools. This salt-pan is also flooded by freshwater during the wet season as strong flows from adjacent streams spill over the flats. However, at the time of sampling the pools were isolated and salinities ranged from 29-90 ppt.

Collating lower estuary and permanent freshwater assemblage data

Lower estuary and freshwater assemblage data were collated from the best available datasets in the published literature featuring species count data. Lower estuary assemblage data could be extracted from a single extensive study, featuring cast net data from the lower portions of eight estuaries in North Queensland over 15 months, representing all seasons (Sheaves et al. 2010). These estuaries spanned a 225 km stretch of coastline encompassing all of the transitional wetland sites sampled in the present study. Freshwater assemblage data were collated from five studies, as a single spatially extensive survey from the North Queensland region did not exist. These five studies sampled a total of 7 freshwater river/stream systems, distributed across the same 225 km stretch of coastline. This included the permanent freshwater section of the Ross River, directly upstream of Annandale Wetland. Surveys of freshwater assemblages varied in sampling design, but employed gears and mesh sizes which targeted a similar component of the fish assemblage (Table 2.1).

Table 2.1: Sources of data used to estimate assemblages of species in lower estuarine reaches and permanent freshwater streams of the bioregion.

	Study	Sampling sites	Gear	Sampling duration/no. of sampling occasions	Sampling effort (no. of samples/estimated area sampled per occasion)
Lower estuary	(Sheaves et al. 2010)	8 small estuary channels	Cast net (3 mm mesh)	~2 years/5 occasions	~200 nets/950 m^2
Freshwater	(Pusey et al. 1998)	Extensive sampling of a large river catchment	Electro-fisher Seine net (10 mm mesh)	~3 years/5 occasions	12 samples/~300 m total stream length
	(Perna & Pearson 2008)	2 small streams	Visual surey	~2 years/8 occasions	6 snorkels/~300 m total stream length
	(Beumer 1980)	Extensive sampling of Black River freshwater catchment	Electro-fisher Large seine net (13 mm mesh)	~2.5 years/24 occasions	5 samples/~150 m total stream length
	(Johnston & Sheaves 2006)	Ross River (Aplin's Weir, Black's Weir)	Cast net (10 mm mesh)	<1 year.4 occasions	~250 nets/~1125 m^2

2.3.2 Data analysis

Assemblage composition

Initially, species lists were compared among the three reaches (pooled over sites) to assess the degree of overlap or discreteness in species occurrences.

Differences in assemblage composition across the three reaches were analysed with a multivariate classification and regression tree (mCART, Bray-Curtis dissimilarities) (De'ath 2002) based on rank abundances (emphasising relative abundances of species among reaches). Basing composition on rank abundances rather than absolute numbers down-weights the influence of extreme values resulting from gear selectivity, and at least partly compensates for intrinsic differences in the way different sampling techniques emphasise the occurrence of different species. For each site (lower estuary, n=8; transitional wetland, n=4; freshwater, n=5) the 20 highest ranking species (ranked in descending order) were used to represent assemblage composition. Rather than coding different sites by reach type (i.e. lower estuary, transitional wetland, freshwater), assemblage compositions coded by site were fed into the mCART, and the grouping of sites at each split subsequently examined. This enabled a more objective assessment of the level of difference/similarity in assemblage composition among the three reaches.

Details of assemblage compositions were then compared by producing a composite histogram of species' rank abundance by reach. Lower estuary and freshwater compositions were represented by averaging rank abundances of species across sites, and presenting only

the 20 highest ranked species from these average ranks. The transitional wetland assemblage was represented by displaying rank abundances of the 20 highest ranked species in Annandale Wetland, and overlaying the 20 highest ranked species averaged across the three supplementary sites. Data from Annandale Wetland and the three supplementary wetlands were not pooled, since catches from the supplementary sites only represent the assemblage in a single season. Instead data from these supplementary sites were complementary in providing a broader overview of the transitional wetland assemblage.

Distribution patterns

From the composite histogram, distribution patterns along the river-estuary profile could be interpreted by comparing relative abundance of species across reaches. Since this histogram was largely based on a broad meta-analysis of available data, fine-scale quantitative comparisons of relative abundance among reaches could not be reliably interpreted. Caution was exercised when interpreting differences in relative abundance among reaches, focussing conservatively on clear patterns. For example, if a species was dominant in the lower estuary (among the 20 highest ranking species) but was absent in other reaches, this would be interpreted as a downstream-restricted species. However, if this species was recorded as present in transitional wetlands, but not as one of the dominant species, this would be interpreted as a downstream-bias. By framing these distribution patterns in the context of known spawning locations (Table 2.2), and thus point of entry into the estuary, distribution patterns could be interpreted as 'modes of dispersal'.

2.3 RESULTS

2.3.1 Assemblage composition

In total, 180 species were recorded across the three reaches (Fig 2.4). The majority of these species (123) were found in the lower estuary, another 44 species were found in permanent freshwater reaches, while an additional 13 species were found in both lower estuary and freshwater reaches (amphidromous species). No species were exclusive to transitional wetlands. Instead, the transitional wetland assemblage was composed of a mixture of species from the lower estuary (52) and freshwater (12) reaches, together with the 13 amphidromous species.

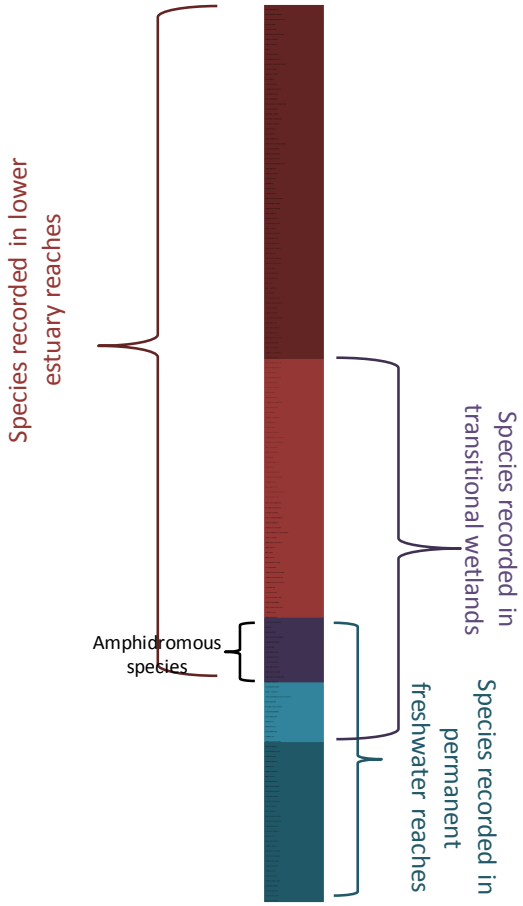

Figure 2.4: Overlap of species recorded in each of the three reaches. Different colour bars are scaled to represent the number of species recorded in each of the reaches, as a proportion of the total species richness of the study.

The mCART of assemblage composition indicated that different reaches had distinctly different assemblage compositions (Fig 2.5). All lower estuary sites were grouped together on the same branch of the primary tree split (n=8), suggesting that lower estuary composition was markedly different from the freshwater composition, and to a large extent the transitional wetland composition. However, one supplementary transitional wetland site (Althaus Creek) was grouped on the same side of the split as lower estuary sites, indicative of an assemblage composition that was more characteristic of the lower estuary than other transitional wetland sites. The secondary tree split clearly separated transitional wetland sites (n=3) from freshwater sites (n=5), indicating that these two reaches also have distinctly different assemblage compositions.

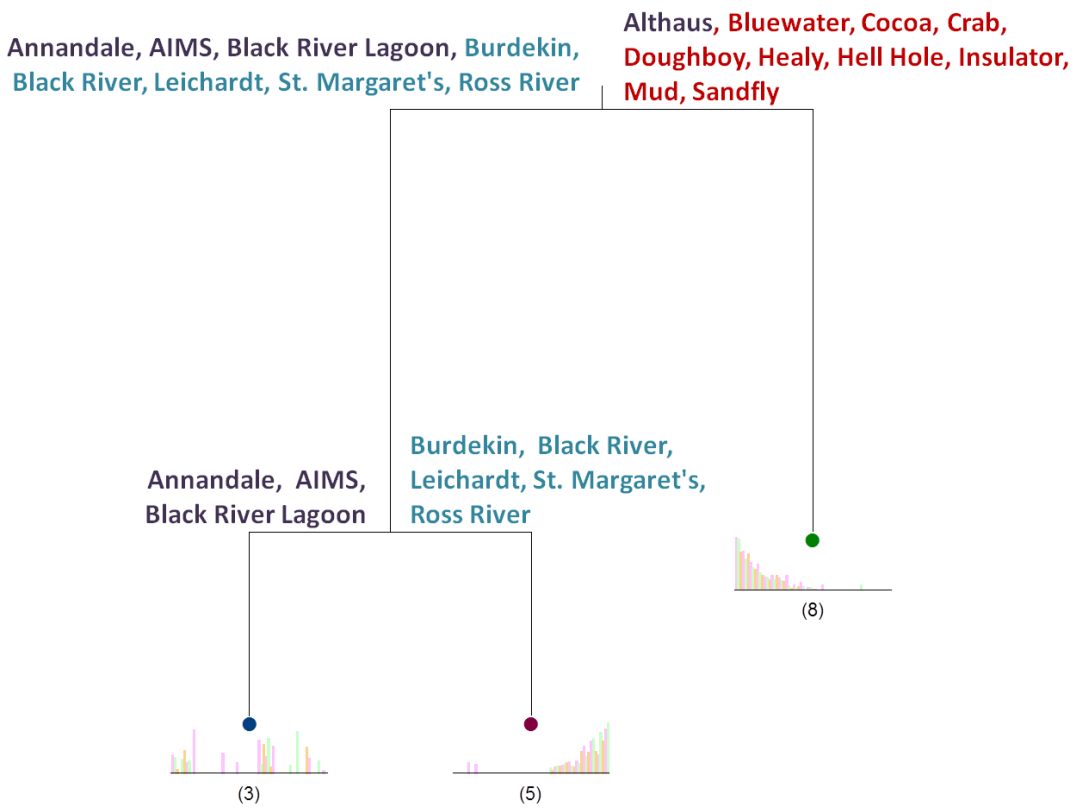

Figure 2.5: mCART of assemblage composition (based on Bray-Curtis dissimilarities) across the all lower estuary (red), transitional wetland (purple), and freshwater (blue) sites. Sites partitioned at each side of assemblage splits are displayed above each branch. Histograms at each terminal node represent average rank abundances of species across all sites grouped at the corresponding branch, illustrating differences in assemblage composition among site groupings. Details of assemblage differences are not displayed in this figure, but details of assemblage composition by reach are displayed in Fig 2.6.

Histograms of relative abundance revealed that lower estuary and freshwater assemblage compositions were largely distinct (Fig 2.5), with only *Gerres filamentosus* and *Pseudomugil signifer* occurring in high relative abundance (among 20 highest ranked species) in both reaches. Although transitional wetlands were largely composed of sub-sets of species which also dominated the lower estuary and freshwater reaches, the assemblage also comprised an additional suite of species that were not abundant in these surrounding reaches.

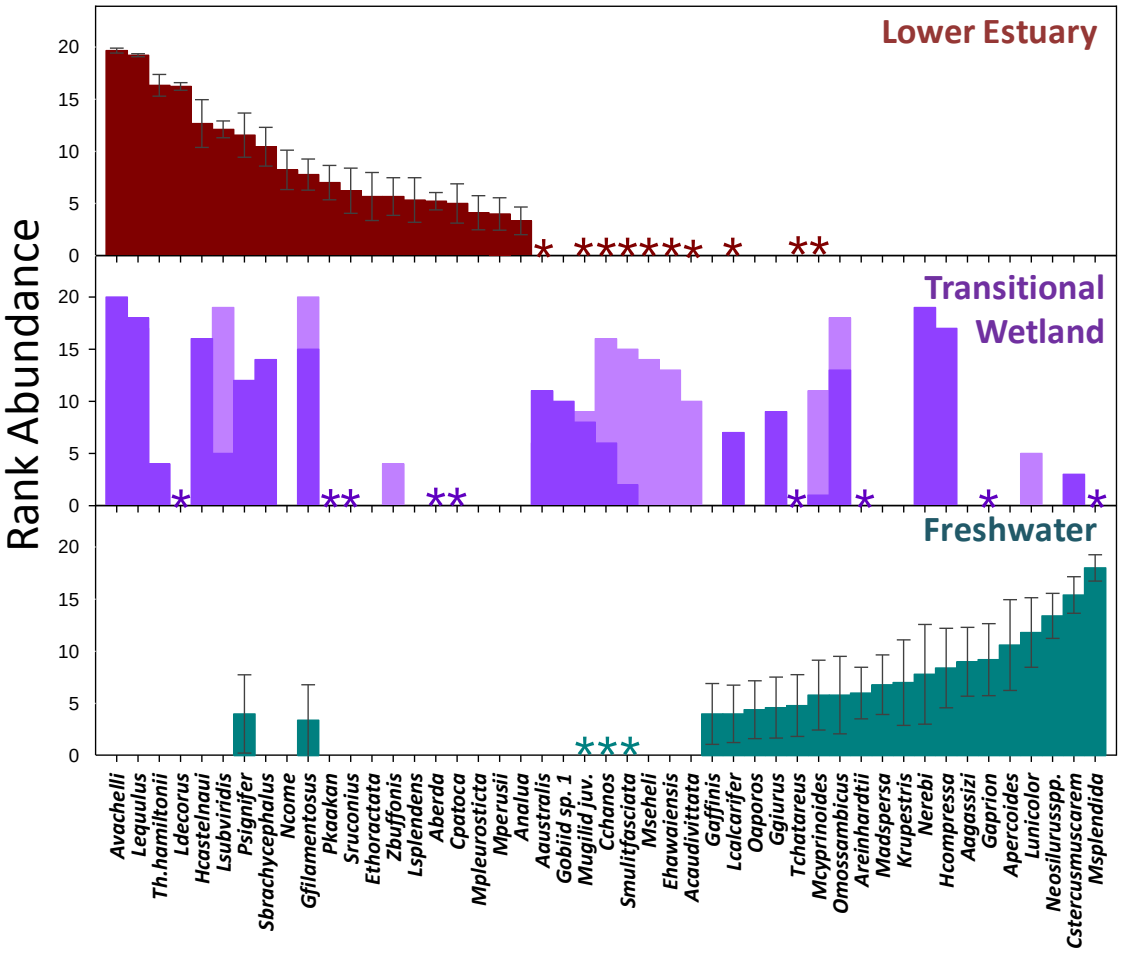

Figure 2.6: Composite histogram of rank abundances (20=most abundant) of dominant species in each reach (±1 S.E. for lower estuary and freshwater rank abundances, which have been averaged over sites). Dark purple bars represent rank abundances in Annandale Wetland, and light purple bars represent rank abundances averaged across the three supplementary transitional wetlands. Asterisks signify species which were present, but not among the dominant species.

2.3.2 Distribution patterns

Histograms of relative abundance across reaches (Fig 2.6) coupled with existing knowledge of recruit sources (i.e. spawning location) (Table 2.2), provided the basis to identify 7 different modes of dispersal along a river-estuary gradient (Fig 2.7):

Marine-spawned

1. *Downstream restricted*

   Six marine-spawned species (*Nuchequula gerroides, Eubleekeria splendens, Nematalosa come, Escualosa thoractata, Ambassis nalua,* and *Moolgarda perusii*) all occurred exclusively in the lower estuary, suggesting they are restricted to downstream reaches.

2. *Downstream biased*

   Five marine-spawned species (*Thryssa hamiltonii, Pomadasys kaakan, Secutor ruconius, Acanthopagrus pacificus,* and *Chelonodon patoca*) were present in both

lower estuary reaches and transitional wetlands, although occurred in higher relative abundance in the lower estuary, suggesting abundances taper upstream.

3. *Estuary pervasive*

   Four marine-spawned species (*Leiognathus equulus, Herklotsichthys castelnaui, Liza subvridis, Gerres filamentosus,* and *Stolephorus* spp.) all occurred in similar relative abundances in the lower estuary and transitional wetlands, indicative of widespread occurrence through the entire estuary.

4. *Upstream biased*

   Eight species which spawn at the mouths of estuaries, adjacent coastal waters, or offshore waters (*Acanthopagrus australis*, Mugilid (juveniles), *Chanos chanos, Selenotoca multifasciata, Moolgarda seheli, Elops hawaiensis, Lates calcarifer,* and *Megalops cyprinoides*), all occurred in higher relative abundance in transitional wetlands than in the lower estuary. Meanwhile, two of these species (*Lates calcarifer* and *Megalops cypronoides*) also penetrated into permanent freshwater reaches.

Estuary-spawned

5. *Ubiquitous estuary-residents*

   Two estuary residents (*Ambassis vachelli* and *Pseudomugil signifer*) displayed similar patterns of distribution to the '*estuary pervasive'* group. However, since these species spawn within the estuary, these patterns may be the result of self-recruitment in each reach, rather than dispersal.

Freshwater spawned

6. *Freshwater migrants*

   Three obligate freshwater-spawned species (*Craterocephalus stercusmuscarum, Leiopotherapon unicolor, Nematalosa erebi*), and three freshwater/facultative estuary-spawned species (*Hypseleotris compressa, Oreochromis* mossambicus, and *Glossogobius giurus*) occurred in freshwater reaches and transitional wetlands in similar relative abundances.

7. *Freshwater restricted*

   Eight species (*Melatoneia splendida, Neosilurus spp., Amniataba percoides, Glossamia aprion, Ambassis agassizi, Kuhlia rupestris, Mogurnda adspersa, Anguilla reinhardtii*) exclusively occurred in permanent freshwater reaches, and were not recorded in estuaries.

Table 2.2: Spawning locations of various species, assisting the identification of the different dispersal modes. M=marine-spawned, including species that spawn offshore, coastally, or around the mouths of estuaries; e=estuary-spawned, including species that spawn within the estuary interior; f=freshwater-spawned, including species which spawn in permanent freshwater reaches. These data were sourced from: (Moore 1982, Sheaves et al. 1999, Staunton-Smith 2001, Pusey et al. 2004, Whitfield et al. 2006, Froese & Pauly 2012).

Species	Spawning location	Species	Spawning location
Nuchequulus gerroides	m	*Elops hawaiensis*	m
Eubleekeria splendens	m	*Lates calcarifer*	m
Nematalosa come	m	*Megalops cyprinoides*	m
Escualosa thoractata	m	*Ambassis vachelli*	e
Ambassis nalua	m	*Amniataba caudivittata*	e
Moolgarda perusii	m	*Pseudomugil signifer*	e/f
Thryssa hamiltonii	m	*Glossogobius giurus*	e/f
Pomadasys kaakan	m	*Oreochromis mossambicus*	f/e
Secutor ruconius	m	*Hypseleotris compressa*	f/e
Acanthopagrus pacificus	m	*Craterocephalus stercusmuscarum*	f
Chelonodon patoca	m	*Leiopotherapon unicolor*	f
Leiognathus equulus	m	*Nematalosa erebi*	f
Herklotsicthys castelnaui	m	*Melatoneia splendida*	f
Liza subvidiris	m	*Neosilurus* spp.	f
Gerres filamentosus	m	*Amniataba percoides*	f
Stolephorus spp.	m	*Glossamia aprion*	f
Acanthopagrus australis	m	*Ambassis agassizi*	f
mugilid spp.	m	*Kuhlia ruprestris*	f
Chanos chanos	m	*Mogurnda adspersa*	f
Selenotoca multifasciata	m	*Anguilla reinhardtii*	f
Moolgarda seheli	m		

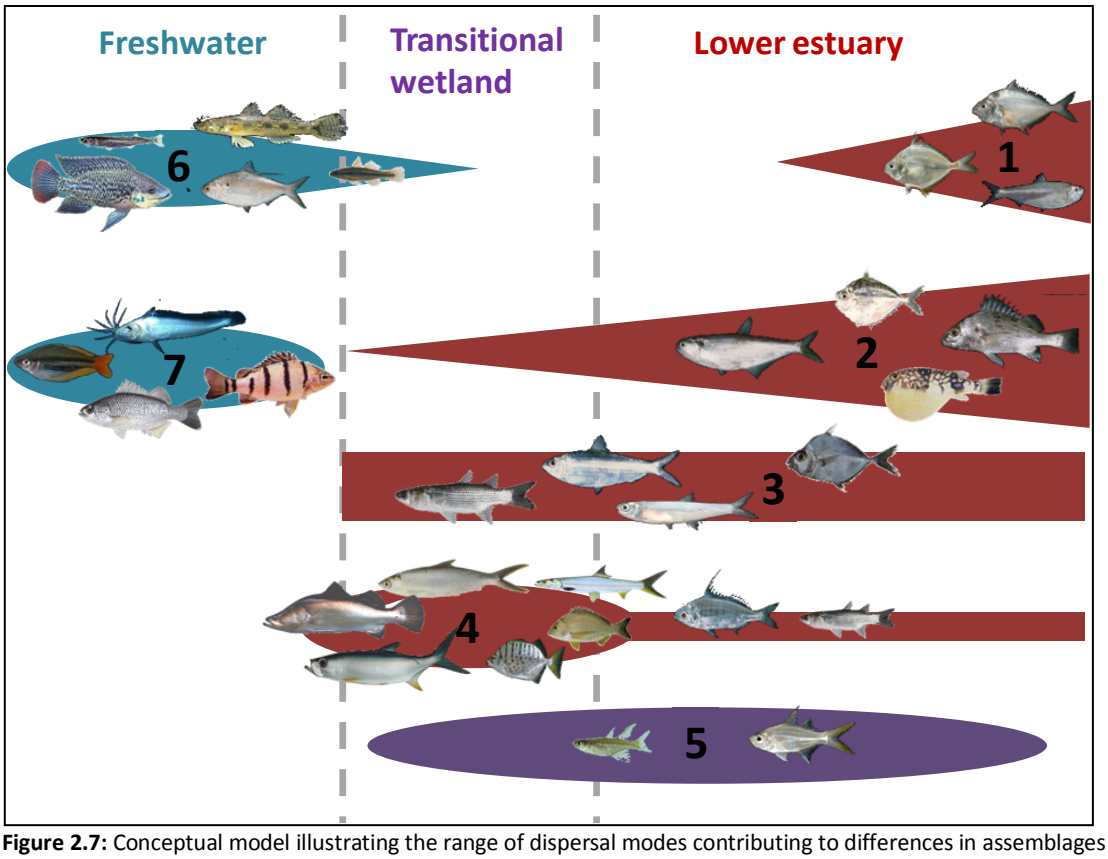

Figure 2.7: Conceptual model illustrating the range of dispersal modes contributing to differences in assemblages composition among reaches. Species characteristic of each mode are shown.

2.4 DISCUSSION

Different reaches of the river-estuary gradient hosted very different fish assemblages, characterised by broad changes in species occurrences and assemblage compositions along the river-estuary profile. Of the 180 species recorded, 123 species occurred in the lower estuary, 44 species occurred in permanent freshwater reaches, while an additional 13 amphidromous species were common to both of these reaches. Assemblage compositions at either ends of the river-estuary profile were highly distinct, with little overlap in the species dominating the lower estuary and freshwater reaches. Transitional wetlands hosted a mixture of species from surrounding reaches, including 52 species found in the lower estuary, 12 species found in freshwater reaches, together with the 13 amphidromous species. However, dominant species from the lower estuary and freshwater reaches did not simply interface in the middle to compose the transitional wetland assemblage. Interestingly, the transitional wetland assemblage was also characterised by a component of species found in low abundances in surrounding reaches. This represents a distinctive transitional wetland fauna that to my knowledge has not previously been reported in equivalent studies from other parts of the world, and certainly not in Australia's tropics.

2.4.1 Modes of dispersal

Underlying the patterns of assemblage composition, seven general modes of species dispersal were apparent, defined by patterns of distribution along the estuary profile relative to source of recruitment (i.e. spawning location; marine, freshwater, and estuary). Resolving these modes of dispersal provided enhanced insight into the processes regulating assemblage differences and producing the distinctive transitional wetland fauna.

Marine-spawned

The majority of species typical of downstream estuarine reaches spawn in marine waters (around estuary mouths, coastally, or offshore) (Table 2.2) and subsequently occupy the estuary as a nursery for several months (Sheaves et al. 2013). Different modes of dispersal demonstrated how these species penetrate variously through the estuary. While some species, (including *Escualosa thoractata, Nematalosa come, Ambassis nalua* and *Leiognathus decorus*) were restricted to the lower portions of estuaries, others penetrated farther upstream into transitional wetlands, tapering in an upstream direction (including *Thryssa hamiltonii, Pomadasys kaakan, Secutor ruconius,* and *Acanthopagrus pacificus*), or occurring

relatively evenly through the entire estuary (including *Leiognathus equulus, Herklotsichthys castelnaui, Liza subvridis,* and *Stolephorus* spp.).

Patterns of marine-spawned species decreasing in richness and abundance in an upstream direction are common features of both tropical and temperate estuaries (Cyrus & Blaber 1987a, Thiel et al. 1995, West & King 1996b, Barletta et al. 2005). Such patterns are commonly attributed to variable species responses to salinity gradients (and occasionally turbidity gradients) that develop along estuary profiles (Whitfield et al. 2012). While this mechanism is supported by shifts in distribution in response to spatio-temporal shifts in physical gradients (Garcia et al. 2003, Whitfield et al. 2006), a phenomenon previously observed in the Ross River (Sheaves et al. 2007b), the patterns could equally be driven by processes mediated by or correlated with physical gradients (e.g. the tracking of shifting food sources). Since many species reliant on estuaries are adapted to withstand the broad range of physical conditions typically experienced within them (Bamber & Henderson 1988, Whitfield et al. 2006), much of the assemblage is likely to be distributed independently of immediate physical conditions, with distributions more likely to reflect historical rather than current drivers (Sheaves 1998). Invertebrate prey sources however, are sensitive to pronounced salinity fluctuations experienced upstream (Whitfield et al. 2006, Sheaves in prep), and may regulate fish distributions by bottom-up control processes. Such a mechanism may explain the restriction of several planktivorous species to downstream reaches in the present study.

Relationships between species' distributions and processes linked to physical condition mean that some patterns of dispersal described in this study are likely to shift, both seasonally and among years with different river flows. However, processes independent of physico-chemical condition altogether may also shape some of the observed patterns, leading to more consistent patterns of distribution. A partial independence of salinity-mediated drivers is evident from South African estuaries, where patterns of fish distributions are similar between estuaries characterised by typical salinity gradients, and those which have effectively become homogenous 'arms of the sea' (Ter Morshuizen & Whitfield 1994). This suggests other more consistent factors are also important in shaping distributions of individual species, such as limited penetration of recruits into the estuary (Bell et al. 1988, Martino & Able 2003, Faunce & Serafy 2007), recruitment to habitats only available in particular reaches (Richardson et al. 2006, Whaley et al. 2007), and perhaps innate life-history movements (Moore 1982).

Marine-spawned species that were pervasive throughout the estuary (including *G. filamentosus, L. equulus, L. subvirids, H.castelanui,* and *Stolephorus* spp.) possibly represent

euryhaline generalists that are relatively unaffected by the aforementioned estuary-level processes, similar to Atlantic Croaker (*Micropogonius undulatus*) and Spot (*Leiostomus xanthurus*) in mid-Atlantic estuaries (Rozas & Hackney 1984). However, since patterns were integrated over time, the apparent ubiquitous distributions of these species could also represent seasonal use of each reach as conditions become suitable.

Unexpectedly, another group of marine-spawned species (including *Chanos chanos, Selenotoca multifasciata, Elops hawaiensis, Lates calcarifer, Megalops cyprinoides,* and *Acanthopagrus australis*) were biased towards upstream reaches, contributing to the unique assemblages found in transitional wetlands. The addition of this group contrasts with the concept proposed for temperate systems, that transitional wetlands represent 'species minimum zones' (Odum 1988, Attrill & Rundle 2002, Whitfield et al. 2012), where conditions are sub-optimal for species originating from both marine and freshwater sources (Barnes 1989, Attrill & Rundle 2002). Upstream biases in the present study may reflect either an innate drive to exploit upstream reaches, or a preference for reduced salinities more likely to be encountered upstream. The larvae and post-larvae of *L. calcarifer, S. multifasciata,* and *M. cyprinoides* have previously been found in abundance in both saltwater pools following large tides, and also brackish and freshwater swamps following seasonal flooding (Nair et al. 1974, Moore 1982, Russell & Garrett 1983, Davis 1988). Meanwhile, *C. chanos* and *E. hawaiensis* are frequently found in salt-pan pools subject to hypersaline conditions (Hiatt 1947, Schuster 1960). This suggests that early life phases of these species may migrate upstream into transitional wetlands regardless of salinities. This assertion is supported by the fact that three of the transitional wetland sites supported relatively high abundances of these species despite being subjected to very different salinity regimes, encompassing gradual returns to marine conditions following floods (Annandale Wetland), steady fresh-oligohaline conditions (Black River Lagoon), and extreme fluctuations among fresh, marine, and hypersaline conditions (AIMS culverts).

The presence of an apparent 'specialist' transitional wetland fauna has not previously been recognised in Australia's tropics, and indicates that these portions of the estuary provide a specific nursery function for several marine-spawned species. Similar life-history strategies, characterised by upstream biases of marine-spawned recruits have also been observed in sub-tropical US estuaries for red drum (*Scianeops ocellatus*), ladyfish (*Elops saurus*), and snook *(Centropomus undecimalis*) (Peters & McMichael 1987, McBride et al. 2001, Stevens et al. 2007), and in South-African estuaries for cape stumpnose (*Rhabdosargus holubi*) and full

moony (*Monodactylus falciformis*) (Ter Morshuizen & Whitfield 1994). Ladyfish and snook are close relatives of two members of the 'upstream biased' group (*Elops hawaiensis* and *Lates calcarifer* respectively). This suggests that marine-spawned species in many parts of the world may benefit by exploiting transitional wetlands during early life phases, and that this life-history strategy may be common to certain families of fish.

These same parts of the estuary are also under high risk from anthropogenic activities, including the construction of weirs, dams, bund walls and other flow regulation structures which can sever or disturb hydrological connections (both marine and freshwater) to transitional wetlands (Sheaves et al. in review). This emphasises a pressing need to further resolve the nursery function of transitional wetlands, to reveal whether these reaches are critical *per se*, or merely valuable conduits between fresh and marine waters for diadromous species. Distinguishing between these two very different functions will be paramount in reliably informing management and remediation protocols. For instance, the implementation of weirs often 'drown-out' transitional wetlands, effectively resulting in a discrete separation of freshwater and lower estuary reaches either side of the weir (Boys et al. 2012). In this scenario, function for diadromous fish may be partially re-instated by constructing a fishway to facilitate fish passage between the two reaches (Kowarsky & Ross 1981, Stuart & Mallen-Cooper 1999). However, if species are reliant on habitat features particular to transitional wetlands, nursery function would only be re-instated by removal of the weir and restoration of the drowned habitats.

Freshwater-spawned

From the other end of the system, a small subset of obligate freshwater-spawned species dispersed downstream into transitional wetlands (including *N.erebi, C. stercusmuscarum,* and *Leiopotherapon unicolor*), yet did not penetrate extensively into the estuary. Freshwater-spawned fish using estuaries are generally less capable of withstanding salinity changes than marine- or estuary-spawned species, and are often limited to oligohaline reaches (Peterson & Ross 1991, Whitfield et al. 2006, Whitfield et al. 2012). The majority of species dominating freshwater reaches did not occur in any considerable abundance in transitional wetlands, despite extensive freshwater flows throughout the study period. This suggests that several freshwater species strategically avoid being entrained in downstream flows where they may suffer in variable physical conditions.

Some freshwater species found in the transitional wetlands (including *Glossogobius giurus, Oreochromis mossambicus,* and *Hypseleotris compressa*) are capable of spawning in brackish water. Occurrences of these species in the transitional wetlands could reflect a mixture of downstream dispersal and self-recruitment.

Estuary-spawned

Two estuary residents, which spawn within the estuary (including *Ambassis vachelli* and *Pseudomugil signifer*) were found uniformly distributed across the estuary. Estuary residents are likely to benefit from superior salinity tolerances (Strydom et al. 2003), enabling spawning and persistence through the spectrum of physical conditions typically experienced (through time and space) in their host estuaries. These life-history characteristics mean that estuary residents often dominate abundances of upstream estuary assemblages (Wasserman & Strydom 2011, Bilkovic et al. 2012). However, in the present study the contribution by estuary residents was downplayed by the high relative influence of the 'estuary-pervasive' and 'upstream-biased' marine-spawned species.

2.4.2 Conclusion

Species from the three different recruit sources (marine, estuary, and freshwater) disperse variously through the estuary. The resulting stratification of species along the river-estuary profile means that habitats embedded in different reaches of the estuary will be subjected to different species mixes.

While this study provides a general overview of where species are likely to be found along the river-estuary profile, distribution patterns are not fixed through time. Many species distributions are seemingly mediated by physical gradients, which shift in position and intensity seasonally and inter-annually. Consequently, a single reach within an estuary will be subjected to different species mixes in response to migration of the salt-wedge along the estuary axis. Assemblage compositions are likely to vary most in transitional wetlands, which experience the greatest physical fluctuations and periodically receive direct connection to freshwater recruit sources. Distribution patterns will be further complicated through the year due to varying spawning schedules and resulting seasonal availabilities of recruits (Sheaves et al. 2010), and also through fish ontogeny due to changing biotic and abiotic requirements with development (Miller & Dunn 1980). These combined sources of variability highlight the need for temporally and ontogenetically resolved analyses to better understand the processes shaping assemblage structure across and within reaches of tropical estuaries.

Chapter 3 *This chapter has been published in PLoS ONE*

Temporal utilisation of estuarine wetlands with complex hydrological connectivity

3.1 ABSTRACT

The physical and faunal characteristics of coastal wetlands are driven by dynamics of hydrological connectivity to adjacent habitats. In dry-tropical and sub-tropical regions, wetlands in the transitional zone between estuary and freshwater reaches are particularly dynamic, driven by a complex interplay of tidal marine connections and seasonal freshwater flooding, often with unknown consequences for fish using these habitats. To understand the patterns and subsequent processes driving fish assemblage structure in such wetlands, I examined the nature and diversity of temporal utilisation patterns of 12 species/genera representing 12 families, over three annual cycles in a tropical Australian estuarine wetland system. Four general patterns of utilisation were apparent based on CPUE and size-structure dynamics: (i) classic nursery utilisation (use by recently settled recruits for their first year) (ii) interrupted peristence (iii) delayed recruitment (iv) facultative wetland residence. Despite the small self-recruiting 'facultative wetland resident' group, wetland occupancy seems largely driven by connectivity to the subtidal estuary channel. Variable connectivity regimes (i.e. frequency and timing of connections) within and between different wetland units (e.g. individual pools, lagoons, swamps) will therefore interact with the diversity of species recruitment schedules to generate variable wetland assemblages in time and space. In addition, the assemblage structure is heavily modified by freshwater flow, through simultaneously curtailing persistence of the 'interrupted persistence' group, establishing connectivity for freshwater spawned members of both the 'facultative wetland resident' and 'delayed recruitment group', and apparently mediating use of intermediate nursery habitats for marine-spawned members of the 'delayed recruitment' group. The diversity of utilisation pattern and the complexity of associated drivers means assemblage compositions, and therefore ecosystem functioning, is likely to vary among years depending on variations in hydrological connectivity. Consequently, there is a need to incorporate this diversity into understandings of habitat function, conservation and management.

3.2 INTRODUCTION

Increasing knowledge of temporal utilisation patterns of functional groups, and of the underlying processes regulating their occurrence has led to great advances in our understanding of the functioning of estuarine fish assemblages (Elliott et al. 2007). Such studies have primarily concerned subtidal estuary channels (hereafter referred to simply as 'estuary channels'), however the coastal and estuarine system acts as a mosaic of inter-connected habitats, linked through fish migrations at a range of scales, including feeding and refuge, ontogenetic, and life-history migrations (Sheaves 2009). Consequently, complete understanding of estuarine function will not be achieved without understanding the utilisation of other important estuarine habitats (Gehrke & Sheaves 2006).

Occurring adjacent to estuary channels worldwide are a variety of fringing wetlands with varying potential for fish utilisation. Vegetated intertidal wetlands (i.e. mangroves and saltmarshes) are prominent and iconic components of estuarine systems, and provide tidally available habitat for fauna inhabiting the estuary channel (Rountree & Able 2007). Periodic tidal emersion means that temporal utilisation patterns are a function of seasonal dynamics in the main estuary, modified by tidal-driven migration patterns (Ellis & Bell 2008). Estuarine systems worldwide also contain a variety of 'off-channel' wetlands (including a mixture of pools, lakes, and lagoons) that connect to the subtidal estuary channel over a range of spatial and temporal scales. Although such wetlands are recognised as important nurseries for fish (Brockmeyer et al. 1996, Menon et al. 2000), detailed knowledge of utilisation patterns is scant. These wetlands often provide relatively permanent habitats (persisting through tidal and annual cycles) which nekton potentially use for longer periods, spanning tidal visits to periods of years, depending on wetland persistence, and the frequency and duration of hydrological connection to the estuary channel. Consequently, off-channel wetlands provide alternative habitats to the subtidal estuary channel, providing the possibility of separate nursery function, and different patterns of occupation.

In dry-tropical and sub-tropical regions, off-channel wetlands dominate the transitional zones between the upstream estuary channel and lower freshwater reaches. Low annual rainfall in these regions means that 'transitional wetlands' exist as a fragmented series pools for much of the year, either in a linear sequence upstream of continuous subtidal reaches (Beumer 1980), or (in areas of low relief) scattered laterally across floodplains (Fig 1.5) (Sheaves et al. 2007a, Sheaves & Johnston 2008). The dynamic regimes of hydrological connectivity characteristic of these transitional wetlands, featuring the interplay of tidal

marine and freshwater connections, results in variable physical conditions, and simultaneously provides corridors for fish recruitment from both estuarine and freshwater systems (Sheaves & Johnston 2008). Dislocation from freshwater reaches, and reduced tidal connectivity, means there is an increased propensity to become hypersaline towards the end of the dry season (Ridd & Stieglitz 2002). Discrete wet season characterised by increased freshwater flows (~January-March) can then induce abrupt and severe drops in salinity, and shifts in other physical parameters (Ram et al. 2003), while establishing or enhancing connections to both freshwater and estuarine sources (Sheaves & Johnston 2008). Conditions then become increasingly saline through the rest of the year as freshwater is progressively replaced by coastal marine water (Ridd & Stieglitz 2002). The consequences of these extreme changes for fish utilisation patterns are poorly understood, however these dynamics are likely to interact with variable physiological tolerances of organisms to modify patterns of wetland utilisation for many species (Cyrus & Blaber 1992, Barletta et al. 2005).

Pools on estuary floodplains have previously received some attention in Australia's tropics (Russell & Garrett 1983, Davis 1988) and sub-tropics (Sheaves & Johnston 2008), with a focus on the nursery function for the commercially and recreationally important barramundi, *Lates calcarifer*. *L. calcarifer* spawn in coastal waters and mouths of estuaries during wet season months, coinciding with periods when connectivity and habitat availability of fragmented coastal wetlands is greatest (Moore 1982). Consequently, juvenile barramundi recruit to estuarine pools during wet season months (Russell & Garrett 1985). They remain until the advent of the dry season, although it is unclear whether this represents a life-history emigration or if occupancy is curtailed by declining water levels or water quality. Despite the past focus on *L. calcarifer,* wetland fish fauna are taxonomically diverse (Russell & Garrett 1983, Davis 1988, Sheaves et al. 2007a). Components of estuarine wetland assemblages show a variety of spawning schedules (Robertson & Duke 1990b, Sheaves et al. 2010) and life-history strategies (Whitfield 1990), which together with variable physical tolerances mean assemblages are likely to display a diversity of pool occupation patterns, featuring modified timing and age of recruitment, and subsequent persistence of different species.

To develop an understanding of the patterns and underlying processes driving the fish assembage of transitional wetlands in Australia's tropics, I examined the nature and diversity of temporal utilisation patterns (timing and age at recruitment, and subsequent persistence) at a species level over three annual cycles that incorporated strong physical change. The study focused on a natural wetland system comprised of 20 discrete pools situated on a salt-marsh

of the Ross River in North Queensland, Australia. Data from the main channels of estuaries in the region were used to provide a utilisation pattern 'null model', to investigate whether observed patterns were typical of estuary channel use, or if different sets of processes influenced transitional wetland utilisation.

3.3 METHODS

3.3.1 Study site

The study was conducted in Annandale Wetland (the main details of study site are given in Ch. 2). Weather patterns in the study region can be divided into 4 periods (Sheaves et al. 2010): (1) a pronounced hot wet season, generally concentrated around January-March, yet occasionally extending into neighbouring months. During years where there is sufficient rainfall Aplin's Weir (located 0.9 km upstream) overflows, blanketing the wetland in a sheet of freshwater. (2) A post-wet season (~April-May), where conditions begin to cool. During this transition period as floodwaters naturally recede (hereafter referred to as draw-down), the system of pools become discrete semi-isolated units connected to each other and to the Ross River to varying extents during high tides. This state of alternating marine connection and disconnection continues though (3) a cool dry season (June-September); and (4) a pre-wet season (October-December) where conditions begin to warm prior to the commencement of the wet season.

3.3.2 Fish Sampling

Sampling of all 20 pools commenced after wet season floodwaters receded in March 2010, and was repeated on a monthly basis until the commencement of the following wet season in December. Monthly sampling in the first three months following draw-down was undertaken during 2011, to incorporate likely complexity associated with this transition period, followed by bi-monthly sampling until the end of the year. A third annual sample was collected for the first month after floods in April 2012.

The main details of sampling in Annandale Wetland are as per Chapter 2, although there were some additional details of specific pertinence to the present study. Upon catch, fish numbers and their sizes were measured in 10 mm fork length (FL) size classes, and reported as size-class minimums (e.g. 27 mm FL = 20 mm). Fish <10 mm FL were excluded from analyses as a large proportion were below mesh selection size, and unlikely to be well represented. Catches were rapidly returned to the water alive, as extraction may substantially influence catch in subsequent months. Salinity, water temperature, and visibility (Secchi

depth) were recorded in each pool on each sampling occasion as potential explanatory variables of fish dynamics. Freshwater flow data over Aplin's Weir through the study period were also provided by North Queensland Water.

Data collected across the complete lengths of 9 small North Queensland estuary channels as part of a previous study (Sheaves et al. 2010) were interrogated to develop a null model of expected wetland utilisation patterns. Many species of fish using transitional wetlands are widespread across the region's coastal and estuarine system (Ch. 2; Blaber et al. 1989), and any difference in utilisation pattern between the wetland and the estuary channel null model provided an insight into processes shaping wetland utilisation. For instance, it enabled assessment of whether any disparity in utilisation pattern was a function of different regimes and severities of physical change between the two habitats.

Fish were quantitatively sampled from the estuary channels using cast nets (5 mm mesh size) during 12 sampling trips between November 2007 and January 2009; the complete methodology can be found in Sheaves et al. (2010). Since cast nets and seine nets are both effective at sampling the main components of the small fish assemblage in tropical estuaries (Johnston & Sheaves 2007), general comparisons of temporal population dynamics (from which utilisation patterns could be interpreted) could be made for well represented taxa. To standardise the range of analysed size classes with the Annandale Wetland seine data, fish <10 mm FL were also excluded. Data were not available for the Ross River channel, and sampling the channel in addition to the pools was beyond the scope of the present study. However, the objective was not to make a direct comparison between pool and channel habitat within a system, but rather to assess whether patterns in Annandale Wetland reflected general patterns of estuary use.

3.3.3 Data analysis

The most commonly captured species' were selected for analysis, along with some larger less-abundant species of commercial and recreational importance (*Lates calcarifer, Chanos chanos, Megalops cyprinoides, Elops hawaiensis*), which commonly utilise off-channel habitats during early life-history stages (Moore 1982, Davis 1988, Bagarinao 1994). To identify general patterns of wetland utilisation parallel dynamics of catch per unit effort (CPUE) and size class at a species or genus level (where identification to species level was not possible) were examined over three annual cycles. Plotted together as a time series, CPUE and modal size-class data enabled the examination of demographic trajectories and shifts within the

populations of taxa through time. These dynamics in turn allowed interpretation of the processes underpinning wetland utilisation patterns. Such processes included recruitment (defined here as an annual population peak, dominated by the smallest recorded size class for that cycle), growth, mortality and emigration. Similar methods have previously been applied to identify functional groups within the estuarine fish assemblage (Robertson & Duke 1990b).

CPUE was calculated as an average abundance over the 20 replicate pools in each month. For larger pools requiring multiple net hauls, only data from the net containing the greatest abundance of a species was used. Since certain individuals within a pool may have been released and recaptured in subsequent hauls, taking the net of greatest abundance ensured individuals were not accounted for more than once. Monthly CPUE and associated error structure were plotted against modal size-class trends for each taxon. Modal size classes were extracted from monthly plots of size-class distribution, fitted with a generalised additive model (GAM), for which the specified degrees of freedom were adjusted based on the size-class range. Where GAM curves were bimodal, two modal size classes were extracted for a single month. Size-class distributions were based on the sum of each 10 mm size-class increment across the 20 pools in each month (with the net of maximum abundance taken to represent each increment in the larger pools). *Stolephorus* spp. and *Acanthopagrus* spp. data were only resolved to the genus level due to difficulties distinguishing between early life-stages of species in the field. Laboratory identified specimens of *Stolephorus* were mostly *S. comersonii* and *S. brachycephalus*, while *Acanthopagrus* spp. was composed of ~70% *A. australis* and ~30% *A. pacificus*.

For species sufficiently abundant in both the wetland and regional estuaries, CPUE vs. size-structure plots were qualitatively compared. Any large-scale disparities between the plots were considered as different utilisation patterns.

3.4 RESULTS

3.4.1 Physical data

Salinity in the wetland responded negatively to freshwater flow, ranging from 0-4 ppt directly after the wet season to >30 ppt pre-wet season (Fig 3.1). Visibility was also loosely correlated with freshwater flow and water temperature displayed seasonal variation, yet these two variables provided little explanation of fish dynamics.

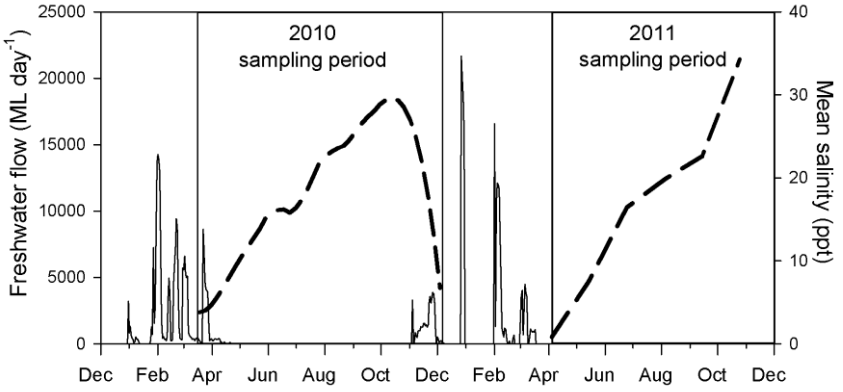

Figure 3.1: Freshwater flowing over Aplin's Weir (solid line plot) from December 2009 to December 2011 (measured as mega-litres per day), and the resulting salinity changes (smoothed with a Loess) in Annandale Wetland (dashed line) during the sampling periods (grey boxes) of 2010 and 2011. Freshwater flow data were provided by North Queensland Water. However, due to gauge-failure data were unavailable for much of December 2010 and all of January 2011, although the weir was flowing throughout these months.

3.4.2 Patterns of fish utilisation

Sampling produced 101 fish taxa, with 33 taxa collectively constituting 99.2% of the total catch (see Appendix B). There were 10 dominant taxa, however two of these were small-bodied species (*Pseudomugil signifer* and *Hypseleotris compressa*) which were unsuitable for analysis since they were below gear selection size for substantial proportions of their life-cycles. The remaining 8 taxa (*Ambassis vachelli, Leiognathus equulus, Nematalosa erebi, Gerres filamentosus, Stolephorus* spp*., Herklotsichthys castelnaui, O. mossambicus* and *Acanthopagrus* spp.), together with the four commercial/recreational species, can be categorised into four groups based on CPUE vs. modal size-class plots (Figs 3.2-3.5): (i) Classic nursery utilisation, (ii) Delayed recruitment, (iii) Interrupted persistence, and (iv) Facultative wetland residence. These groups represent the dominant temporal utilisation patterns for the wetland, independent of taxonomic or life-history identities.

Classic nursery utilisation

Four taxa (*L. equulus, Acanthopagrus* spp., *Elops hawaiensis,* and *G. filamentosus*) displayed a pattern of classic nursery utilisation (CNU), typified by cycles of recruitment at small size classes, followed by growth and then emigration. Taxa in the CNU group recruited as larvae and postlarvae (Fig 3.2; Table 3.1), illustrated by heightened CPUE's dominated by small size classes during peak recruitment periods. The timing and duration of recruitment varied between taxa. *Acanthopagrus* spp. and *E. hawaiensis* (Fig 3.2) had relatively discrete recruitment periods, occurring August-September and November-December respectively, as illustrated by the progressive increase in modal size from the time of first recruitment, mirrored by simultaneous declines in abundance. Other CNU species displayed extended recruitment. For these, growth trajectories were periodically masked by the extended

Table 3.1: Approximate body lengths at important life-history landmarks for taxa recruiting to the wetland at small size classes (<40 mm FL), to determine how wetland utilisation patterns relate to life-histories. Settlement from planktonic to demersal forms is displayed; for pelagic species this is assumed from the length of larval-juvenile morphological transformation. This information allows developmental stage of recruitment to be interpreted. Common adult lengths follow FishBase (TL=total length; SL=standard length).

Taxa	Length @ settlement	Source	Common adult length
Leiognathus equulus	15 mm	(Froese & Pauly 2013)	200 mm TL
Acanthopagrus spp.	14 mm	(Leis et al. 2009)	300 mm TL
Elops hawaiensis	35 mm	(Pollock et al. 1983)	500 mm SL
Gerres filamentosus	10 mm	(Sato & Yasuda 1980)	150 mm SL
Stolephorus spp.	23-27 mm	(Miskiewicz 1998b)	85 mm SL
Herklotsichthys castelnaui	21-33 mm	(Miskiewicz & Neira 1998)	140 mm SL
Ambassis vachelli	10 mm	(Miskiewicz 1998a)	60 mm SL
Oreochromis mossambicus	-	-	350 mm TL

dominance of smaller size classes, suggesting numerous recruitment-growth cycles staggered over several months. *L. equulus* had an extended summer recruitment period, illustrated by the dominance of 10-30 mm FL size classes during the pre- and post-wet season. However, due to the sampling hiatus it remains uncertain whether this recruitment continued through the wet season itself. *G. filamentosus* also demonstrated an extended summer recruitment in 2010, but in 2011 displayed year-round recruitment, illustrated by year round dominance of 20-40 mm FL size classes.

CNU taxa displayed similar patterns between Annandale Wetland pools and estuary channels (Fig 3.2). These taxa displayed no apparent response to wet season floods (Fig 3.1); CPUE's and modal size classes directly after floods followed regular cycles of recruitment, growth and emigration (i.e. no sharp decreases or increases were observed directly after the wet season).

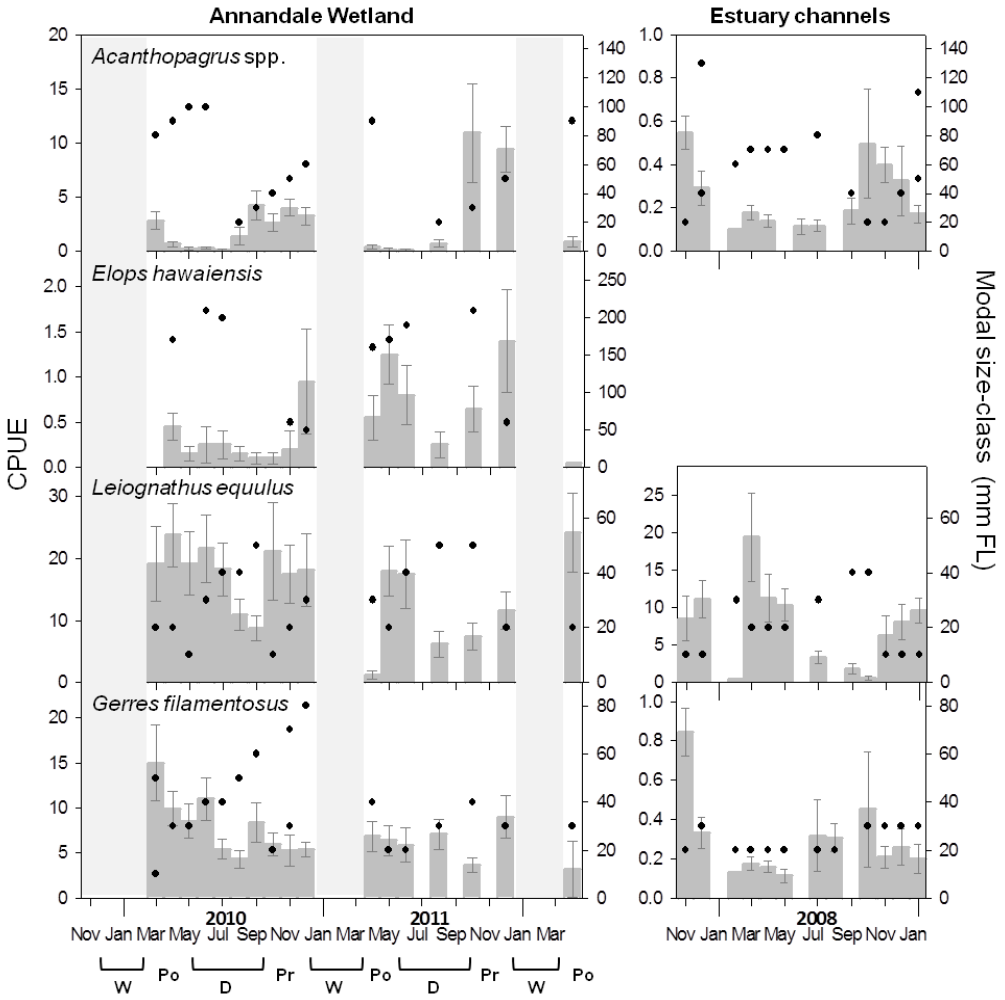

Fig 3.2: CPUE and modal size-class dynamics for taxa exhibiting patterns of classic nursery utilisation (CNU). Profiles of CPUE (±1 S.E.) (darker grey bars) averaged over the 20 pools in Annandale Wetland from March 2010–April 2012, matched with modal-size classes (filled black circles; measured as fork length (FL)). Where size-distributions were bimodal, two modes (black circles) are displayed for the same month. Sampling hiatuses are shaded in light grey, and generally represent periods when the salt-marsh surface was flooded with freshwater. Seasons have been labelled below the x axis (W = wet; Po = post-wet; D = dry; Pr = pre-wet). No data were collected in July, September, and November of 2011. Equivalent data are displayed for CPUE (±1 S.E.) and modal-size class averaged over the main bodies of 9 estuaries in the North Queensland region, over an extended annual cycle from pre-wet season 2007 to the 2008/2009 wet season. *Elops hawaiensis* was not caught in sufficient abundance in the 9 regional estuaries to display temporal dynamics.

Delayed recruitment

Three species, *L. calcarifer, M. cyprinoides, C. chanos*, were caught exclusively as advanced juveniles (i.e. beyond postlarvae; all modal sizes were >100 mm FL) (Fig 3.3), despite sampling overlapping with spawning seasons (spanning pre-wet season to the end of the wet season (Table 3.2)). These species comprise the delayed recruitment (DR) group. In the present study the smallest recorded size classes dominated annual population peaks during post-wet season months. Whether this represents discrete post-wet season recruitment is unclear as potential recruitment during the wet season sampling hiatus cannot be accounted for. However in 2010 it was evident that the bulk of recruitment of these species was delayed

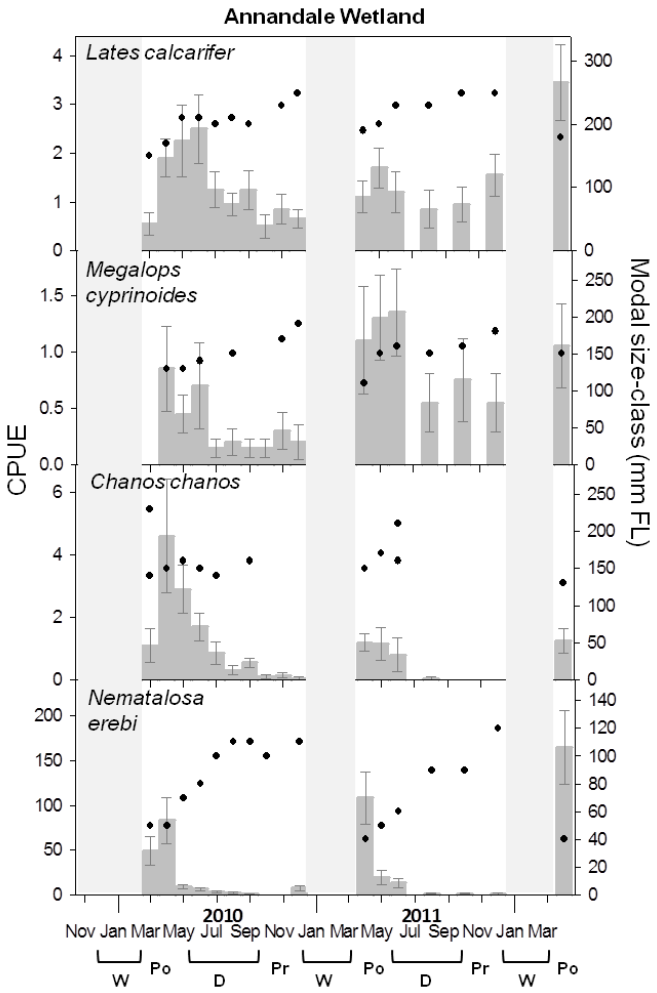

Figure 3.3: CPUE and modal size-class dynamics for taxa exhibiting patterns of delayed recruitment (DR).
Details as per Figure 3.2. These taxa were not caught in sufficient abundance in the 9 regional estuaries to display temporal dynamics.

until the second month of sampling in April (Fig 3.3). In contrast, *N. erebi* CPUE was relatively high from first sampling in March (Fig 3.3), and despite the smallest recorded size classes being 40-50 mm FL (representing advanced juveniles; Table 3.2), observed patterns are likely to represent the tail of a wet season recruitment dominated by smaller size classes. For each of these species, recruitment was followed by a maturation period where modal size increased as abundances declined through the year. However, *C. chanos* and *N. erebi* persisted for shorter periods than the other two species in this group.

Table 3.2: Early life history parameters of species only caught at advanced sizes. Spawning periods refer to knowledge of periodicity in the tropics, for broadly distributed species. Sizes in March-April are only considered for tropical Australian estuaries and refer to post-wet season sizes. This information is necessary to gauge the developmental stage of these delayed recruiting species.

Species	Spawning period	Source	Size in March-April (mm)	Reference	Source	Reference
Lates calcarifer	Nov-Mar; Oct-Feb	(Moore 1982)	~200	(Reynolds 1982)	~300	(Reynolds 1982)
Chanos chanos	Nov-Mar	(Leis & Reader 1991)	-	-	>150	(Davis 1984)
Megalops cyprinoides	Oct-Feb	(Moore 1982, Davis 1988)	~100	(Kowarsky & Ross 1981)	-	-
Nematalosa erebi	Little seasonality; peaks early in wet	(Kumagai et al. 1985)	-	-	~100	(Bishop et al. 1986)

Interrupted persistence

Two taxa (*H. castelnaui* and *Stolephorus* spp.) recruited as larvae or post-larvae in the pre-wet season (the interrupted persistence (IP) group), illustrated by large peaks in CPUE dominated by size classes of 20-30 mm FL (Table 3.1) in November-December (Fig 3.4), followed by a complete absence directly after wet season freshwater flows (Fig 3.4), with varying extents of re-colonisation of larger size classes (60-80 mm FL) post-wet-early dry season. This trend contrasted with more consistent patterns of CPUE in local estuaries (Fig 3.4).

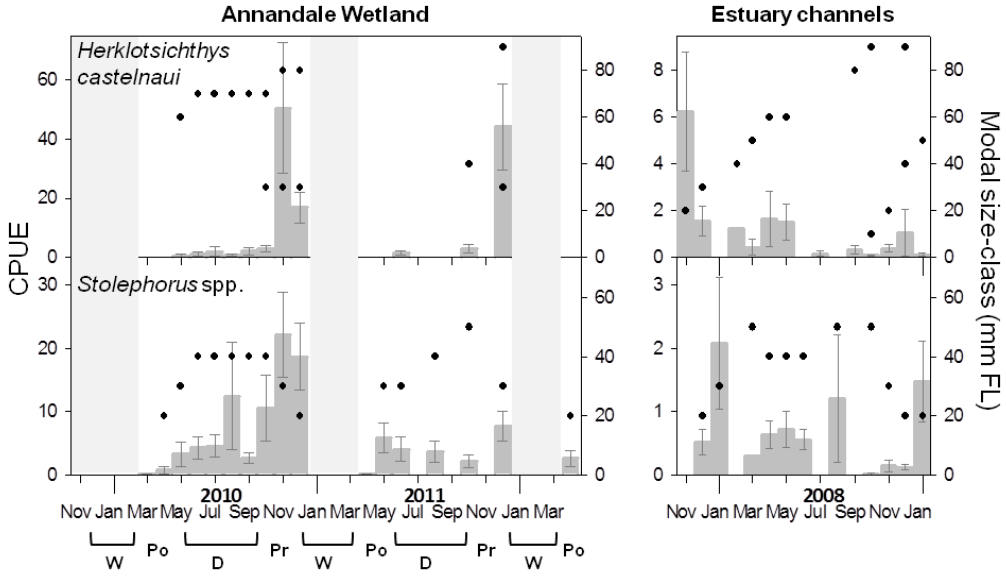

Figure 3.4: CPUE and modal size-class dynamics for taxa exhibiting patterns of interrupted persistence (IP). Details as per Figure 3.2.

Facultative wetland residents

Two species (*A. vachelli* and *O. mossambicus*) displayed fluctuating CPUE's through the year that matched with consistent size structures (facultative wetland resident (FWR) group). These trends reflected year-round occurrence of early post-settlement stages (represented by modal size classes of 20-30 mm FL for *A. vachelli*; <90 mm FL for *O. mossambicus* (Table 3.1)), in addition to larger juveniles and adults (Fig 3.5). The simultaneous presence of both juveniles and adults is evident in the discrete bimodal size structure of *O. mossambicus* populations, represented by consistent occurrence of modal sizes of ~300 mm FL in addition to <90 mm FL (Fig 3.5; Table 3.1). Although not evident from the figure, *A. vachelli* was also present as adults year round, with consistent presence of 50 mm FL size classes (Table 3.1). Furthermore, *A. vachelli* exhibited similar trends of fluctuating abundance and constant size-structure in local estuaries (Fig 3.5), while *O. mossambicus* was absent in samples from those estuaries.

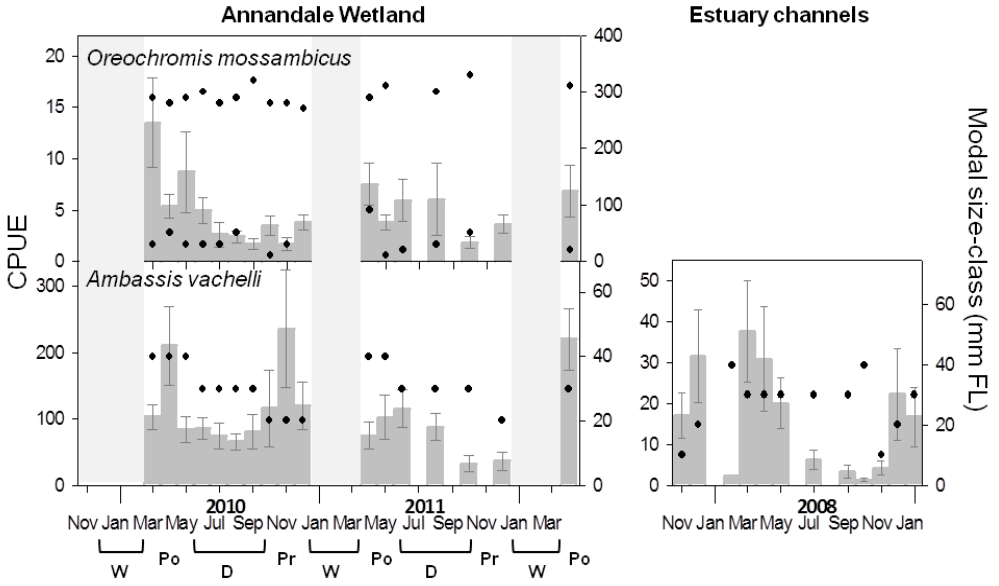

Figure 3.5: CPUE and modal size-class dynamics for taxa exhibiting patterns of facultative wetland residence (FWR). Details as per Figure 3.2.

3.5 DISCUSSION

There were diverse patterns of utilisation among the 12 taxa analysed, defined by taxa-to-taxa differences in the details of CPUE and size-structure dynamics. Despite differences in detail these taxa could be broadly categorised into four groups based on similar patterns of wetland usage. Most taxa demonstrated a surprising tolerance to the severe and abrupt shifts in salinity, although for many taxa, utilisation patterns were strongly modified by other effects of freshwater flow. In general, utilisation patterns reflected the relationship of life-history schedules, physical tolerances, and habitat requirements with variations in hydrological connectivity, physical conditions, and habitat availability mediated by the interplay of tidal and freshwater flow.

3.5.1 Patterns of utilisation

Four taxa (*L. equulus, Acanthopagrus* spp.*, G. filamentosus,* and *E. hawaiensis*) display CNU patterns, following cycles of post-larval recruitment, growth, and assumed emigration to other habitats upon reaching critical juvenile sizes (Staunton-Smith et al. 1999). This pattern has previously described by Robertson & Duke (1990b) for fish using a tropical Australian estuary. The uninterrupted nursery dynamics and mutuality of pattern between Annandale Wetland and the main channel of estuaries in the region, suggest that CNU taxa are tolerant of the abrupt marine-freshwater shifts experienced in estuarine pools, and are simply

using the wetland as they would the estuary channel. The possible exception is *E. hawaiensis,* which has not been captured in abundance in previous studies sampling estuary channels across numerous systems in the region (Ch. 2, Robertson & Duke 1990b, Sheaves & Johnston 2009).

Two taxa, *H. castelnaui* and *Stolephorus* spp., display classic nursery ground dynamics in the main channels of regional estuaries, but in Annandale wetland, utilisation was interrupted by the advent of the wet season. Although estuary channel data were averaged over the full length of the estuary, details of the distribution of these species suggest they move downstream after freshwater flow events (Sheaves et al. 2010). These are plantkivorous fish, so it is likely that freshwater flows push food aggregation zones farther downstream (Ueda et al. 2004). Studies in temperate estuaries have attributed aggregations of planktivorous fish to the accumulation of plankton around the maximum turbidity zone (MTZ) (North & Houde 2006). MTZ's form at the fresh-saltwater interface of estuaries (Sanford et al. 2001), and are spatially variable, shifting downstream during periods of high freshwater input. Consequently, restricted wetland utilisation by these planktivorous species probably reflects occupation limited to periods when conditions are suitable for them or when their food source is present.

Four species (*L. calcarifer, M. cyprinoides, N. erebi,* and *C. chanos*) display a delayed recruitment to the wetland, arriving at advanced-size juvenile stages during wet or post-wet season months. Consequently, it is implicit that these species initially settle as post-larvae elsewhere. For *N. erebi,* settlement occurs in permanent freshwater reaches (e.g. above Aplin's Weir), due to exclusive freshwater spawning (Pusey et al. 2004). While it is possible that *N. erebi* recruited as early post-settlement juveniles during the wet season sampling hiatus, recruitment to tidal wetlands is essentially decoupled from life-history schedule, and the exact size at recruitment is dependent on the relationship between timing of spawning and the timing of freshwater flows, which allow movement to the wetland. The other three species (*L. calcarifer*, *C. chanos,* and *M. cyprinoides*) spawn in coastal marine waters (Moore 1982, Leis & Reader 1991, Shen et al. 2009). While little is known of the early life-history of *M. cyprinoides* and *C. chanos, L. calcarifer* has a complex early-life history linking multiple coastal habitats. *L. calcarifer* and *M. cyprinoides* post-larvae recruit to shallow habitats associated with elevated wet season water levels, including supra-littoral depressions on saltpans and ephemeral freshwater and brackish swamps (Moore 1982, Russell & Garrett 1983). Recruitment of advanced juvenile *L. calcarifer* into subtidal estuarine habitats synchronises

with draw-down of these ephemeral habitats at the end of the wet season (Russell & Garrett 1985). Meanwhile juvenile *M. cyprinoides* migrate upstream during post-wet season months (Kowarsky & Ross 1981, Bishop et al. 1995). The delayed patterns of recruitment in the present study suggest that a similar habitat progression may occur in the Ross River, with recruiting individuals having previously occupied flooded ephemeral wetlands earlier in the wet season. This ephemeral wetland could potentially be the seasonally flooded areas of salt-marsh surrounding the pools on Annandale Wetland.

Following recruitment, *L. calcarifer* and *M. cyprinoides* persist and grow on the wetland through the year, yet persistence of *N. erebi* and *C. chanos* is particularly brief, with an absence or negligible abundance from post-wet season to early dry season. Brief persistence may be the result of mortality without ability for re-colonisation, or alternatively migration to other habitats. Falling water levels during this period could cause *N. erebi* to migrate to preferred deeper waters (Johnston & Sheaves 2008) or expose them to elevated predation from both avian (Houston 2006) and piscine predators. *L. calcarifer* is a major predator of *N. erebi* (Sheaves et al. 2006) and recruits to the wetland during this period. Furthermore, despite the capability of *N. erebi* to persist when captive in hypersaline lakes (Ruello 1976), increasing salinities may cause sub-lethal stress and trigger emigration to other habitats. *C. chanos* on the other hand is an active roving fish, and may be restricted by the limited volume of the pools as water levels drop in the post-wet season (Bagarinao 1994), prompting emigration.

In contrast to the nursery-orientated utilisation of the rest of the assemblage, two facultative wetland residents (FWR) (*A. vachelli* and *O. mossambicus*) were present in the wetland year-round both as young juveniles and adults. Continual presence of young juveniles suggests spawning may occur within the wetland or perhaps adjacent habitats. For *A. vachelli* these trends occur at the scale of the entire estuary (this study and (Molony & Sheaves 1998)), and recruitment may reflect both colonisation from the estuary channel and spawning within the wetland. *O. mossambicus* however is generally considered a freshwater-spawning species and appears to primarily recruit to Annandale Wetland from freshwater reaches during the wet season. However, the surprising resilience in the number of both adults and juveniles through the year (despite removal upon capture) is indicative of re-colonisation from adjacent estuarine habitats, and subsequent spawning in the wetland. The shallow, sheltered nature and soft sediment common in the wetland appears to provide ideal habitat for the formation of breeding arenas (circular depressions in the sediment called ‘Leks’) (de Silva & Sirisena

1988), which were frequently observed in wetland pools during the sampling period (pers. obs.). Studies of *O. mossambicus* distributions in similar tropical estuaries suggest they are capable of spawning in seawater salinities, but are limited to torpid waters in the upper estuary or enclosed water bodies (Whitfield & Blaber 1979).

3.5.2 Linking pattern and process

Transitional wetlands are essentially satellite habitats. With the exception of the two facultative wetland residents, which are possibly capable of self-recruitment and resilient to the prolonged periods of isolation often experienced in lesser-connected wetland units (Hyland 2002), the majority of taxa use tidal pools exclusively as juveniles and are dependant on connectivity to other habitats**.** The large contribution of juveniles dependant on connectivity to other habitats probably explains why Sheaves & Johnston (2008) found that re-colonisation based factors were more important than local factors in driving fish assemblages of sub-tropical pools. The main source of recruits for estuarine pools is the estuary channel, for which the assemblage itself is governed by multiple processes influencing different faunal components (Sheaves et al. 2010). However, from the perspective of fringing habitats the estuary channel can simply be perceived as source of recruits from which recruits are drawn.

The nature of connection between estuary channels and transitional wetlands will play a large role in structuring the wetland assemblage. For the members of the CNU group, which use pools indiscriminately as just another estuarine habitat, the regime (i.e. frequency and timing) and physical integrity (i.e. depth and presence of physical barriers) of connections to the estuary channel are likely to be the sole regulators of wetland utilisation pattern. In Annandale Wetland estuary channel-to-pool connections were established through most tidal cycles, and utilisation of several taxa mirrored patterns in the estuary channel. However, in reality regimes of estuary connection across estuarine floodplains are highly variable from wetland to wetland, occurring on scales of days, weeks, months, and sometimes years (Sheaves & Johnston 2008). This variety of connection regime among off-channel wetlands is likely to result in spatio-temporal asymmetries in assemblage compositions, through matching and mismatching of connection events with the availability of different taxa to recruit, particularly larval and post-larval stages which are highly abundant for short windows (Botsford et al. 1998). However, this effect may be tempered somewhat by the general overlapping of spawning and recruitment with elevated wet season water levels, which may enable estuarine taxa to access off-channel wetlands that would otherwise be inaccessible via tidal connections alone.

Beyond the simple effect of enhancing connection depths and durations, other effects of wet season freshwater flows appear to modify wetland utilisation patterns and assemblage structures. Flows move certain planktivorous species (IP group) out of the wetland system, and simultaneously donate many *N. erebi* and *O. mossambicus* from permanent freshwater sources. Meanwhile, the extent of freshwater flooding will regulate use of ephemeral wetlands that certain members of the DR group initially recruit to. Effective use of these intermediate habitats is likely to modify the extent, timing, and size of recruitment of these larger and mostly predatory species (*L. calcarifer* and *M. cyprinoides*) to tidal pools.

Despite the presence of Aplin's Weir directly upstream of the study site, the wet season flow dynamics observed in the study are similar to dynamics in unregulated river systems (Sheaves et al. 2007b). In unregulated river systems however, weaker rainfall is more likely to initiate stream flow (Sheaves et al. 2007b), and freshwater spawned species will have greater opportunity to repopulate tidal wetlands more frequently through the year. However, there are few rivers on Australia's North East coast without weirs or dams (Walker 1985), and so the patterns observed in this study are likely to be representative of the functioning of estuarine systems in the region.

The pivotal role of freshwater flow in mediating key physical and biological processes of estuarine pools adds a profound layer of variability to wetland functioning since wet season rainfall in dry tropical and sub-tropical regions is inter-annually inconsistent, following a loose cycle of wet and dry climactic periods spanning multiple years, largely associated with ENSO cycle (Cai et al. 2001). Extended periods of negligible freshwater flow into dry- tropical and sub-tropical estuaries are not uncommon (Sheaves et al. 2007b), and reliability of flow is expected to become increasingly erratic with climate change (Kothavala 1999), a phenomenon exacerbated by the widespread regulation of river systems (Walker 1985). Further work is required during dry climactic periods to uncover the full influence of flow denial on wetland utilisation patterns. The response of the DR group to a drought period is of particular interest, since the use of intermediate habitats (i.e. seasonally flooded lowlands) will be disabled (Staunton-Smith et al. 2004). In addition, a clearer understanding of the ontogenetic sequence of habitat use is required for these species' to fully understand the processes regulating nursery function.

Additional processes operating at finer spatio-temporal scales are likely to further complicate assemblage structure and dynamics of transitional wetlands, such as taxonomic and ontogenetic differences in locomotory capabilities (Thomas & Connolly 2001, Hohausová

et al. 2010), movement-based behaviours (Bretsch & Allen 2006, McGrath & Austin 2009) and sub-habitat associations (Allen et al. 2007, Johnston & Sheaves 2007). Consequently, further work is required to establish the recruitment potential of the fish assemblage to wetlands of varying connectivity and morphology, through examining among-pool spatial patterns. Additionally, the potential homogenising effect of freshwater floods on assemblages of transitional wetland pools needs to be explored (Gomes et al. 2012).

This study demonstrates the diversity of utilisation pattern and complexity of associated drivers inherent in a coastal nursery habitat characterised by dynamic physical conditions and a high taxonomic diversity. It is evident that the processes regulating the occurrences of fish are not mutual across the assemblage, but vary among taxa, with different species responding differently to the same hydrological connectivity event. Therefore any future change in hydrological regime in this system, driven by natural fluctuation, climate change or water regulation, will have differing impacts on different members of the assemblage. Consequently, the assemblage composition and ecological function of transitional wetlands is prone to variation among years, and there is a need to incorporate the diversity of assemblage drivers into understandings of habitat function. The results of this study may not have clear implications for conservation and management strategies. However, since transitional wetlands seem to provide the greatest value to members of the DR group (Ch. 2), managers should prioritise the resource and connectivity requirements (including reliance on physical cues) of these species in their strategies, while recognising that an ecosystem approach is needed to conserve the food sources of these species and subsequently nursery function. Before this can be done, we need to develop a mechanistic understanding of how freshwater flow influences the behaviour, movement patterns, growth, and survivorship of members of the DR group, and also identify the intermediate nursery grounds that they initially recruit to. With this information managers will be able to protect and rehabilitate essential habitats and connectivity pathways, and also structure the timing and extent of freshwater releases around the requirements of these commercially important species.

Chapter 4 *This chapter has been published in MEPS*

Seascape and metacommunity processes regulate fish assemblage structure in coastal wetlands

4.1 ABSTRACT

Faunal complexity is an impediment to understanding the function of coastal wetlands. Conceiving faunal communities as part of a larger network of communities (or a metacommunity) helps to resolve this complexity by enabling simultaneous consideration of local environmental influences and 'regional' dispersal-driven processes. I assessed the role of local vs. regional factors on fish assemblage structure of a wetland system comprising 20 tidal pools. In equivalent freshwater metacommunities, regional factors often override local influences, resulting in patterns of nestedness among patches as species and individuals are progressively filtered out along gradients of isolation. While the tidal pool assemblage was primarily structured by regional processes, patterns deviated from freshwater systems as two faunal groups exhibited contrasting responses to tidal connectivity. A subset of typical estuary channel fauna was restricted to better connected pools at lower elevations, which connect to the estuary channel or other pools on most neap high tides. Frequent connections among these pools subsequently enabled sorting of species relative to preferred environmental condition (including depth and substrate). Contradicting models of nestedness, a distinct faunal group including salt-marsh residents and juvenile marine-spawned taxa occurred in greater abundances in more isolated higher elevation pools, which connect to the estuary channel or other pools only on larger spring high tides. These higher elevation pools represent a functionally unique seascape component, and colonisation by marine-spawned taxa seems to reflect an innate drive to ascend upstream gradients to access them. This illustrates how seemingly similar patches within coastal wetlands may perform considerably different nursery functions due to their position in the landscape. Together, metacommunity and seascape frameworks offer complementary perspectives in understanding the role of spatial ecology in structuring coastal ecosystem function and productivity.

4.2 INTRODUCTION

Considering habitat units as a component of a broader landscape/seascape is essential for understanding the range of processes driving faunal assemblage compositions. Most habitats exist as a fragmented series of patches (e.g. forest patches in an agricultural matrix), and faunal communities within individual patches are often connected by the exchange of individuals with other patches, or dispersal from a 'mainland' stock of colonists. Consequently, we need to expand our focus from local scales to conceptualise habitats as a group of communities inter-connecting across a landscape, or 'metacommunity'. Within metacommunities, the structure and dynamics of local communities are shaped by the interplay of processes operating at both local patch scales, including species responses to habitat heterogeneity and physico-chemical conditions, as well as processes operating at broader regional scales, i.e. dispersal to and between patches. Theories and understandings of how local and regional processes interact to structure communities fall under the umbrella term 'metacommunity ecology' (Leibold et al. 2004).

Metacommunity concepts have been developed through empirical studies in fragmented freshwater wetlands (De Meester et al. 2005, Logue et al. 2011), which have provided greater insights into processes driving fish community structure (Snodgrass et al. 1996, Magnuson et al. 1998). The balance between local and regional influences shifts depending on the extent of inter-patch connectivity in a system. Local patch processes are often more influential in systems characterised by low inter-patch connectivity (i.e. infrequent hydrological connections, large inter-patch distances, low exchange of organisms), while in better connected systems (i.e. with frequent connections, proximate patches, high exchange of organisms) regional dispersal often masks local effects (Magnuson et al. 1998, Brown & Swan 2010). A high influence of dispersal generally results in patterns of nestedness forming among patches (Snodgrass et al. 1996, Taylor 1997), whereby assemblages of more isolated patches are subsets of those in better connected patches, due to the filtering out of species and individuals with progressive isolation. Nestedness is strongest in systems where recruitment to patches depends on connection to a common source of colonists (i.e. through a mainland-island dynamic), particularly where communities in patches are frequently reset by disturbances (Snodgrass et al. 1996, Baber et al. 2002).

In contrast to the developed understanding in freshwater systems, less is known about how local and regional processes interact to structure the assemblages of fragmented coastal habitats, where the influence of tidal pulsing and complex life-history/habitat use schedules may lead to different trends (Kneib 1994, Rozas 1995, Rountree & Able 2007). Although similar multi-

scale landscape principles have recently been applied to components of the coastal ecosystem, such as mangroves and seagrass meadows (Boström et al. 2011, Pittman et al. 2004), these components are not conducive to explicit examination under a metacommunity framework; since there are no definite barriers to fish movement in these open systems it is difficult to define what a patch is, and what a dispersal pathway is (Connolly & Hindell 2006). Instead, these coastal habitats have been more effectively studied in the broader context of seascape ecology, whereby the coastal ecosystem as a whole is perceived as a mosaic with different habitat types providing complementary resources for fish (Nagelkerken et al. 2013, Olds et al. 2012). Pools scattered across transitional wetlands of tropical estuaries (henceforth referred to as 'tidal pools') on the other hand, are more conducive to metacommunity applications (De Meester et al. 2005), providing a tractable system of discrete units with defined boundaries to both patches and connectivity pathways. These characteristics of tidal pools, coupled with their situation as a component of a broader coastal ecosystem, mean that metacommunity and seascape processes (movements of species among different habitat types of the coastal ecosystem) may interface to drive community dynamics of these systems.

Tidal pools are an important component of the coastal seascape (Ch. 2, Russell & Garrett 1983, Davis 1988, Sheaves & Johnston 2008), but are yet to be the focus of a spatially-explicit study, so it is not known whether different pools provide for the estuarine assemblage in different ways. Pool colonists predominantly comprise juveniles of species spawned in other habitats, including the estuary channel, coastal marine waters, and from freshwater reaches during wet season flows (Ch. 2, Sheaves & Johnston 2008, Davis et al. 2012). Pools therefore operate as a network of 'island' units because colonisation predominantly depends on periodic connections to the estuary channel as a source of colonists (i.e. a 'mainland') (Ch. 3, Davis et al. 2012). Subsequent dispersal among pools however, may further influence community assembly. Different species colonise pools at different times of the year, and generally use pools for less than a year before individuals make ontogenetic migrations to other habitats, resulting in a high annual turnover of individuals (Ch 3; Davis et al. 2012). This mainland-island dynamic and frequent faunal re-setting is likely to foster a metacommunity dynamic driven by regional dispersal processes (i.e. re-colonisation of pools), and freshwater systems with similar characteristics are characterised by clear patterns of nestedness.

The cyclical pulsing of tides means hydrological connectivity between pools and the estuary channel is spatio-temporally complex (Davis et al. 2012). However, dispersal pathways and

movement patterns of fish through tropical intertidal habitats are not well understood. Therefore, a number of potential pathways must be considered when defining patch connectivity, beyond simple inter-patch distances considered in studies of other wetland systems (Astorga et al. 2011, Warfe et al. 2013; but see Olden et al. 2001). This includes a consideration of the spatial configuration of patches (i.e. structural connectivity), the depth of connection, temporal connectivity variables, as well as the potential influence of episodic freshwater floods which can briefly cause extensive hydrological connection over the tropical intertidal landscape. The variation in level of tidal connectivity also modifies physico-chemical regimes within pools (Sheaves & Johnston 2008). For example, more isolated pools connecting only on larger tides will potentially experience wider fluctuations in temperature and salinity than those connected on smaller tides and therefore buffered by more frequent flushing with tidal waters. Pools also vary in morphology, marked by different depths, surface areas, substrates, types and extent of fringing vegetation. In South Carolina salt-marshes morphological features of intertidal channels, such as depth, breath, and flow velocity have a strong influence on nekton abundance (Allen et al. 2007). However the relative influence of these factors on patterns of fish community structure and dynamics in tropical salt-marsh systems remains largely unknown.

To better understand the patterns and processes behind community assembly in an estuarine wetland system, and how generally applicable patterns reported from freshwater wetlands are to these systems, I sampled 20 tidal pools scattered across a tropical salt-marsh system over three annual cycles. I examined the extent to which assemblages differed between pools, and then considered extent to which assemblage patterns were explained by local patch processes (responses to pool morphology and physico-chemical condition) and regional system-scale processes (responses to hydrological and structural connectivities). If drivers are similar to those in better studied freshwater systems, then I predict a pattern of nestedness in assemblage structure along connectivity gradients. However, the influence of tidal connections may contribute further complexity, leading to the emergence of different trends.

4.3 METHODS

4.3.1 Study site

The study was conducted in Annandale Wetland (Fig 4.1; the main details of study site are given in Ch. 2). For much of the year the pools exist as an array of semi-isolated units connected to the Ross River and each other to varying extents on high tides. The level (frequency, duration, and

depth) of tidal connectivity a pool receives is largely governed by its position along the intertidal radient from the estuary channel to the terrestrial-aquatic ecotone. However, tidal connectivity is modified by topographic heterogeneity within the gradient. Many pools connect by narrow channels of different lengths and depths providing regular, but variable connections during most lunar tidal cycles. Others have no defined channel connections and are only connected during spring tides that flood over the salt-marsh surface at shallower depths and for shorter durations. Additionally, some pools may connect directly to the estuary channel, while others may rely on connection through a series of intermediate pools. This spatio-temporal variability in connectivity modifies colonisation potential for fish and imposes different regimes of physical condition across pools. If there has been sufficient rainfall during wet-season months (~ January-March) Aplin's Weir (located ~0.9 km upstream) overflows, blanketing the wetland in a sheet of freshwater. This complete connectivity presents an opportunity for faunal composition and conditions to homogenise across the system. After these floods draw-down, revealing the array of pools, the water table remains relatively high for a month or two, with greater pool depths than during drier periods later in the year. Based on these complex features, various descriptors of hydrological and structural connectivity can be derived, pertaining to the level of tidal connection, connection distances, and the configuration of pools (described in Table 4.1).

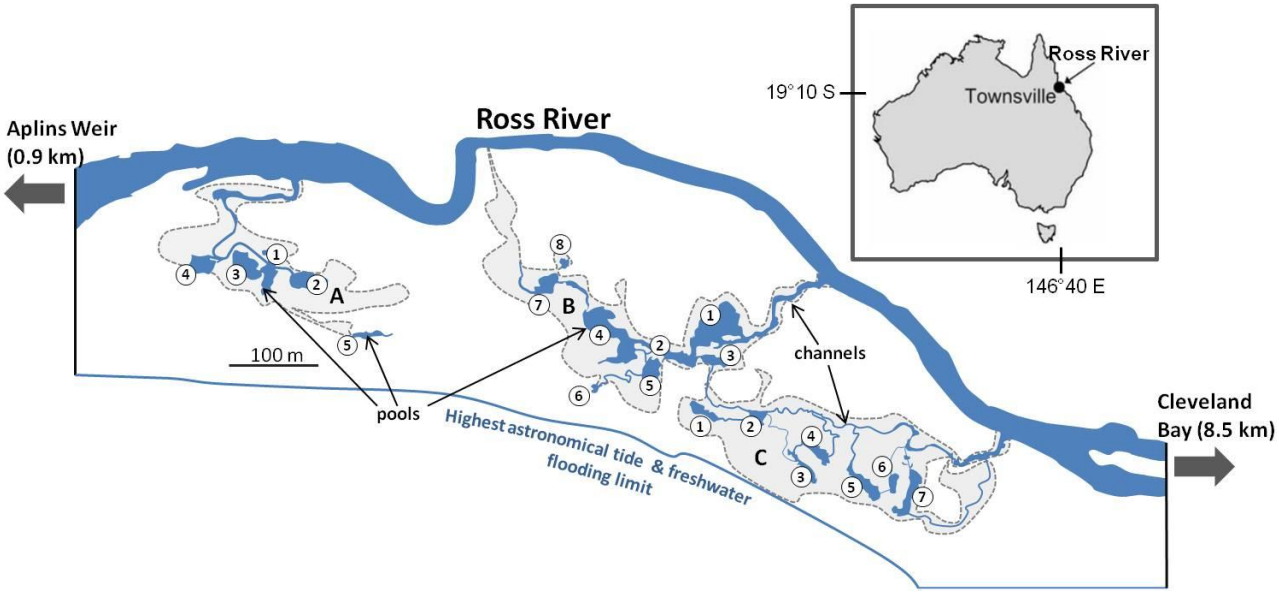

Figure 4.1: Annandale Wetland containing the 20 wetland pools adjacent to the Ross River, Australia. The wetland extends from the subtidal channel of the Ross River, south to the uppermost tidal limits (highest astronomical tide ~4m; occurring during January and February), indicated by the blue boundary at the bottom of the figure. An embankment also contains freshwater floods within these limits. The areas of salt-marsh surface flooded during regular high spring tides (3.6-3.8 m; occurring for a few days during one spring tide period a month) are shaded in light grey, and were central to the delineation of the 3 Networks (A, B, and C; see Table 1). These salt-marsh flooding patterns were evident from aerial maps of the study site, and were ground-truthed at the top of a 3.7 m tide. Within each network, pools were assigned numbers such that each pool could be referred to by a unique alpha-numeric code.

4.3.2 Fish Sampling

Fish were sampled from all 20 pools over three annual cycles, as described in Chapter 2. Sampling over multiple years enabled assessment of inter-annual consistency and subsequently the determinism of observations. This was central to discerning between systematic structuring processes and stochasticity. Sampling occurred during the new moon period of the lunar tidal cycle, when hydrological connectivity and hence the potential for fish exchange is greatest. However, since spatial patterns remain consistent through lunar cycles (Appendix C), samples from this period are representative of the whole month.

The main details of sampling are given in Chapter 2. Fish numbers and size-classes (in 10 mm increments) in each haul were quickly recorded, resolved to the lowest identifiable taxonomic level. Some multi-species genera and families (e.g. mugilids) were difficult to differentiate at smaller size-classes, and were resolved to genus level, although larger conspecifics could be resolved by species. To control for possible recaptures of the same individuals in pools requiring multiple hauls on a single sampling occasion, for each taxon only the maximum count across hauls was used to represent the abundance of a taxon in a pool for a given sampling date. This sampling provided monthly/bimonthly catch-per-unit-effort (CPUE) data for a range of fish taxa across 20 pools, from March/April-December over 2 annual cycles (and a third annual cycle for April).

4.3.3 Explanatory variables

Three groups of explanatory variables were measured to examine for correlation with the spatial structure of fish assemblages. This included a range of regional dispersal (i.e. hydrological and structural connectivity) metrics, and also local patch variables, which included pool morphology and physico-chemical variables (Table 4.1). Due to the multifaceted nature of hydrological connections, via channels and flooded salt-marsh surfaces, and through complex configurations of pools, a variety of connectivity metrics were derived in an attempt to capture the full spectrum of connectivity processes that may regulate spatial dynamics. All of these variables were normalised to standardise the degree of variation amongst variables.

Table 4.1: Description of the explanatory variables derived to explain spatial structure of the fish assemblage. These were formed *a priori*, based on the defining physical features of Annandale Wetland, previous understanding of fish community structure in fragmented wetland systems and estuarine intertidal zones, and knowledge of mechanisms shaping nekton distributions within the main body of North Australian estuaries.

Variable	Description	Unit	Method	Underlying ecological/biological hypothesis
CONNECTIVITY				
Freshwater overbank distance	Shortest linear distance from Ross River to a pool	m	GIS	Assemblage structure is determined by proximity to main channel (source of recruits) during wet season flood events that overtop the whole wetland with freshwater
Tidal overbank distance	Shortest path from Ross River to a pool through tidally inundated basins (Fig 1) which form on high spring tides	m	GIS + ground truthing	Fish exchange predominantly occurs over the tidally flooded salt-marsh surface, and is limited by distance from source
Channel distance	Shortest path from Ross River to a pool via channelised connections. Channels were defined as water courses connecting pools to the Ross River or other pools. For two pools this included water courses running over vegetated salt-marsh.	m	GIS	Fish exchange predominantly occurs via channels, and is limited by distance from source
Critical tidal connection	Minimum tidal height required for a pool to receive aquatic connection to Ross River	m	Pool depths were continuously logged over a tidal sequence. Depth fluctuations were plotted against realised tide data (courtesy of Townsville Port Authority). The lowest high tide peak at which pool depth rose was taken as the critical tidal connection, accounting for lag between time of realised tide peak and time of high water in Annandale Wetland.	Assemblage is structured based on a tidal/elevation gradient, irrespective of the nature and distance of connection pathways. Fish exchange is dependent on frequency, depth, and duration of connection. Different species and sizes of fish are restricted by depth in different ways.
Network	Wetland divided into clusters of pools based on the rivulet which connects them to the Ross River, and the basins which form around them on high spring tides (Fig 1).	three network categories defined: A, B, and C.	GIS + ground truthing	Differences in assemblage between pool clusters are greater than differences between individual pools within clusters, due to upstream/stochastic disparities in colonisation followed by little connectivity between the 3 networks.

Variable	Description	Unit	Method	Underlying ecological/biological hypothesis
CONNECTIVITY				
Pool order	The number of intermediate pools an individual would need to pass through to colonise the destination pool from the Ross River	number of pools	GIS	The colonisation of a pool may be reduced by the number of intermediate pools between a given pools and Ross River. Intermediate pools may provide enhanced settlement opportunity, reducing the number of individuals available to colonise a given pool.
Stream position	Pools connect to upstream pools (mid-stream), or are the most upstream pool in a network (terminals)	binary variable: mid-stream vs. terminal	GIS + ground truthing	Pools at the upstream terminals of networks may accrue different compositions over time if certain species are inclined to colonise new habitat patches by moving progressively upstream with the tide
Nearest neighbour	Distance to nearest pool via tidal overbank connections	m	GIS	Pools at the upstream terminals of networks may accrue different compositions over time if certain species are inclined to colonise new habitat patches by moving progressively upstream with the tide
POOL MORPHOLOGY				
Maximum depth	Maximum depth of a pool at low ride	cm	Measuring staff	Fish may only remain in a pool if it exceeds a critical depth
Surface area	Low tide surface area of pool	m^2	GIS	Fish may be restricted by habitat availability
Dominant substrate	Most pools were comprised of multiple substrate types. Only substrates which constituted >40% of the pool bed were considered.	5 categories, in order of coarseness: rubble/sand, sand, mud/sand, mud, fine mud.	Visual survey	Fish will only remain in pools with appropriate substrate

Variable	Description	Unit	Method	Underlying ecological/biological hypothesis
POOL MORPHOLGY				
Mangrove fringe	The proportion of pool perimeter fringed by mangrove	m	GIS	Certain species may remain in a pool based on the services provided by the amount of mangrove fringing a pool
Relative area of ephemeral wetland	Area of ephemeral wetland (salt-marsh flooded at high tide that dries out between tidal cycles) that drains into a pool, divided by the area of that pool	m^2	GIS	Ephemeral wetland may provide intermittent habitat for a distinct set of species which may recede into the nearest permanent pools
PHYSICO-CHEMICAL				
Salinity	-	ppt	Portable refractometer	Fish limited to pool within tolerable range
Visibility	-	cm	Secchi disc	" "
Temperature	-	Degrees Celsius	Thermometer	" "

4.3.4 Data analysis

The 22 most abundant taxa which together comprised >95% of the total catch were selected for assemblage-level analysis. Two taxa (*O. mossambicus* and *Elops hawaiensis*) showed strong bimodal size structure, with each mode representing a different life-phase. This enabled ontogenetically resolved analysis of distribution pattern by examining each life stage separately. *O. mossambicus* was split into juvenile (0-90 mm) and adult (>200 mm) stages, and *E. hawaiensis* was split into small juvenile (0-110 mm) and larger juvenile (150-300 mm) stages. Although many other species occurred on the wetland in a range of sizes, their size-distributions were unimodal, and so any ontogenetic separation would have been arbitrary. The assemblage CPUE data were log(x+1) transformed to down-weight the influence of highly abundant taxa, favouring a more assemblage-orientated analysis (Clarke 1993).

Assemblage structure (CPUE x pool x month) was analysed with multivariate classification and regression trees (mCART) (De'ath 2002) based on Bray-Curtis dissimilarities, using the R 'mvpart' package. mCART's are accepted as a simple and robust technique for modelling ecological data (De'ath & Fabricius 2000), and have previously been used to explain nekton assemblage structure (Sheaves et al. 2010). Initially a tree was constructed using pool codes (consisting of network and pools number; see Fig 4.1 caption), months, and years as explanatory variables to examine the spatio-temporal patterns of dissimilarity among pools. Even though the study focus was on spatial dynamics, the temporal variables 'month' and 'year' were included as explanatory variables. This enabled the strength of spatial structuring processes to be assessed against temporal structuring processes, and also enabled assessment of the temporal consistency of spatial phenomena. The tree model was selected using 10-fold cross-validation (CV), which estimates the prediction error for the tree output at each size that minimises dissimilarity. The final model was selected as the smallest tree within 1 standard error of the tree with the lowest CV-error.

The mCART model was then re-run with pool codes replaced by the explanatory variables (see Table 4.1), to help explain the processes driving spatial assemblage structure. Comparison of the similarity in tree splits and level of variance explained between this model output and the previous model output (at equivalent tree sizes) allowed evaluation of the success of the explanatory variables in accounting for the observed assemblage patterns. The influence of each variable was evaluated by its order of occurrence in the tree.

Each species was also analysed individually with univariate CARTs, using log(CPUE+1) data and the same suite of explanatory variables, to investigate the spatial distribution of rarer taxa which may have been highly pool specific or only abundant for short periods. Such species may not have been influential in the multivariate analyses, but may be important in understanding species-specific functioning of the wetland system.

4.4 RESULTS

Ninety species were captured throughout the study. The 22 most abundant taxa comprised >95% of the total catch and were included in further analyses. *Ambassis vachelli, Leiognathus equulus, Nematalosa erebi, Hypseleotris compressa, Metapenaeus bennettae, Herklotsichtyhys castelnaui, Gerres filamentosus* and *Stolephorus* spp. together constituted >85% of the assemblage.

4.4.1 Assemblage structure

General patterns in assemblage structure

Assemblages varied considerably among pools. The dominant split in the mCART formed at the 'pool' level (Fig 4.2), suggesting spatial organisation of fish on the wetland explained more assemblage variability than any temporal change (i.e. 'month' and 'year'), and that spatial patterns were consistent. This split was characterised by a minority of pools (A5, B6, B8, C3) consistently harbouring a different assemblage to the rest of the wetland.

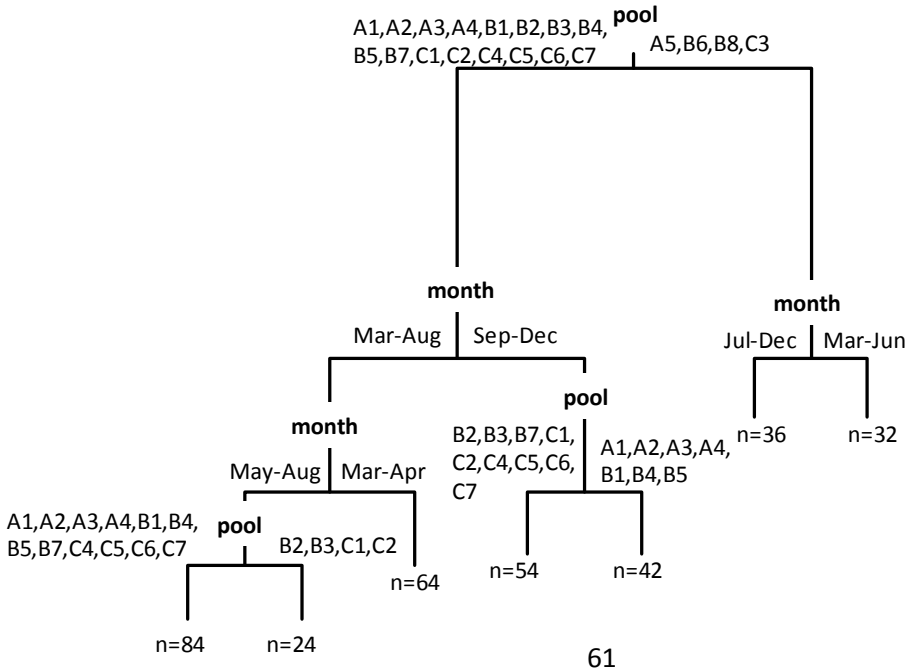

Fig. 4.2: mCART of log(CPUE+1) based on pool codes (network and pool number), month, and year, explaining 21% of the variation in assemblage structure. Factors responsible for splits are indicated in bold above branch points. Codes above branches indicate levels of factors split in each direction. The 'n' number represents the number of pool x month x year cases grouped in each terminal branch.

Explaining patterns

Explanatory variables modelled with mCART (see Table 4.1) successfully accounted for the observed patterns in assemblage structure, explaining a similar degree of variability in assemblage composition as the model based on pool codes (at the same tree sizes: 21% explained variability for the initial 'pool code' model, 20% for the 'explanatory' model). The mCART output suggested that a connectivity metric 'critical tidal connection' was the key structuring variable (Fig 4.3a). Critical tidal connection refers to the minimum tidal height at which a pool connects to the Ross River (or other pools), and is a function of the relative position of a pool along an elevation gradient from the Ross River to the aquatic-terrestrial ecotone. Pools connected to the Ross River during tides >2.8 m (henceforth referred to as 'higher elevation pools'), harboured an assemblage distinct from the rest of the wetland, where pools connected to the Ross River <2.8 m tides (henceforth referred to as 'lower elevation pools'). Although no species was exclusive to either pool type, species profiles at the terminal nodes of the mCART (Fig 4.3a) indicated the presence of two groups of taxa: those associated with higher elevation pools and those associated with lower elevation pools. Lower elevation pools were characterised by greater abundances of *L. equulus*, *A. vachelli, G. filamentosus, Stolephorus* spp., *H. castelnaui,* adult *O. mossambicus*, *gobiid* sp. 1*, Penaeus merguiensis, Acanthopagrus* spp., *Lates calcarifer*, *Glossogobius circumspectus,* and *Thryssa hamiltonii*. Higher elevation pools were characterised by greater abundances of *Hypseleotris compressa, N. erebi, Pseudomugil signifer,* juvenile *O. mossambicus,* small juvenile mugilids, and small juvenile *E. hawaiensis*).

When 'critical tidal connection' was excluded from the mCART analysis, another connectivity metric 'stream position' emerged as the primary structuring variable, explaining similar degrees of variability as the initial output featuring critical tidal connection (Fig 4.3b). 'Stream position' is a binary variable referring to whether a pool is (1) the most upstream pool (i.e. a terminal pool) in a sequence of pools, or (2) connects to more upstream pools at higher elevations. 'Stream position' therefore pertains to a similar phenomenon as 'critical tidal connection, relating to upstream position of pools defined by topology rather than elevation. Based on this alternative model output, pools located at the 'terminals' of networks, including the higher elevation pools and two additional pools in Network C (Fig 4.4), harboured a different composition to the rest of the wetland. However, where higher elevation pools had assemblages that were highly distinct from the lower elevation pools (Fig 4.3a), the two additional 'terminal' pools in Network C harboured an intermediate assemblage (Fig 4.3b). This intermediate

assemblage was characterised by high abundances of taxa typical of both higher elevation pools (juvenile *O. mossambicus*, *H. compressa, P. signifer*, small juvenile mugilids, and small juvenile *E. hawaiensis*) and lower elevation pools (including *Acanthopagrus* spp.. and *A. vachelli* (Fig 4.3b)), but also the diminished abundances of other lower elevation taxa (*L. equulus*., *Stolephorus* spp., *H. castelnaui*). It is also worth noting that these terminal pools in Network C are incidentally the two shallowest pools on the wetland (max. depths <60 cm).

Both model outputs displayed similar secondary splits that reflected seasonal dynamics (Fig 4.3a & b). Seasonal assemblage shifts occurred in both more isolated (higher elevation/terminal pools) and better connected pools (lower elevation/mid-stream pools). These shifts were partially caused by the high abundances of the freshwater-spawned *N. erebi* across the whole wetland early in the year (Fig 4.3a & b). In more isolated pools seasonal assemblage shifts were also caused by higher abundances of juvenile *O. mossambicus* during post-wet season months (March-May/June) (Fig 4.3a & b). Meanwhile, in better connected pools seasonal assemblage shifts were also caused by the influx of *Acanthopagrus s*pp., *Stolephorus* spp., *T. hamiltonii* and *H. castelnaui* to the wetland later in the year (September-December). These late-year recruits consistently occupied Network A in higher abundance than Network C, illustrated by the tertiary Network split (Fig 4.3a & b), indicative of finer-scale structuring among better connected pools.

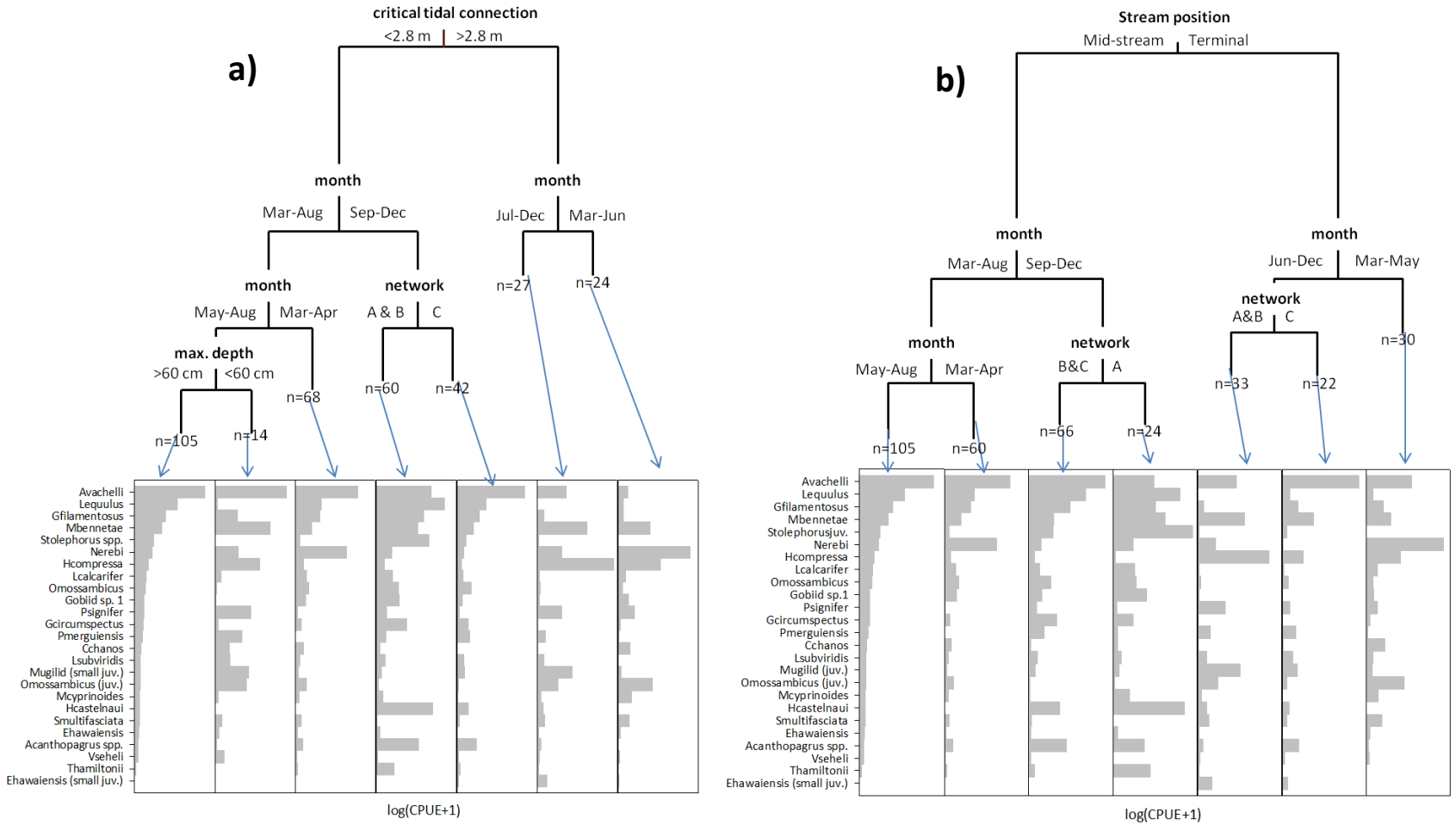

Figure 4.3: mCART of log(CPUE+1) based on (a) explanatory variables (see Table 1) and (b) all explanatory variables except 'critical tidal connection'. Both models explain 20% of the variability in assemblage structure. Factors responsible for splits are indicated in bold above branch points. Codes above branches indicate levels of factors split in each direction. The 'n' number represents the number of pool x month x year cases grouped in each terminal branch. Species profiles below represent the species CPUE's corresponding to each of the terminal branches.

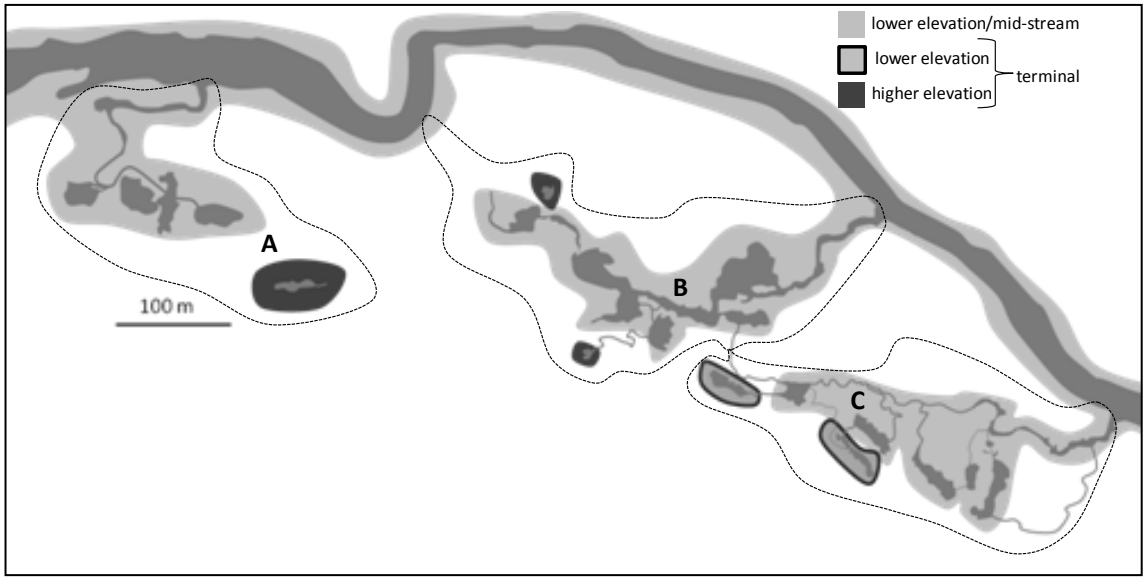

Figure 4.4: Map of the wetland illustrating heterogeneity in fish assemblages, derived from pool groupings in Figs 4.3 a & b. Light grey indicates an assemblage which mirrors that of the estuary channel, including the 'lower elevation pools'. Dark grey indicates a unique 'higher elevation' assemblage, connected to the Ross River at tides >2.8 m. Light grey with black margins indicates an intermediate assemblage occurring in the two shallowest pools (<60 cm max. depth), which also represent the upstream 'terminals' of the C Network. The dark grey pools are also terminal pools in their respective networks. The network boundaries are shown with a dotted black line.

4.4.2 Individual Species distribution

Univariate CART's revealed that distributions of individual species were predominantly structured according to 'critical tidal connection', 'stream position', and 'network' corresponding with overall assemblage patterns. However, some species were distributed independently of assemblage level patterns (Table 4.2).

Megalops cyprinoides primarily responded to 'critical tidal connection' but at a different level to the overall assemblage split. *M. cyprinoides* was more abundant in pools connected by tides >2.4 m (as opposed to >2.8 m), and among these pools was biased towards deeper pools (>85 cm depth).

Two species of gobiid, *G. circumspectus* and gobiid sp. 1, were structured according to unique connectivity metrics. *G. circumspectus* occurred in higher abundance in closely clustered pools (<17 m nearest neighbour), while Gobiid sp. 1 occurred in higher abundance in pools connected to the Ross River over relatively short distances (<210 m), particularly those connecting more frequently (<2.2 m critical tidal connection). *C. chanos* also responded to an alternative connectivity metric, occurring in higher abundances in pools located farther from Ross River (freshwater overbank distance >210 m) during post-wet season and early dry-season months. *P. merguiensis* on the other hand occurred in greatest abundance in pools connected to Ross River by short distances over the tidally flooded salt-marsh surface (tidal overbank distance <150 m).

Other species were also structured at finer scales according to local habitat attributes of pools. Among mid-stream pools where *L. equulus* and *O. mossambicus* were most abundant, they were primarily found over mud or muddy sand, rather than coarser sandy or rubble substrates.

Table 4.2: Results from univariate CART's of log(CPUE+1) of individual species. The explanatory variables responsible for primary and secondary splits in the regression tree are shown, followed by an indication of whether the relationship between the variable and CPUE is positive (+) or negative (-), and in parentheses, the critical level at which the variable splits the population of a species. Where categorical variables were responsible for splits, only the category associated with positive CPUE is shown. Blank cells indicate the absence of splits.

Species	Primary split	Secondary split (+ve branch)	Secondary split (-ve branch)
A. vachelli	critical tidal connection - (2.8 m)	-	-
G. filamentosus	critical tidal connection - (2.8 m)	-	-
M. cyprinoides	critical tidal connection + (2.4 m)	max. depth + (85 cm)	-
H. compressa	terminals	-	year (2011)
L. calcarifer	mid-stream	channel length + (290 m)	-
***O. mossambicus* (adult)**	mid-stream	substrate (mud/muddy sand)	-
L. equulus	mid-stream	substrate (mud/muddy sand)	tidal overbank - (180 m)
mugilid (small juv.)	terminals	month (July-December)	
***O. mossambicus* (juv.)**	terminals	-	-
Gobiid sp. 1	tidal overbank - (210 m)	critical tidal connection - (2.2 m)	-
***Acanthopagrus* spp.**	month (September-December, March)	critical tidal connection - (2.8 m)	-
C. chanos	month (March-July, September)	freshwater overbank distance + (210 m)	-
***E. hawaiensis* (small juv.)**	month (November-December)	terminals	-
H. castelnaui	month (November-December)	network (A & B)	-
M. bennettae	month (June, August-November)	year (2011)	-
N. erebi	month (March-April)	year (2011)	critical tidal connection + (2.68 m)
P. signifer	month (June-October)	network (B) & max. depth (<60 cm)	-
G. circumspectus	neast neighbour - (17m)	month (June, August-December)	-
***Stolephorus* spp.**	Network (A)	critical tidal connection - (>3.1)	-
P. merguiensis	tidal overbank - (150 m)	month (June-Sepetember, December)	-
***E. hawaiensis* (large juv.)**	No viable model		
L. subviridis	No viable model		
S. multifasciata	No viable model		
T. hamiltonii	No viable model		
V. Seheli	No viable model		

4.5 DISCUSSION

Different pools across the salt-marsh system harboured distinctly different assemblages, with a high level of inter-annual consistency in spatial pattern, indicative of deterministic processes. Spatial factors explained considerably more assemblage variability than temporal factors, despite the extensive seasonal changes in assemblage composition characteristic of the system (Ch. 3; Davis et al. 2012). This pronounced spatial variability indicates the operation of key ecological processes at the scale of the wetland system.

Connectivity-based processes took primacy over local processes in regulating these spatial patterns, although two correlated connectivity metrics similarly accounted for pattern. Analyses initially identified 'critical tidal connection' as the primary driver of spatial pattern, with higher elevation pools, connecting to the Ross River only on spring high tides, harbouring a distinct assemblage from the rest of the wetland, which generally connected to the Ross

River on neap high tides. Assemblages in these higher elevation pools were dominated by *H. compressa,* juvenile *O.mossambicus,* small juvenile mugilid*s* and *E. hawaiensis, P. signifer, N. erebi* , and *M. cyprinoides*. This seems to be a 'specialist' tidal pool fauna, not previously recorded in abundance in surveys of the estuary channel. Meanwhile species dominating lower elevation assemblages (*A. vachelli, L. equulus, G. filamentosus, H. castelnaui* and *Stolephorus* spp.,) comprise a subset of typical estuary channel fauna (Robertson & Duke 1990a, Sheaves & Johnston 2009), representing an estuary 'generalist' component.

When 'critical tidal connection' was removed from the analysis an alternative connectivity metric 'stream position' emerged as a key variable. 'Stream position' similarly separated the higher elevation pools from the rest of the wetland, with the addition of the two most upstream (i.e. terminal) pools in Network C, which harboured an intermediate assemblage featuring some 'specialist' taxa and some 'generalist' taxa. This suggests that in the absence of higher elevation pools, certain species aggregate in the most upstream pools of a network. Consequently, major assemblage splits seem to be driven by the tendency of a few taxa to move in a general upstream direction, ascending gradients of elevation. This trend contrasts with models of nestedness typical of topologically similar freshwater systems (Fig 4.5a), which predict patterns of assemblage attenuation along gradients of isolation.

4.5.1 Regional processes

Critical tidal connection effectively describes the elevation of a pool relative to the estuary channel. This relationship modifies the frequency, duration, and depth of tidal connection, and also regimes of physico-chemical condition mediated by tidal connectivity. Such factors are likely to have restricted generalist taxa to lower elevation pools, either because these taxa are either less dispersive, or are limited to the more stable physico-chemical conditions of these pools. Gradients of elevation similarly govern function over temperate salt-marsh systems (Rountree & Able 2007). In these systems subtidal creeks intersecting marshes function like lower elevation pools, harbouring a subset of marine-spawned estuary channel fauna (Kneib 1997). Habitats at higher elevations in Atlantic salt-marsh systems are primarily utilised by a specialist 'resident' component featuring Cyprinodontids and Fundulids. These taxa feed on the marsh surface at high tide and withdraw to nearby marsh depressions at low tide (Rozas & Reed 1993). In a similar way marsh residents *P. signifer* and *H. compressa* actively use the tropical marsh surface (Connolly et al. 1997), advancing with the leading edge of water at high tide (Sheaves, unpublished data), before retreating to the nearest pools and ephemeral depressions as the tide recedes (Morton et al.

1988). This explains their greater abundance in higher elevation and terminal pools in the present study. However, other more 'transient' taxa concentrating in higher elevation pools are probably structured by broader-scale processes.

Greater abundances of other specialist taxa in higher elevation pools appear to be driven by a general proclivity to ascend upstream gradients. This upstream migration may be for the purpose of accessing higher elevation pools as a specific habitat niche, or alternatively to pursue freshwater habitats, aggregating in the upstream limits of the estuary when access to freshwater is denied. It seems reasonable that freshwater species (including *N. erebi* and juvenile *O. mossambicus*) would move in pursuit of lower salinities as conditions become more marine after the wet season, while some marine-spawned taxa (including *M. cyprinoides*, *C. chanos,* and mugilid spp.) are known to move into freshwater reaches to varying extents as young juveniles (Ch. 2, Beumer 1980, Bagarinao 1994, Shen et al. 2009). On the other hand, utilisation of more isolated, upstream parts of the estuary as a specific habitat niche is supported by observations from other studies in tropical and sub-tropical coastal ecosystems. *M. cyprinoides, C. chanos, E. hawaiensis* and mugilid spp. have previously been observed using off-stream tidal pools in the Indo-Pacific region (Russell & Garrett 1983, Davis 1988, Sheaves & Johnston 2008), as well as pools in the upstream tidal reaches of channels (Beumer 1980, Pusey et al. 1998). Moreover, related species (of families Elopidae, Megalopidae, Mugilidae, and Centropomidae) in America's sub-tropics similarly use pools off the main estuary as early nursery habitats (Brockmeyer et al. 1996, Poulakis et al. 2002, Stevens et al. 2007). This is best demonstrated by *Centropomus undecimalis,* which initially recruits to more isolated marsh ponds, moving through to better connected marsh ponds as they mature, before rejoining the main estuary (Stevens et al. 2007). This suggests that the use of supralittoral estuarine habitats as crucial early life-history nurseries could be a common phenomenon across the world's tropics and sub-tropics. Species and life-stages capable of tolerating the more demanding physical environment of these niches may benefit from reduced competition or predation.

The primacy of elevation and low influence of distance-based measures of connectivity (e.g. nearest neighbour, tidal overbank distance, and channel distance) suggests that the function of intertidal estuarine wetlands is largely independent of distance between patches, which can be orders of magnitude greater than those encountered in the present study. This assertion is supported by the similar faunal characteristics of equivalent tidal pools across more expansive systems around the world (Sheaves & Johnston 2008, Stevens et al. 2007, Russell & Garrett 1983). However, despite these overriding trends species-specific

dispersal capabilities, resource requirements, and life-history strategies meant that some species were structured independently of general assemblage patterns in the present study. For instance, the distribution of two species of Gobiidae were best explained by distance-based variables (tidal overbank distance and nearest neighbour), which is possibly due to brood-spawning and small home-ranges common to this family (Ray & Lynda 2001). Similarly, *P. merguiensis* was largely restricted to two pools in close proximity to the estuary channel. While this may represent limited dispersal into the wetland, high abundances of *P. merguiensis* in these pools could equally be a function of the dense mangrove fringes skirting these particualr pools (Sheaves et al. 2012).

Floods which are known to homogenise faunal structure across freshwater floodplain pools (Thomaz et al. 2007, Gomes et al. 2012) did not have pervasive effects over the assemblage in the present study beyond the extensive colonisation of the freshwater-spawned species *N. erebi.* Only one species, *C. chanos,* appeared to respond to freshwater overbank distance, to access more upstream habitats during wet season floods. This suggests that freshwater floods are not as important in structuring assemblages of tidal wetlands, or that tidally-mediated processes rapidly overcome the effects of flooding.

4.5.2 Local processes

Among lower elevation pools, there was evidence of sorting based on local environmental constraints. Frequent tidal connectivity among lower elevation pools provides the freedom for species to continually redistribute relative to preferred conditions (i.e. 'species-sorting'), and also probably allowed species to colonise and persist in pools of sub-optimal habitat condition (i.e. 'mass-effects' (Leibold et al. 2004)) (Fig 4.5b). The biggest split among lower elevation pools was due to certain taxa colonising particular networks in higher abundance during the late dry – pre-wet season. The drivers of this network split are unknown, but may be related to seasonal and spatial changes in food supply, as the taxa responsible for splits are predominantly planktivorous Clupeids and Engraulids (*H. castelnaui, Stolephorus* spp., and *T. hamiltonii*).

Many species appeared to avoid particularly shallow pools (<60 cm max. depth), including *L. equulus, Stolephorus* spp., and *H. castelnaui*, while *M. cyprinoides* was biased towards particularly deep pools (>85 cm max. depth), according with previous observations of habitat selection in tropical rivers (Coates 1987). While these behaviours may be related to factors such as avian predation risk, feeding strategy, and tolerance to thermal fluctuations, the specific drivers are unclear.

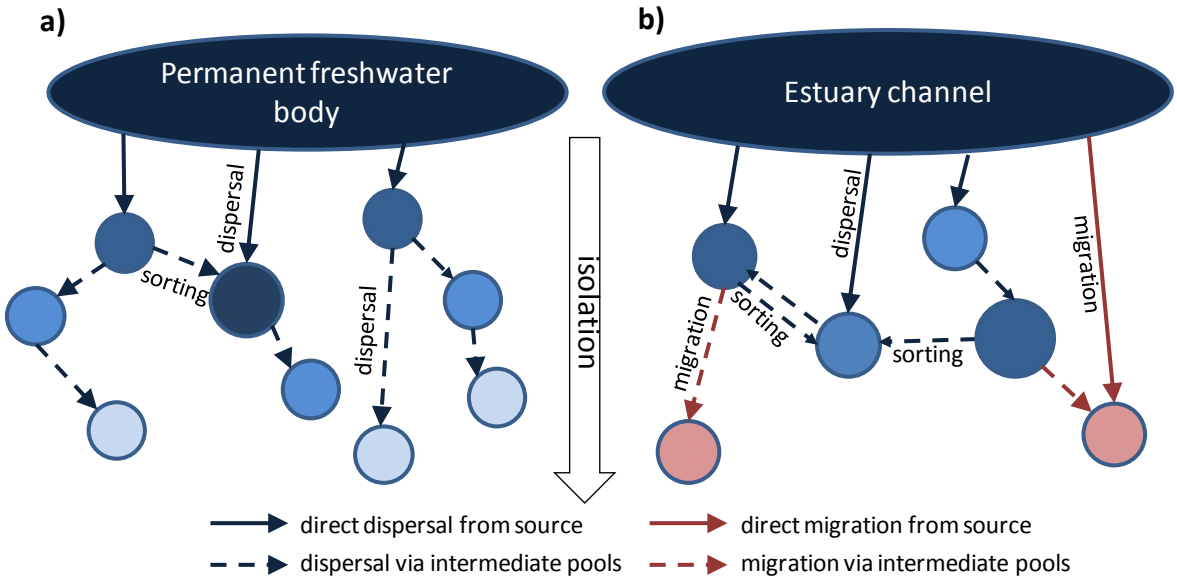

Figure 4.5: Conceptual models illustrating how assemblages are structured in (a) freshwater mainland-island type metacommunities, based on trends reported in the literature (Snodgrass et al. 1996, Taylor 1997, Magnuson et al. 1998) and (b) in tidal systems of similar topological configuration based on results of the present study. In the freshwater system, species and individuals are progressively filtered out along a gradient of isolation, illustrated by progressively lighter shades of blue in circles (patches) further away from the source pool. Assemblages are further modified by local environmental attributes of a patch, illustrated by slightly different shades of blue in patches of similar connectivity. In the tidal system, similar processes structure a 'generalist' estuary channel subset fauna. Generalist taxa are largely limited to more frequently connected pools at lower elevations (blue circles), and progressively filtered out along a gradient of tidal connectivity, with low abundances and species richness in more isolated pools (red circles). Frequent tidal connectivity among the lower elevation pools allows species to redistribute among patches based on favourable habitat attributes (i.e. species-sorting). Additionally, a 'specialist' faunal component appears to make directed upstream migrations along gradients of tidal connectivity to occupy more isolated pools at higher elevations. This results in a unique assemblage within more isolated pools (illustrated by red circles).

Within-pool substrate type may have also been important for some species; *L. equulus* and *O. mossambicus* were rarely found over coarser sand or rubble substrates. A preference for finer substrates has previously been observed for *L. equulus* in Australian tropical estuaries (Johnston & Sheaves 2007). This is a behaviour that may relate to selective foraging for benthic invertebrates, which form a considerable proportion of their diet (Wilson et al. 2001 Hajisamae et al. 2003). On the other hand, the absence of *O. mossambicus* in pools of coarser substrate may not be a response to substrate *per se*, but the avoidance of high flow velocities (Whitfield & Blaber 1979) that engender coarser substrates.

4.5.3 Model performance

Clear and repeatable patterns of spatial assemblage structure emerged despite the final mCART models only explaining 20% of the total variance. This low level of explained variance is not surprising in such a dynamic ecosystem, and is likely due to high levels of stochasticity in the movements of several species among lower elevation pools, which constitute the majority of the wetland. These species may not be limited by connectivity or

environmental conditions at the scale at which these factors vary among the lower elevation pools. Alternatively, I may have overlooked some important explanatory variables, such as dissolved oxygen profiles, pH, avian predation pressure, and the composition of habitats in adjacent reaches of the Ross River, which could have been influential structuring forces.

4.5.3 Tidal pool vs. freshwater metacommunity dynamics

Assemblages in tidal pools were primarily structured according to regional connectivity processes, akin to freshwater systems of similar topology and disturbance regime. However patterns were more complex than simple patterns of nestedness typical of freshwater systems (Fig 4.5b), due to the contrasting responses to hydrological connectivity of two faunal components: an estuary 'generalist' component and a tidal pool 'specialist' component. The generalist component behaved similarly to the freshwater community, with species and individuals filtered out along gradients of isolation, and abundances among pools modified by sorting relative to local environmental conditions (Fig 4.5b). The specialist component however occurred in greater abundance in more isolated higher elevation pools, contradicting expected patterns of nestedness and manifesting in a distinct pattern of metacommunity structure. These differences in metacommunity structure among tidal and freshwater wetlands highlight the dangers of extrapolating patterns and processes among systems.

Distinct patterns in tidal pools are related to their existence as a functional component embedded in a broader coastal seascape, in which fish rely on multiple patch types throughout their life-history (Pittman & McAlpine 2003), as opposed to networks of freshwater lakes and ponds in which a single lake or pond can stage entire fish life-cycles. Different species move among habitats of the coastal seascape in different ways, relative to varying life-histories, behaviours, and niche-breadths (Boström et al. 2011, Pittman & McAlpine 2003). Higher elevation pools seem to represent a unique functional component within the coastal seascape, providing distinct nursery habitat for specialist taxa, rather than an additional patch of available habitat for the estuary channel assemblage.

4.5.4 Conclusions

The clear assemblage distinction among higher and lower elevation pools illustrates how otherwise similar patches of coastal wetland habitat may perform very different functions due to their position in the landscape, supporting different species and life-stages. This highlights the need to incorporate understandings of spatial ecology into coastal management,

conservation, and restoration strategies. For instance, when selecting zones for conservation and offsetting purposes, rather than simply considering local site factors (such as areal extent or vegetation density) as a proxy for habitat value, managers also need to consider the spatial context of patches relative to movement behaviours and life-history requirements of subject species.

Ultimately, a holistic understanding of community structure and function in coastal wetlands requires recognition of the interplay of processes operating at multiple scales. The seasonal variation in recruit availability inherent in coastal systems modifies the source pool of colonists through the year (Ch. 3). The structural and hydrological connectivity between the source of colonists and patches, and among patches themselves, then determines the spatial distribution of taxa across a wetland system. The relative abundances of taxa across the wetland system are further modified by suitability of local patch conditions. Consequently, understanding how spatial arrangement and hydrological connectivity between patches (and between patches and sources) supports both the secondary production of a wetland system (e.g. McNeill & Fairweather 1993) and the active selection of particular patches by certain species or life stages, is central to maintaining crucial ecosystem function.

Chapter 5 *This chapter has been published in MEPS*

Bottom-up control modifies patterns of fish connectivity and assemblage structure in coastal wetlands

5.1 ABSTRACT

In this chapter I examined the potential for patterns in invertebrate prey distribution to act as a key driver of fish distribution across a coastal wetland system. Seascape and metacommunity approaches recognise that faunal assemblages in coastal and freshwater systems are structured by responses to multi-scale connectivity and local environmental conditions. However, we currently have a poor understanding of how different groups of aquatic organisms affect each other's distribution. Most fish in freshwater and coastal wetland systems feed predominantly on benthic invertebrates and zooplankton. To investigate the extent to which these invertebrate taxa exert control over fish distribution, fish, benthic invertebrate and zooplankton assemblages were sampled across 13 inter-connected pools on a salt-marsh in North Queensland, Australia. There were strong and inter-annually consistent spatial concordances among the three faunal components, characterised by higher densities of benthic invertebrates and zooplankton in pools at lower elevations on the salt-marsh - reflected by high densities of planktivorous and benthivorous fish, and lower densities of benthic invertebrates and zooplankton in pools at higher elevations - reflected by dominance of fish species trophically de-coupled from these taxa (detritivores, insectivores, and herbivores). Further supporting the idea of trophic linkages, the two most invertebrate-rich pools also harboured the greatest densities of benthivorous and zooplanktivorous fish, which in turn attracted the wetland piscivores, *Lates calcarifer* and *Megalops cyprinoides*. This is indicative of bottom-up forcing acting across three trophic levels, a process that is likely facilitated by the frequent tidal connections among pools, which allows for regular redistribution of fish. Prey availability should be considered as a key component of the spatial ecology processes that shape fish assemblages across coastal and freshwater wetland systems.

5.2 INTRODUCTION

Fish distributions and connectivities across patches of habitat (e.g. stream reaches, pools, lakes, seagrass patches, mangrove stands) embedded in wetland landscapes (e.g. river basins, floodplains, salt-marshes, sandy substrate) are often analysed in a metapopulation framework, recognising that populations within patches are not closed, but linked by dispersal. Metapopulation approaches examine the interplay of local patch processes (such as fish preference for local environmental conditions) and regional landscape processes (such as movement among patches) in structuring populations across wetland systems. This multi-scale perspective improves understanding of connectivity criteria necessary to sustain species' populations, and highlights patches of key conservation value (Hanski & Thomas 1994, Hanski 1999), providing essential knowledge in the face of accelerated rates of landscape fragmentation (Morita & Yamamoto 2002, Valentine-Rose et al. 2007). However, metapopulation approaches do not explicitly consider the influence of biological interactions, which can be important in structuring fish distributions across a landscape (Tonn 1990, Snodgrass et al. 1996, Tejerina-Garro et al. 1998).

Emerging 'metacommunity' approaches have begun to incorporate species interactions into metapopulation models to better represent processes driving organism distributions (Cottenie et al. 2003, Leibold et al. 2004). In these models, biological interactions are perceived as local-scale processes that modify communities within patches (Shurin 2001, Cottenie et al. 2003, Brown et al. 2011, Warfe et al. 2013). However, classic theories predicting species' distributions (e.g. ideal free distribution, optimal foraging theory) suggest that interactions among species, particularly predator-prey relationships, will also influence patch selection by an individual. Consequently, if inter-patch hydrological connectivity is sufficient to allow species to redistribute based on abiotic and biotic preferences (Leibold et al. 2004, Grober-Dunsmore et al. 2009), then prey availability is likely to be a key determinant of fish distribution patterns.

Most species of fish feed primarily on benthic or zooplanktonic invertebrates (Parrish 1989, Vadeboncoeur et al. 2002, Zagars et al. 2013). However, very few studies have explored the relationship between the spatial dynamics of fish and invertebrate prey at the scale of a wetland system, in either freshwater or marine settings (Grober-Dunsmore et al. 2009). Studies that have observed parallel dynamics of fish and invertebrates in freshwater systems have generally been confounded by scale, linking distributions across broad spatial scales (e.g. among separate river systems, drainage networks, or distant lakes) that far exceed fish dispersal capabilities (Tonn 1990, Heino 2002, Beisner et al. 2006, De Bie et al. 2012), and

provide limited opportunity to identify patch selection processes. On the other hand, in open estuary and coastal seascape systems, oscillating priorities for feeding and refuge drive frequent tidal movements between patches and habitat types. Therefore feeding grounds may only constitute a small proportion of a fish's home-range (Pittman & McAlpine 2003, Sheaves 2009) making it difficult to isolate and quantify the structuring influence of prey availability (Grober-Dunsmore et al. 2009). Top-down influences however have been observed to exert control on the distribution of juvenile blue crabs (*Callinectes sapldus*) and bay scallops (*Argopecten irradians*) in US seagrass systems (Hovel & Regan 2008), where predation pressure is modified by structural landscape attributes and levels of fragmentation (Hovel & Lipcius 2001, Hovel & Fonseca 2005, Irlandi et al. 1995).

Networks of tidal pools scattered across tropical transitional wetlands however, provide a tractable system where the balance between hydrological connectivity and discreteness of patches is ideal for examining bottom-up control influences. Tidal pools exist as an array of semi-enclosed study units, where predator and prey distributions can be representatively sampled and reliably compared. Relatively frequent tidal connections to the estuary channel and among pools (generally connecting during most daily tidal cycles) provide potential for faunal populations to access each pool, and facilitate redistribution relative to preferred conditions. Moreover, samples of community structure from different years can be considered independent, as pool fauna is annually reset by two main processes: (1) ontogenetic migrations of fish from the salt-marsh system results in residence times of <1 year (Davis et al. 2012), and (2) periodic wet season floods flush many species of fish (Davis et al. 2012) and benthic invertebrates (Janine Sheaves pers. comm.) from the system. Independent replication is a feature lacking in previous empirical studies of metacommunity dynamics (Logue et al. 2011), but is key to identifying repeatable pattern and deterministic processes.

To examine the extent to which patterns of fish assemblage structure and realised connectivity across a wetland system (i.e. the patterns described in Ch. 4) are driven by predator-prey interactions, the parallel distributions of fish, benthic invertebrates, and zooplankton were compared across 13 tidal pools scattered across a North Queensland salt-marsh (Annandale Wetland). If prey availability exerts considerable control over fish distribution, I expected to find spatial concordances between benthivorous fish and benthic invertebrates, and planktivorous fish and zooplankton taxa, respectively. The study was conducted over 2 annual cycles during the pre-wet season month of October, to allow invertebrate communities maximum time to re-colonise following freshwater flushing.

5.3 METHODS

5.3.1 Study site

The study was conducted in Annandale Wetland (Fig 5.1; the main details of the study site are given in Chapter 2).

Extensive floods which blanket the wetland during wet-season months (January-March) prompt extensive faunal shifts, resetting fish assemblages (Ch. 3), exterminating the majority of benthic invertebrate taxa (Janine Sheaves pers. comm.), and flushing zooplankton from the system (Kay 2009). Following floods, re-colonisation of pools primarily relies on multi-faceted tidal connections to the Ross River (described in Ch. 4), which acts as a regional source of colonists (Ch. 3). Subsequent exchange of individuals among pools is also likely to modify pool fauna's to some extent. Although critical tidal connection was identified as the key driver of fish assemblage structure in Chapter 4, different facets of tidal connections (such as frequency, duration, depth and distance of connection) may variously affect distributions of the different faunal groups. Therefore, a range of connectivity metrics were included as explanatory variables in this study, to examine for correlation with biological patterns, along with pool morphology and physico-chemical variables (Table 5.1).

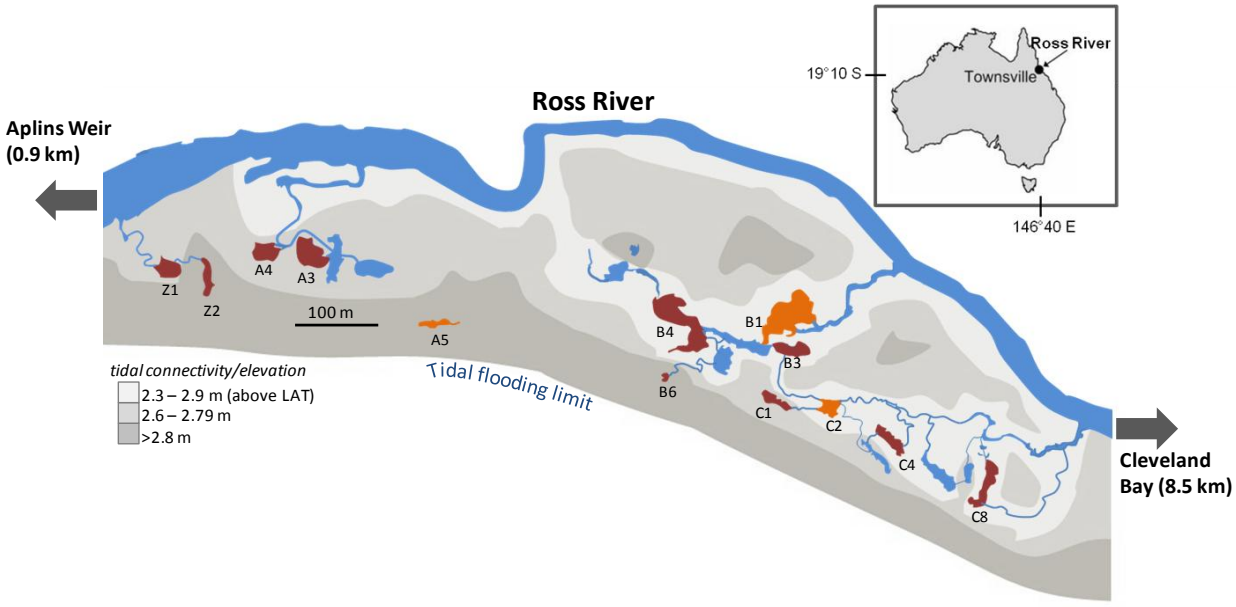

Figure 5.1: Annandale Wetland containing the 22 wetland pools adjacent to the Ross River, Australia. Pools can be loosely decomposed into four groups (Z,A,B,C), based on topographic basins they are set within, and the different arterial channels that connect groups of pools to the Ross River. Pools which were sampled in both 2010 and 2011 are shaded in red, whilst those sampled only in 2011 are shaded orange. The sampled pools were assigned unique alpha-numeric codes to discern between them in analyses. The wetland extends from the subtidal channel of the Ross River, south to the uppermost tidal limits (highest astronomical tide =~4 m). Different shades of grey illustrate the range of tidal heights at which different areas of the wetland are tidally inundated, and pools within them connected. This is essentially a function of elevation differences. Flooding patterns were determined by the deployment of a series of pressure loggers, the data from which were cross-referenced against parallel realised tide data (courtesy of the Townsville Port Authority). LAT = lowest astronomical tide.

Table 5.1: Environmental variables used in the BIO-ENV and CART procedures, to test for correlation with benthic invertebrate, fish, and zooplankton distribution data.

	Variable	Description	Units	Method
Physico-chemical	Salinity	-	ppt	Portable refractometer
	Temperature	-	degrees Celsius	Thermometer
	Visibility	-	cm	Secchi disc
Pool morphology	Substrate class	Dominant substrate type/s	Ranked: 1. silt, 2.mud, 3. mud/sand, 4. sand, 5. rubble	Visual survey
	Maximum depth	Low tide maximum depth of a pool	cm	Measuring staff
	Surface area	Low tide surface area of a pool	m^2	GIS
Connectivity	Critical tidal connection (CTC)	Minimum tidal height required for a pool to receive aquatic connection to the Ross River	cm above lowest astronomical tide (LAT)	Pool depths were continuously logged over a tidal sequence. Depth fluctuations were plotted against realised tide data (courtesy of Townsville Port Authority). The lowest high tide peak at which pool depth rose was taken as the critical tidal connection, accounting for lag between time of realised tide peak and time of high water in Annandale Wetland.
	Channel distance (CD)	Shortest path from Ross River to a pool via channelised connections. Channels were defined as water courses connecting pools to the Ross River or other pools. For two pools this included water courses running over vegetated salt-marsh.	m	GIS
	Tidal overbank distance (TOD)	Shortest path from Ross River to a pool through tidally inundated salt-marsh surface	m	GIS + ground truthing
	Pool order (PO)	The number of intermediate pools separating a pool from the Ross River	number of pools	GIS
	Nearest neighbour (NN)	Distance to nearest pool via channel or over tidally inundated salt-marsh surface	m	GIS

5.3.2 Data collection

Benthic invertebrate, zooplankton, and fish densities (measured as catch-per-unit effort (CPUE)) were sampled in October 2010 in a subset of 10 pools encompassing a representative cross-section of connectivities, and again in October 2011 with the addition of 3 more pools to boost the sample size and strengthen analyses. Pre-wet season sampling ensured that invertebrate taxa had the maximum opportunity to re-establish on the wetland following the deleterious impacts of wet season floods (Janine Sheaves pers. comm.). Pools were sampled at the bottom quarter of the tidal cycle (i.e. around low tide) during the new moon period.

Fish sampling

Details of sampling as per Chapter 4.

Benthic invertebrate and zooplankton sampling

Benthic invertebrates and zooplankton were simultaneously sampled using a manual rope-pulled epibenthic sledge, based on Hessler and Sander's (1967) design (50 x 50 cm mouth opening with a 200 um mesh size). Three replicate 4 m long sledge trawls were taken at each pool, stratifying for pool areas or any variation in substrate type. When the sledge was positioned, care was taken to avoid disturbing the sampling area by the operator walking in an arc around the intended path of the sledge prior to commencing sledge towing. The content of the catch-box was preserved in 4% phosphate buffered formaldehyde for laboratory identification. Specimens were identified under microscope to the lowest practical taxon and quantified. The density of a taxon in a pool was measured as the average count across the three trawls. Since the study focuses on the structuring potential of invertebrates as a food-source for fish, it was considered practical to resolve invertebrate taxa to levels identified as prey items in fish dietary studies. Dietary studies generally do not resolve invertebrate prey types beyond family level, and resort to order and class in some circumstances (Wilson & Sheaves 2001, Baker & Sheaves 2005).

5.3.3 Data analysis

Species which were present in <25% of samples were excluded from analysis to remove undue influence of rare species, as multiple zero's in the data matrix can 'swamp' the analysis, presenting a danger of absences driving model outputs. Faunal CPUE data were log(x+1) transformed to down-weight the influence of very common species (allowing less

common species some influence on analytical outcomes and reducing the influence of extreme observations) (Clarke 1993).

Patterns of distribution were initially analysed separately for each faunal group, and then compared across groups to assess the extent of concordance. Since samples from 2010 and 2011 were independent, distributions were analysed separately. This enabled assessment of the extent of consistency in distribution pattern, and by extension the level of determinism of observed trends.

Zooplankton consisted almost exclusively of the calanoid copepod *Acartia sinjiensis*, so distributions were analysed with univariate classification and regression trees (CARTs), using log(CPUE+1) as the response variable, and pool codes (Fig 5.1) as the explanatory variable. Univariate CARTs operate by successively splitting data into increasingly homogenous groups based on the specified explanatory variables, by minimising residual sums of squares within a group at each split (De'ath & Fabricius 2000). This technique is a robust non-parametric means for analysing relationships where assumptions of conventional linear approaches may be compromised (Breiman et al. 1984). Selection of the final tree model (i.e. determining where to reliably stop splitting data) was conducted using 10-fold cross-validation, selecting the smallest tree within 1 SE of the minimum cross validation error. This is a standard protocol for selecting robust, biologically meaningful trees (Breiman et al. 1984, De'ath & Fabricius 2000). To help explain patterns of distribution the procedure was repeated, replacing pool codes with a suite of environmental variables (Table 5.1).

Benthic invertebrate and fish distributions were analysed using non-metric multidimensional scaling (nMDS) of log(CPUE+1) data, based on Bray-Curtis dissimilarities. Information on the taxa most highly correlated with the configuration of pools in the MDS was displayed by superimposing vectors indicating direction of increasing density onto the ordination biplot. The direction of these vectors was determined by regressing each taxa onto the nMDS space, and vector length was scaled to reflect the strengths of correlation (R value). Only species most highly correlated with the nMDS space ($R > 0.6$) were plotted.

Relationships between distributions of fish/benthic invertebrates and environmental variables were tested using the BIO-ENV procedure in PRIMER, which calculates the combination of environmental variables that best explains patterns in the biological data. BIO-ENV works by generating Euclidean dissimilarity matrices from various combinations of environmental variables, and identifying the subset that maximises Spearman's rank correlation with the biological Bray-Curtis dissimilarity matrix (Clarke & Warwick 1994). For the fish analysis, zooplankton and benthic invertebrate densities were included as additional

environmental variables to assess the extent to which fish assemblage structure could be explained by prey distribution. The combination of variables that best accounted for biological patterns were regressed onto the fish and benthic invertebrate nMDS ordination space and plotted as vectors (in a similar way to the taxa vectors), to assess the strength and direction of relationship between these key environmental variables and distribution patterns.

Patterns of distribution were qualitatively compared across the three faunal groups to assess the degree of concordance in spatial pattern (i.e. whether fish distribution reflected benthic invertebrate and/or zooplankton distribution). Relationships between benthic invertebrate and fish distributions were further explored using the RELATE routine in PRIMER, which is essentially a MANTEL test that calculates the Spearman's rank correlation (ρ) between two similarity matrices (Clarke & Warwick 1994). The drivers of concordances/disparities were then interpreted by examining the key environmental variables that related to distributions of each faunal group.

This combination of qualitative comparison and quantitative examination of environmental/biological drivers was deemed the most effective and reliable means of assessing possible bottom-up control effects. Simply using BIO-ENV (or other techniques that correlate biological pattern with environmental variables and prey data) to explain fish assemblage structure may mask such effects; if all faunal groups co-vary relative to the same environmental variable, there is a danger that this variable may obscure meaningful relationships between faunal groups.

5.4 RESULTS

There were strong concordances in patterns of spatial distribution across the three faunal components (zooplankton, benthic invertebrates, and fish), that were consistent between 2010 and 2011 samples. This was largely characterised by a binary split in faunal characteristics of pools that cut across all three taxonomic groups. In both years, pool Z2 and B6 (and pool A5 which was only sampled in 2011) had consistently lower densities of zooplankton (Fig 5.2) and benthic invertebrate taxa (Fig 5.3) than the majority of pools. These patterns were mirrored by distinct splits in fish assemblage structure (Fig 5.4) (RELATE test between benthic invertebrate and fish nMDS ordinations: ρ = 0.75 and 0.35 for 2010 and 2011 respectively). Pool Z2, B6, and A5 were characterised by greater densities of species that are predominantly detritivorous, herbivorous, and insectivorous (Table 5.2), including: *Hypseleotris compressa, Pseudomugil signifer,* small juvenile mugilid spp., and small juvenile *Selenotoca multifasciata* (Fig 5.4), while the rest of the pools were generally characterised by

greater densities of species that are predominantly planktivorous and benthivorous, including: *Leiognathus equulus, Stolephorus* spp., *Herklotsichthys castelnaui, Gerres filamentosus,* and *Acanthopagrus* spp..

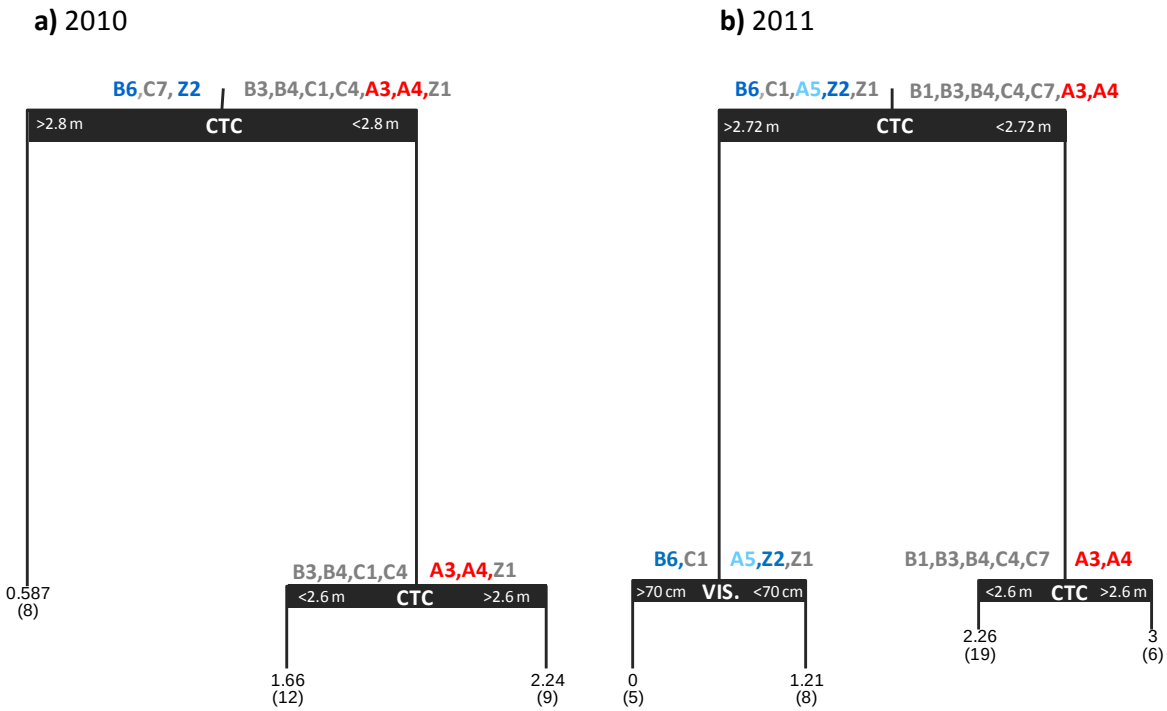

Figure 5.2: Univariate classification and regression trees displaying the distribution of zooplankton (calanoid copepods) in (a) 2010, and (b) 2011, based on log(CPUE+1) data. Mean CPUE and sample sizes (in parentheses) are displayed at each terminal node. Pool groupings have been displayed either side of splits. Pools characterised by consistent high densities are coloured red, and those with consistently low abundances are coloured blue. The pale blue pool code (A5) represents a pool with low densities that was only sampled in 2011. The environmental variables that best explained these splits are indicated in black bars, along with the levels of these variables split in either direction. This information was obtained by re-running the analysis, replacing pool codes with the suite of environmental variables (Table 1). The structure of the tree output remained the same, suggesting that environmental variables successfully accounted for patterns. CTC = critical tidal connection; VIS. = visibility.

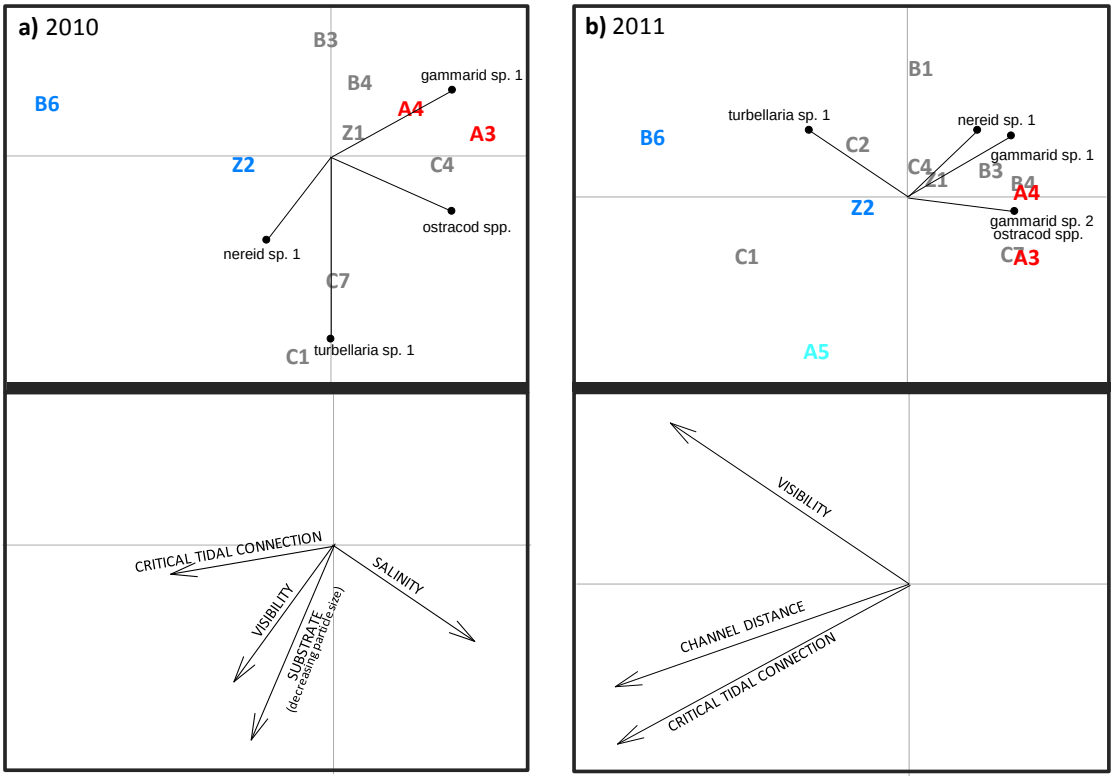

Figure 5.3: Non-metric multidimensional scaling (nMDS) ordination, using Bray-Curtis dissimilarities on log(CPUE + 1) benthic invertebrate assemblage data in 2010 and 2011. Vectors radiating from the intersection of axes relate to taxa densities most highly correlated with the ordination space. Vectors indicate the direction of greatest increase in density, with length proportional to the strength of correlation with the ordination. Red pool codes indicate pools with consistently high densities of benthic invertebrates and blue pool codes indicate pools with consistently low densities of benthic invertebrates. The pale blue pool code (A5) represents a pool with low benthic invertebrate densities that was only sampled in 2011. The combination of environmental variables that best correlated with these data (as identified through the BIO-ENV procedure) are displayed as vectors regressed onto the MDS ordination space, shown on a separate complementary panel. These vectors can be interpreted in similar ways to the taxon vectors.

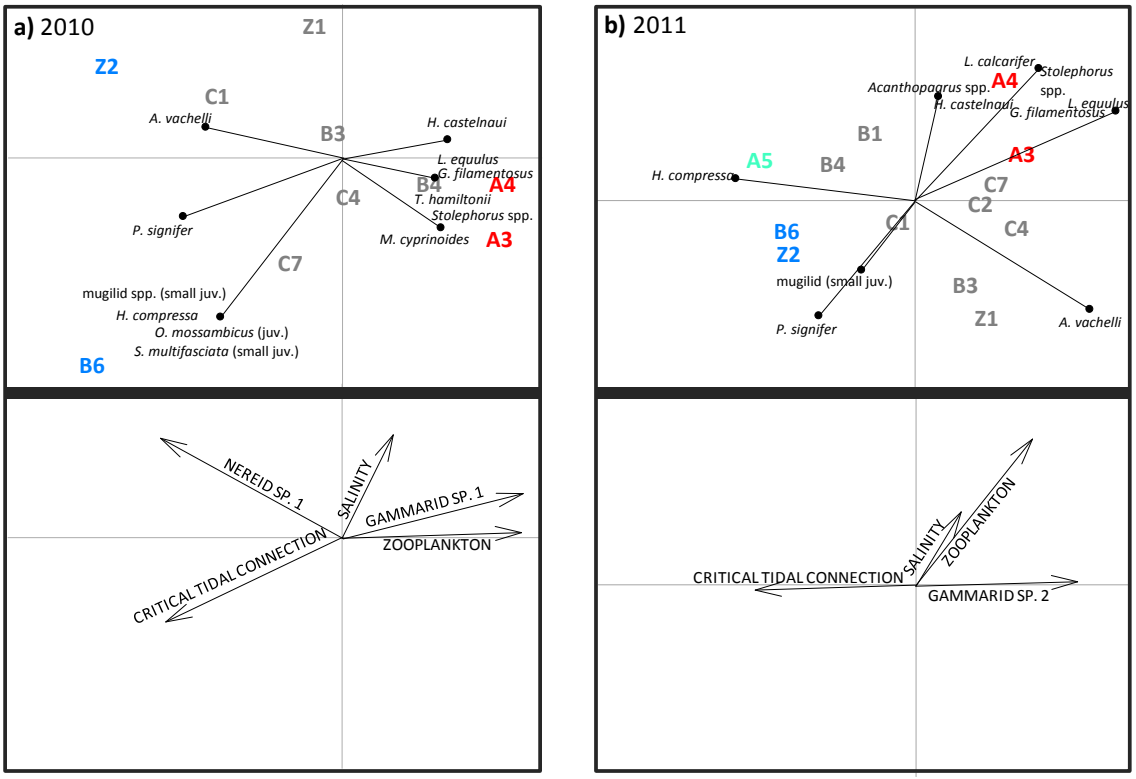

Figure 5.4: nMDS ordination, using Bray-Curtis dissimilarities on log(CPUE+1) fish assemblage data in 2010 and 2011. See Fig 5.3 for further explanation.

Table 5.2: Trophic function of abundant fish taxa in Annandale Wetland (b=benthivore; i=insectivore; zp=zooplanktivore; d=detritivore; p=piscivore; h=herbivore). These categorisations reflect the dominant food types of these taxa at similar developmental stages to those caught in the study, derived from the best available information in the literature.

Taxa	Trophic group	Source
Gerres filamentosus	b/i	(Wilson et al. 2001, Sheaves et al. 2006)
Leiognathus equulus	b/zp	(Staunton-Smith 2001, Wilson et al. 2001, Abrantes & Sheaves 2009)
***Stolephorus* spp.**	zp	(Hajisamae et al. 2003)
Thryssa hamiltonii	zp/b	(Zagars et al. 2013)
Oreochromis mossambicus	d/h/p	(Doupé & Knott 2010)
Ambassis vachelli	zp	(Zagars et al. 2012)
Lates calcarifer	P	(Davis 1985, Sheaves et al. 2006)
mugilid spp.	d	(Eggold & Motta 1992, Sheaves et al. 2006)
Pseudomugil signifer	i	(Booth et al. 1985, Morton et al. 1988, Platell & Freewater 2009, Pusey et al. 2004)
Hypseleotris compressa	i	(Maddern & Gill 2007, Pusey et al. 2004)
Selenotoca multifasciata	h	(Lee et al. 1993)
Megalops cyprinoides	p/i	(Coates 1987)

BIO-ENV (for benthic invertebrates and fish) and CART (for zooplankton) analyses identified 'critical tidal connection' as the key environmental variable explaining this common axis of variability. Critical tidal connection explained the primary split in zooplankton distribution in both years, and also correlated with benthic invertebrate and fish distributions better than any other single variable (Table 5.3). Loading vectors on the benthic invertebrate and fish nMDS ordinations illustrate how 'critical tidal connection' strongly correlates with the split between Z2, B6, and A5 and other pools on the wetland (Fig 5.3 & 5.4). 'Critical tidal connection' refers to the minimum tidal height required to connect a pool to the Ross River, and is essentially a function of the position of a pool along an elevation gradient from the Ross River to the aquatic-terrestrial ecotone. Pool Z2, B6, and A5 are higher elevation pools connecting to the Ross River on tides >2.8 m, which represent medium to large spring high tides (Fig 5.1). Meanwhile other pools on the wetland are at lower elevations, connecting more regularly, during medium to large neap high tides.

Table 5.3: Results of BIO-ENV analyses. The environmental variables that in combination best correlated with the biological data are marked with an 'x', and the single most important variable in the correlation is marked 'X'. Spearman's Rank correlation coefficients (ρ) are given for the best combination and the single best variable. CTC = critical tidal connection; CD = channel distance; ZP =zooplankton.

Faunal group	year	combination (ρ)	single (ρ)	CTC	substrate	salinity	visibility	CD	ZP	gamm. sp. 1	gamm. sp. 2	nereid sp. 1
Benthic invertebrates	2010	0.61	0.43	X	x	x	x					
	2011	0.51	0.43	X			x	x				
Fish	2010	0.83	0.73	x		x			x	X		x
	2011	0.48	0.38	X		x			x		x	

Concordances were not just limited to the higher elevation vs. lower elevation split, but among the lower elevation pools there were consistent productivity hotspots. Two pools (A3 and A4) connecting to the Ross River on larger neap tides (between 2.6m and 2.7 m tides; i.e. at intermediate elevations on the wetland (Fig 5.1)), consistently harboured the greatest densities of zooplankton (Fig 5.2). In the benthic invertebrate and fish ordination plots, these same pools were consistently grouped together opposite high-elevation pools (Fig 5.3 & 5.4). This signifies that A3 and A4 also had the highest densities of dominant benthic invertebrate taxa (gammarid amphipods and ostracods), and also benthivorous and planktivorous fish taxa (*Stolephorus* spp.*, H. castelnaui, L. equulus, G. filamentosus,* and *Thryssa hamiltonii*) (Table 5.2). Additionally, these two pools consistently harboured the highest densities of the piscivorous fish, *Lates calcarifer,* and also the highest densities of the piscivore *Megalops cyprinoides* (Table 5.2) in 2010 (Fig 5.4). Environmental loading vectors indicate that for benthic invertebrates these patterns were consistently explained by low visibilities in A3 and A4 (Fig 5.3), whereas for fish these patterns were consistently explained by the high zooplankton and gammarid amphipod densities in these pools (Fig 5.4).

5.5 DISCUSSION

There were consistent concordances in the distribution of zooplankton, benthic invertebrates, and fish across the wetland system. This was primarily characterised by a binary split in distribution pattern across all three groups that related to variations in the level of tidal connectivity. In both years benthic invertebrates and zooplankton were more abundant in pools at lower elevations, which connect to the estuary channel on medium to large neap high tides, and less abundant in pools at higher elevations, which only connect on large spring high tides. These spatial patterns in invertebrate distribution were mirrored by distinct patterns in fish assemblage structure; lower elevation pools were characterised by greater densities of benthivorous and planktivorous fish (including *Stolephorus* spp.*, H. castelnaui, L. equulus, G. filamentosus,* and *T. hamiltonii*), whereas higher elevation pools were characterised by greater densities of fish species trophically decoupled from benthic invertebrates and zooplankton, instead comprising species that predominantly feed on detritus, insects, or algae (including *H. compressa, P. signifer, S. multifasciata,* mugilid spp., and *O. mossambicus*).

It is unclear whether these concordances reflect biological interactions among faunal groups or simply parallel responses to gradients of elevation/tidal connectivity. If the faunal groups are structured independently of one another, one would expect distribution patterns to vary among groups, due to vastly different life-history characteristics and dispersal modes

(De Bie et al. 2012). However, concordances would still arise if each faunal group was constrained by a different mechanism relating to the elevation gradient. For instance, zooplankton and benthic invertebrates rely on passive transport via water flows to traverse the landscape, and may be limited by the lower frequency and duration of connection to higher elevation pools. Meanwhile, decreasing depths of connection along the elevation gradient may limit the majority of fish species (including benthivores and planktivores) to lower elevation pools (Thomas & Connolly 2001, Bretsch & Allen 2006, Hohausová et al. 2010). Perhaps only a limited number of fish species are capable of accessing the higher elevation pools, and these species demonstrate adaptations to subsist on the alternative food sources there (i.e. detritus, insects, and algae) (Fig 5.5b). However, the possibility remains that benthivores and planktivores are also physically capable of accessing the higher elevation pools, but choose to remain in pools at lower elevations due to higher prey availabilities. This hypothesis could be tested through the manipulation of prey populations in pools at various elevations.

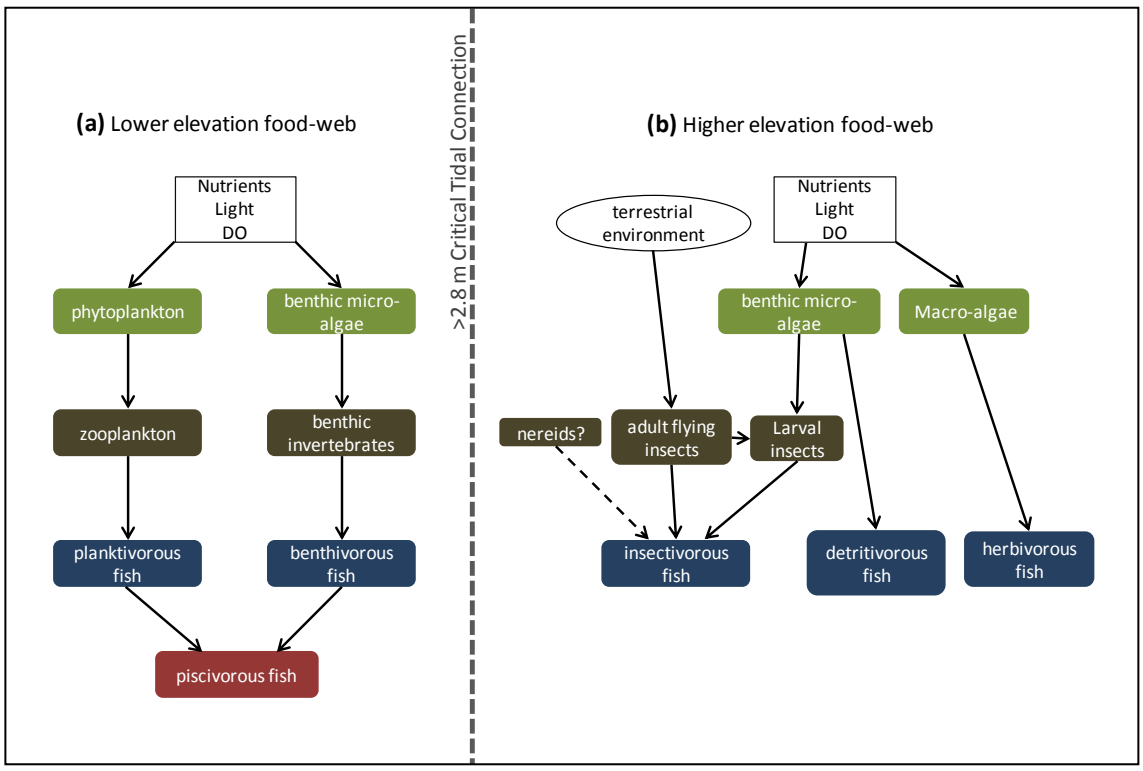

Figure 5.5: Likely food-webs underpinning patterns of community assembly in (a) lower elevation pools, and (b) higher elevation pools. While the majority of benthic invertebrate taxa were rare in higher elevation pools, nereid sp. 1 occurred in relatively high densities in higher elevation pools in 2010 (Fig 5.3). Nereids have therefore been included as a tentative component of the higher elevation food-web, that perhaps subsidise the diet of fish species that are predominantly insectivorous (e.g. *P. signifer*).

Among the lower elevation pools there was another layer of concordance that provided more convincing evidence of bottom-up control effects. Two pools with particularly high densities of benthic invertebrates and zooplankton consistently harboured the greatest densities of benthivorous and planktivorous fish, and also the highest densities of common wetland piscivores, *L. calcarifer* and *M. cyprinoides*. This seems to represent a chain of bottom-up assembly spanning three trophic levels (primary consumer - secondary consumer - tertiary consumer). One can likely extrapolate beyond this to infer that primary productivity in the form of phytoplankton and benthic micro-algae was greatest in these pools (Fig 5.5a), stimulating the settlement and propagation of benthic invertebrates and zooplankton, and in turn attracting secondary and tertiary consumers. The frequent tidal connectivity among lower elevation pools, and between lower elevation pools and the estuary channel, would seem to underpin this process by facilitating regular redistribution of fish relative to preferred conditions and resource requirements. The idea that individuals actively select and remain in pools of favourable condition is partially supported by patterns of *L. calcarifer* movement and pool fidelity, inferred from a tag-recapture study in Annandale Wetland (Appendix D).

Similar bottom-up control processes are also likely to influence patterns of movement and distribution across more open parts of the estuary and coastal seascape. For instance, McIvor and Odum (1998) suggested that salt-marsh fish preferentially use shallow depositional banks at low tide rather than steep erosional banks, due to higher availabilities of benthic invertebrates. Additionally, there is evidence that in some instances bottom-up control processes may override habitat preferences in coastal systems. For example, King George whiting (*Sillaginodes punctata*) in South Australia are typically associated with seagrass beds during early juvenile stages (Bell & Pollard 1989), but at some sites are more abundant over adjacent bare substrates where there are higher densities of meiofaunal food sources (Connolly 1994, Jenkins et al. 1997). Similarly, while Atlantic cod (*Gadus morhua*) are typically confined to waters of 0-5 degrees Celsius, during periods of high prey (capelin *Mallotus villosus*) abundances, they move outside this temperature range to frequent areas where prey are aggegated (Rose & Leggett 1989).

This complexity means that attempting to understand fish distributions based on correlations with landscape structure and physical habitat characteristics alone is unlikely to be successful (Harris & Heathwaite 2012). Biological interactions could obscure or even decouple such species-environment relationships, generating substantial noise. Moreover, by failing to consider prey distribution there is a danger of attributing patterns to irrelevant mechanisms, based on spurious correlations with factors that may covary with prey

availability. For instance, where distributions of fish across coastal landscapes may have previously been attributed to species-specific dispersal capabilities and habitat preferences, it is possible that fish may have actually been indirectly responding to the influence of these factors on their prey sources.

This study also demonstrates how biological interactions are a key component of metapopulation and metacommunity processes. Hydrological and structural connectivity among patches will only result in meaningful realised connectivity (i.e. fish dispersal and colonisation) if both biotic and abiotic conditions are suitable in the destination patch. For instance, in the present study it is likely that fish made forays in to pools during high-tide connections, but did not remain as biological conditions (prey availabilities) were not suitable to sustain them. Equally, in some circumstances fish may avoid patches with high predator densities (Sogard & Olla 1993, Jordan et al. 1997), or patchy distribution of predators may impose asymmetric mortality rates over the landscape (Townsend & Crowl 1991, Rodriguez & Lewis 1997). However, without information on spatio-temporal distribution across trophic levels, such mechanisms cannot be interpreted.

It is clear that spatial ecology studies in coastal and freshwater systems would greatly benefit from conceptualising fish distribution and connectivity within an ecosystem framework, explicitly recognising how different trophic levels may interactively affect each other's distribution. However, incorporating this information into empirical studies is likely to be arduous and require integration of knowledge across disciplines, including input from spatial, food-web, fisheries, and invertebrate ecologists.

Chapter 6 – General Discussion

Developing a holistic understanding of faunal pattern in tropical estuaries

6.1 HIERARCHY OF PROCESSES

The components of this thesis demonstrate how key processes operating over multiple spatial, temporal, and organisational scales structure local nekton communities in tropical estuarine wetlands. Each chapter focuses on a level of process operating at a characteristic spatio-temporal domain, and highlights key sources of spatial, temporal, and taxonomic variability in faunal pattern (represented by different boxes in Figure 6.1). Traditionally, ecological studies in estuaries and coastal systems have addressed these phenomena at single scales in isolation (with a particular bias towards finer-scale phenomena occurring at the site-level; Ch. 1), leading to fragmentary notions of ecosystem function, with poor predictive capacity (Harris & Heathwaite 2012, Nagelkerken et al. 2013). However, integrating multi-scale understandings of pattern and process into a single model can offer improved insight into the faunal dynamic of these complex systems.

Placing the mechanistic understandings emerging from each chapter into a broader ecological context, spanning the spectrum of scales relevant to the life-histories of coastal fish (i.e. from the sub-continent to a single patch of habitat; Fig 6.2), is the first step towards developing a heuristic framework of ecological functioning of tropical estuaries. This will potentially provide the basis for a more complete and holistic understanding of faunal patterns and their drivers in these systems. Considering patterns and processes hierarchically in this framework is the simplest way of conceptualising ecosystem complexity (Allen & Starr 1982), and threading disparate mechanistic understandings into a compound framework. Processes characteristic of broader spatial scales typically operate at slower rates than processes characteristic of finer spatial scales (Urban et al. 1987, Wu & David 2002). This asymmetry in process rate means that patterns and processes at broader scales inevitably constrain pattern at finer scales (Fig 6.2 & 6.3). Thus, in its simplest form, the hierarchy of processes can be perceived as a succession of filters imposed at different scales that sequentially refine the assemblage as levels are descended (sensu Poff 1997). The hierarchy of ecosystem dynamics that need to be considered in the design and interpretation of ecological studies in coastal systems (illustrated in Fig 6.1 & Fig 6.2) are discussed below.

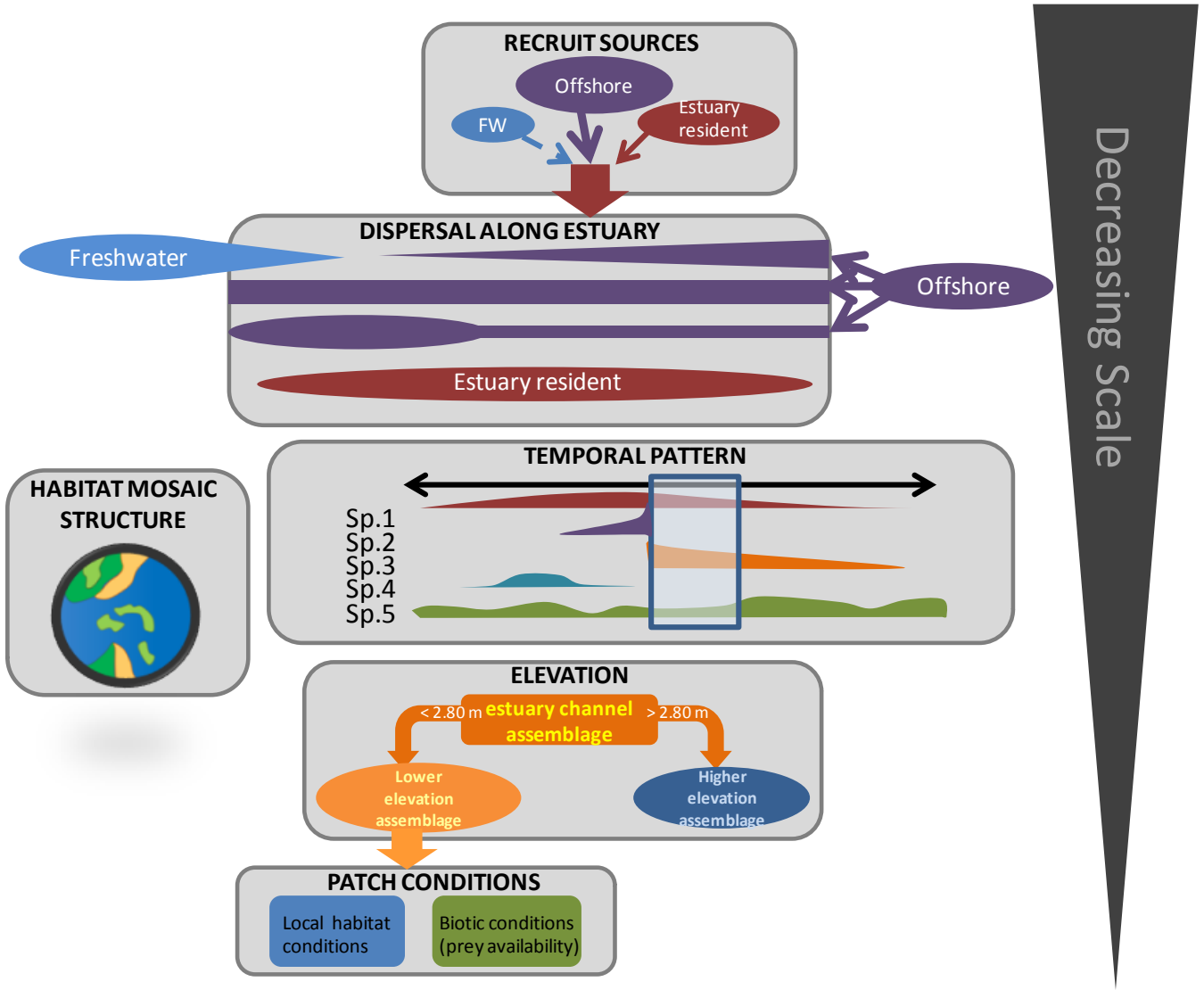

Figure 6.1: Figurative representation of patterns and processes constraining assemblage composition at a range of scales, based on outcomes of the data chapters.

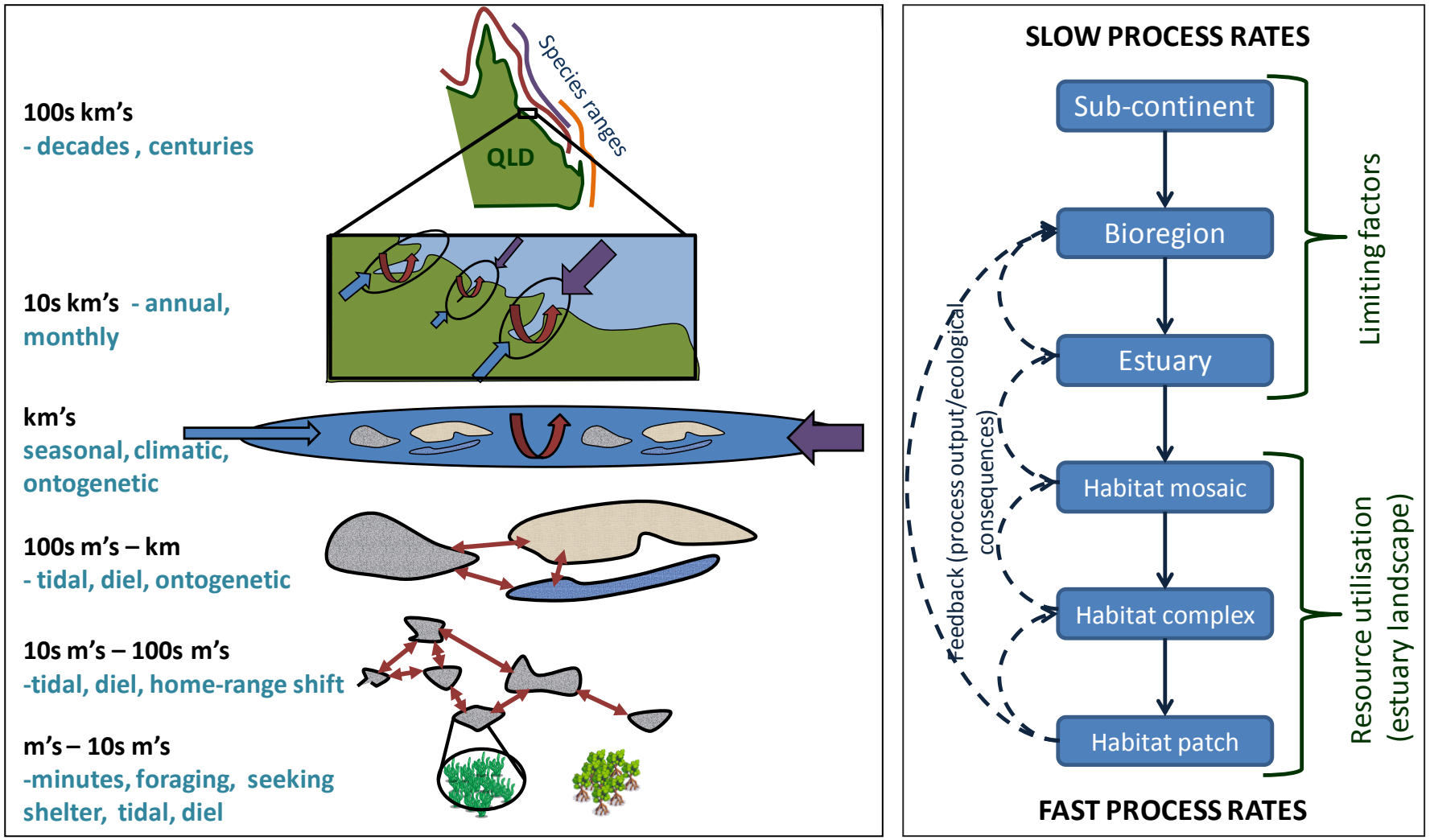

Figure 6.2: a) Hierarchy of organisational scales at which key processes operate. The characteristic rates at which these processes operate are shown on the left hand side of the figure, and b) a hierarchical framework model, illustrating linkages among pattern and process over this multiplicity of organisational scales.

6.1.1. Biogeographical distribution

At the broadest scale, varying species distribution ranges along latitudinal gradients regulate biogeographical species pools, constraining the suite of species available to utilise coastal systems in various regions and climatic zones (Vilar et al. 2013). Species ranges may shift over long (decadal-centennial) time-scales in response to climate change, and are therefore perceived as a constant in ecological studies. However, in Australia's tropics the ranges of many coastal species remain poorly resolved (Sheaves & Johnston 2009). These ranges need to be better defined to avoid erroneously attributing the absence of species in estuaries to finer-scale ecological processes, and to provide a baseline for monitoring anticipated range-shifts (Hickling et al. 2006).

6.1.2 Recruit supply

Within a bioregion, several life-history specific processes act upon the species pool to modify levels of recruitment into individual estuary systems. Most species utilising estuaries spawn offshore and subsequently use the estuary as a nursery for <1 year, before emigrating to coastal waters (Robertson & Duke 1990b, Sheaves et al. 2010). This brief residence time and high turnover of individuals emphasises the role of re-colonisation in shaping assemblages. Therefore, any spatial patterning in larval supply, resulting from the location of spawning grounds and oceanographic features modifying the passage of larvae (Sheaves in review), will generate variability among estuary systems. At a finer scale, within the estuary, assemblages are further modified by the population dynamics of the self-recruiting 'resident' component. The relative contribution from this component is contingent on the historical population dynamics within each estuary (Sheaves et al. 2013), which encourages further assemblage divergence among systems over time. Contribution from the freshwater faunal component will also vary considerably among estuary systems due to spatial variation in assemblages of freshwater reaches (Ch. 2, Pusey & Kennard 1996), and the regimes and extents of river flow that connect them to estuaries. This system-to-system variation is increasingly exaggerated by the widespread implementation of variously sized dams, weirs, and other flow regulation structures which serve to variously restrict estuary-river connections (Walker 1985).

In Australia's tropics recruitment constraints manifest as differences in details of assemblage composition at an estuary-to-estuary scale (Sheaves 2006, Sheaves & Johnston 2009), that are inter-annually consistent, and account for more variability than differences among bays, or even climatic regions (i.e. wet vs. dry tropics)(Sheaves 2006, Sheaves &

Johnston 2009). This suggests that spatial patterning of recruitment is highly deterministic, and an understanding of the mechanisms outlined above can help explain and predict estuary-to-estuary level differences in fauna, without invoking complex ecological processes (Sheaves in review).

There is also a strong temporal element to patterns of recruitment. Availabilities of fish recruiting to estuaries follow seasonal cycles, varying among species (Ch. 3) (Sheaves et al. 2010, Davis et al. 2012) relative to schedules of spawning. Spawning and recruitment of most species in tropical Australian estuaries is concentrated around pre-wet season months (Robertson & Duke 1990b, Sheaves et al. 2010, Sheaves et al. 2013), while some species, (e.g. *Acanthopagrus* spp.) spawn during dry season months (Sheaves et al. 1999), and others recruit continually through the year (Ch. 3).

The predictable pulsing of larvae into the estuary during pre-wet and wet-season months provides the opportunity for settled fish to exploit an easily targeted prey resource at the ocean-estuary interface (Limburg 2001, Baker & Sheaves 2009b). Such biological control of new recruits at this bottleneck is likely to further modify the relative abundance of marine-spawned species to subsequently utilise an estuary (Levin & Stunz 2005, Almany & Webster 2006). This is likely to contribute an element of stochasticity to the otherwise systematic estuary-to-estuary assemblage differences.

Understanding how recruit supply influences spatio-temporal variation in richness and relative abundance of species within estuaries or coastal seascapes is necessary to fully account for assemblage differences among systems, and to avoid erroneously attributing faunal patterns to post-settlement processes. For instance, by incorporating information on distance from suspected spawning grounds in the Gulf of Mexico, Drew & Eggleston (2008) were able to improve their explanation of assemblage composition of mangrove patches in the Florida Keys. However, this level of information is generally unavailable, and is difficult or laborious to establish. Therefore, the influence of variable recruit supply often manifests as noise when trying to relate faunal pattern to coastal seascape structure, despite frequent recognition as a potential source of unexplained variability (Hovel et al. 2002, Kendall et al. 2003).

6.1.3 Patterns of dispersal along estuary profile

Once within the estuary system, species from the three different recruit sources do not disperse evenly or stochastically, but (at the coarsest scale) are systematically structured

along an estuary profile (Ch. 2). Species colonising the estuary from coastal and oceanic spawning grounds, variously disperse upstream, relative to species-specific physiological tolerances (Cyrus & Blaber 1992, Thiel et al. 1995), resource requirements (Whitfield 1986), and life-history schedules (Elliott et al. 2007). One suite of species in tropical Australian estuaries selects upstream reaches as a preferred destination (upstream biased group; Ch. 2), perhaps via transitory settlement and early post-settlement habitats (Ch. 3, Simenstad et al. 2000, Caddy 2008). From the other end of the system, seasonal freshwater flows also donate high abundances of freshwater species to upstream reaches of estuaries (Ch. 2 & 3). Meanwhile, self-recruitment and broad salinity tolerances generally enable the estuary-resident component to occupy the entire length of estuary.

The complex interfacing of these various dispersal patterns means that habitats situated in different reaches will be subject to different species mixes. However, since distributions of many species are regulated by gradients of physical condition, either directly or indirectly (e.g. mediated by prey dynamics), patterns are not fixed, but are prone to variation both seasonally and among years with varying river flow. For example, clupeiod fish (*H. castelnaui* and *Stolephorus* spp.) move downstream in response to freshwater flows, and subsequently return to upstream habitats in response to increasing salinities (Ch. 3). In this regard, the estuary can be perceived as a landscape of physical structure overlaid by a dynamic and variable aquatic medium. This variable medium constrains which parts of the estuary a species can utilise, even if habitat conditions are otherwise suitable; a species is only capable of occupying physical conditions it is adapted to withstand.

More consistent constraints on habitat utilisation may also be imposed by dispersal limitation, if the supply of recruits attenuates away from the point of entry into the estuary, rather than relative to along-stream gradients in conditions. Patterns of declining abundances and species richness away from estuary mouths, oceanic inlets and passes are common to coastal systems and estuaries worldwide (Whaley et al. 2007, Faunce 2008). However, the extent to which these patterns reflect dispersal limitation rather than other covariants such as prey distribution or habitat suitability remains unclear. Dispersal limitation is perhaps a mechanism more characteristic of micro-tidal systems where there is limited exchange of larvae (Drew & Eggleston 2008) and reduced potential for selective tidal transport following settlement (Forward & Tankersley 2001, Faunce 2008).

6.1.4 Estuarine landscape structure

After species' distributions have been constrained by biogeographic factors, recruit supply, and estuary-level gradients, subsequent organisation occurs relative to resource utilisation. Landscape structure within the estuary can be perceived as a heterogeneous mosaic of interacting components and resources, the patchiness of which is central to nursery function and fundamental to the organisation of fish communities, populations, meta-populations (Levin 1992, Sheaves 2009). In order to simplify understandings of relationships between this complex environmental heterogeneity and faunal pattern, landscape structure can be loosely decomposed into nested scales of interacting functional components, with different scales (or levels) broadly relevant to key ecological processes operating at different rates. However, since different species, life-stages, and even individuals perceive and respond to patchiness at different scales and in different ways, linkages between landscape structure, scale, and functional processes are complex (Levin 1992) and difficult to define and decompose in a non-arbitrary way; different species may perform similar activities, such as daily home-range movements, at different scales.

For the purpose of providing a general overview of landscape-assemblage relationships in tropical estuaries I have defined estuary landscape structure at three primary scales, likely to explain assemblage structure without excessive loss of information. The broadest of these scales is the habitat mosaic, nested within this is the habitat complex, and a finer scale still are the local environmental characteristics of individual patches.

Habitat mosaic

While not directly quantified within this thesis, both composition and configuration of different habitat types (e.g. saltmarsh, mangrove, seagrass, sandbars, deep-water channels) are central to meso-scale structuring of assemblages within the estuary (Sheaves 2009) and coastal seascape (Grober-Dunsmore et al. 2009). Within estuaries, species are likely to be faithful to areas where aggregations of suitable habitats types are located (Blaber et al. 1989, Rozas & Minello 1998, Bloomfield & Gillanders 2005). Such species-habitat associations may explain the site-by-site differences in fish assemblage structure previously recorded along the profile of the Ross River estuary (Sheaves et al. 2007b). Species which rely on multiple habitat types throughout a diel or tidal cycle may select areas of the estuary where complementary habitats occur in close association (Parrish 1989, Pittman et al. 2004, Skilleter et al. 2005), minimising predation risk through inter-habitat migrations across hostile landscape (Turgeon

et al. 2010). Equally, species making ontogenetic shifts between habitat types may favour more proximate destinations (Dahlgren & Eggleston 2000, Cocheret de la Moriniere et al. 2002).

Mosaic effects have previously been demonstrated in coastal systems through interactive influence of neighbouring habitat types on each other's assemblage structure. For example, species richness and abundances in intertidal mangroves and salt-marshes are often positively affected by proximity to areas of subtidal seagrass, and vice-versa (Irlandi & Crawford 1997, Pittman et al. 2004, Skilleter et al. 2005). Similarly, the configuration of habitat units within salt-marsh systems can also play a substantial role in shaping faunal pattern. For instance, marsh-residents occur most densely in areas of flooded marsh nearby intertidal channels, which offer refuge habitat at low tide (McIvor & Odum 1988, Kneib 2003).

The scale and manner in which fish respond to the spatial arrangements of habitats will vary in a species- or life-history specific way relative to different resource requirements, dispersal capability, physiology, and niche breath (Pittman et al. 2007a, Drew & Eggleston 2008, Faunce 2008, Grober-Dunsmore et al. 2009, Meyer & Posey 2009). Therefore, an organism-centric approach that defines and scales habitat mosaics relative to the home-ranges and ontogenetic movements of subject species will likely offer improved predictions of species-landscape relationships. For instance, defining habitat mosaics at the scale of different 'habitats classses' (e.g. mangrove forests, seagrass beds, and saltmarshes) may be useful for explaining faunal patterns of sparid or sciaenid fish, however the same focus is unlikely to offer sufficient habitat resolution to account for the resource requirements of a gobiid.

Habitat complex

Abundances and richness of fishes using particular habitat complexes will be constrained by surrounding seascape structure. At finer spatial scales, the landscape structure of a single habitat type will interact with environmental attributes within patches, to exert control on the distributions of species and life-stages over multiple time-scales. For example, during tidal excursions into intertidal nursery habitats, habitat complexes with varying levels of fragmentation, size, shape, and edge density, as well as local attributes such as shoot density, epiphyte biomass, and sediment characteristics, will offer different foraging and shelter opportunities (Pittman et al. 2004, Green et al. 2004), resulting in core areas of fish utilisation within the complex (Nagelkerken et al. 2013). On a broader time-scale, resident fishes (species that spend life-stages or entire lives in a single habitat type) in fragmented habitats

may relocate their home-range to occupy a different patch in response to changing biotic and abiotic conditions (Sogard 1989, Kramer & Chapman 1999, Chapman et al. 2000). The nature and direction of these movements will likely reflect the interacting constraints of local environmental conditions within patches and structural connectivity, modified by the spatial configuration of patches in the landscape (Hovel et al. 2002, Jackson et al. 2006a).

In the present study assemblage structure in the tidal pool complex was governed primarily by landscape-level processes, and secondarily by local environmental conditions within pools (Ch. 4). In particular, patterns were driven by varying responses to the extent (frequency, duration, and depth) of tidal connectivity to the estuary channel, which was the primary source of colonists. These findings demonstrate how spatial context has profound implications for local assemblage dynamics and nursery roles of patches. These general principles are likely to be transferable to complexes of other habitat types within the coastal and estuarine ecosystem, however the specific nature of the drivers will differ. For example, in seagrass meadows, dispersal will likely be limited by the extent of 'inhospitable' bare substrate separating patches of seagrass (Turgeon et al. 2010). Where patches are closely clustered, species-sorting and mass-effects are likely to shape resident communities, as individuals have the freedom to 'sample' the internal habitat qualities of patches (e.g. density of vegetation, seagrass blade length, epiphyte biomass). On the other hand, isolated patches may act as population sinks as settling individuals are limited to a prescribed set of potentially sub-optimal local conditions, e.g. more isolated patches of salt-marsh act as sinks for the marsh resident *Fundulus heteroclitus* (Meyer & Posey 2009).

Prey dynamics can also play key role in structuring assemblages in habitat complexes. For example, Chapter 5 demonstrated how benthivorous and planktivorous fish were attracted to pools with greatest concentrations of benthic invertebrate and zooplankton prey resources, ultimately drawing the piscivore, *L.calcarifer,* to the same pools. Prey distribution has often been suggested as a potential driver of fish distribution in estuarine wetlands (Kneib 1984, Rozas 1995), but this is one of the first studies to explicitly demonstrate measurable effects of bottom-up control processes at the scale of a wetland system (but see York et al. 2012). This has profound implications, as responses to prey dynamics may obscure, or even decouple species-environment relationships, compromising interpretations from studies that lack spatial data across multiple trophic levels.

Within patch post-assembly processes

After communities within patches have been assembled by the aforementioned processes, several biological processes occurring within patches may further modify details of assemblages, independent of connectivity. In the tidal pool complex this was most evident in the apparent self-recruitment by *A. vachelli*, *O. mossambicus, P. signifer,* and *H. compressa* (Ch. 2 & 3), which boosted the resident component within pools. Direct quantification of other post-assembly processes, such as competition, predation, and mortalities was beyond the scope of the present study. However, in estuarine systems where dispersal is usually supported by frequent connectivity, and nursery function drives frequent re-assortment between patches, these processes are likely to only be influential in highly isolated patches. For instance, during prolonged disconnections water quality in pools can degrade to fatal levels, prompting extensive fish kills (Hyland 2002, Sheaves et al. 2006), while falling water levels also render communities vulnerable to intensive avian predation (Sheaves et al. 2006). However, predation within estuaries is generally focussed around spatio-temporal prey bottlenecks in accordance with foraging arena theory (Kneib et al. 2002, Sheaves 2005), e.g. at initial recruitment into estuaries (Limburg 2001), or during predictable constrained movements through corridors in and out of habitats (Kneib et al. 2002, Baker & Sheaves 2009b).

6.2 FUNCTIONING OF THE HIERARCHY

The realised assemblage composition in a given point of the estuary at a given juncture in time ultimately reflects the integrated function of all the aforementioned layers of pattern and process acting in concert. Therefore, we can often offer improved insight into faunal complexity by considering more levels of the hierarchy in ecological studies. However, when attempting to link pattern with processes we must consider the extent to which observed patterns result from top-down cascades through the hierarchy of scales, or mechanisms feeding back up through the hierarchy.

6.2.1 Top-down cascade

Process outcomes at broader scales inevitably percolate down to constrain the assemblage available to utilise landscape units at finer spatial scales. Consequently, for a detailed holistic understanding of the patterns and process at finer scales, we need an explicit consideration of how processes operate at a range of broader scales. For example, to reliably compare the fish assemblage composition of an impacted mangrove forest in a polluted

estuary versus a control mangrove forest in a pristine estuary, it is inadequate to purely consider processes operating at the level of the impact and/or the level of the site (e.g. substrate, mangrove cover, root density, DO). Instead, we must also consider the spatial context that these sites are set within, including the mosaic of adjacent habitats that each mangrove site interacts with, the position of the site along the estuary profile, and the characteristic assemblage composition of the specific estuary that site is embedded within. If we fail to consider this suite of broader-scale processes, we may be left with substantial levels of unexplained variability, or worse, erroneously attribute a phenomenon to a processes operating at the wrong scale based on spurious correlations with irrelevant factors.

6.2.2 Bottom-up mechanisms

Conversely to the hierarchical cascading effect, the functional outcome of processes occurring at finer organisational scales may also feed back to influence faunal pattern at broader scales. This is mainly driven by the nursery function of estuaries; many estuarine species have multipartite life-cycles involving numerous ontogenetic habitat shifts within the estuary and coastal system (Nagelkerken et al. 2013), and each shift is generally accompanied by an expanding home-range (Kendall et al. 2003, Faunce & Serafy 2007). Therefore, asymmetric survivorship of different species, resulting from processes at finer scales (e.g. utilisation and linkages between spatial units within the complex or mosaic) will inevitably feed back to alter assemblage composition at broader scales (e.g. the reach and estuary before individuals emigrate to adult habitats). For example, early survivorship of *E. hawaiensis* may be enhanced if post-larvae can access higher elevation pools for brief periods during the pre-wet season (Ch. 4; Fig 6.3). This will in turn enhance the stock of larger juveniles available to subsequently colonise the reach that the pool is set within, and survivorship at the reach-level may yet influence the relative contribution of *E. hawaiensis* to adjacent adult habitats outside the estuary (Gillanders 2002).

Since different seascape formations suit different species (Grober-Dunsmore et al. 2009), processes occurring at the habitat mosaic or habitat complex level may ultimately feed back to alter the assemblage composition of the estuary as a whole. Fish are presumably unaware of the spectrum of habitats they are destined to encounter when recruiting into an estuary system, and following high recruitment periods, during pre-wet and wet season months, assemblages of tropical Australian estuaries are most similar (Sheaves 2006). Assemblages then begin to diverge thereafter in ways that are repeatable between years (Sheaves 2006), suggesting that fixed features varying between estuaries (i.e. the composition

and configuration of habitats), play a role in shaping assemblage structure into the dry season. Mangrove area has been identified as one potentially important factor contributing to such estuary-to-estuary variation in both tropical Australian (Sheaves & Johnston 2009) and Brazilian estuaries (Vilar et al. 2013). However, the myriad combinations of habitat structure within estuaries are likely to have diverse implications for secondary productivity of individual systems (Meynecke et al. 2008). It has even been suggested that patterns of habitat use within estuaries, and the structural connectivity among habitat units that underpins this, will ultimately feed back to measurably alter coastal fisheries catches (Manson et al. 2005, Meynecke et al. 2008).

In the case of estuary-residents (e.g. *A. vachelli*), the functional outcome of finer scale processes will ultimately shape population dynamics of subsequent generations within the same estuary. Since life-cycles of estuary-residents are enclosed within estuaries, alterations in survivorship will by extension modify the size of the spawning stocks. Mechanisms at finer scales may also transfer up the hierarchy indirectly through trophic relay (Kneib 1997). For instance, populations and growth rates of predatory species within an estuary system may benefit from finer scale processes that foster favourable prey dynamics within individual habitat complexes.

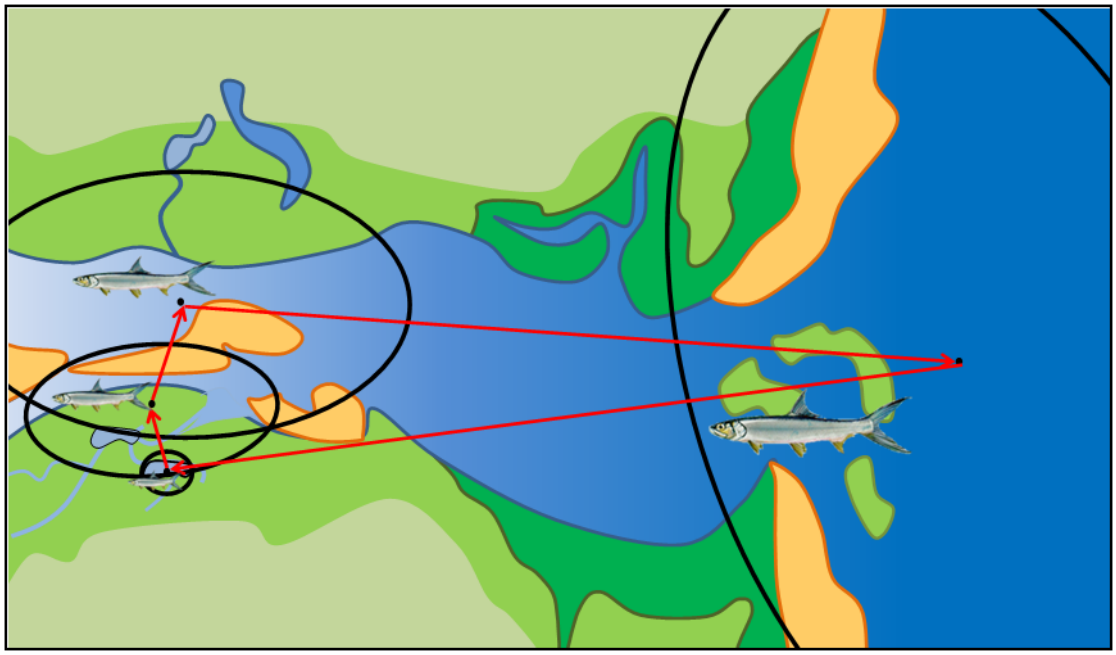

Figure 6.3: A conceptual life-history schedule of *E. hawaiensis* illustrating ontogenetic migrations (red arrows), and home-range extents (black ovals).

6.3 PERIODIC DISTRUBANCES TO HIERARCHCICAL FUNCITONING

In the previous section I explained how the tropical estuary ecosystem can be conceptually decomposed into a range of organisational scales relevant to functioning for the fish assemblage. This is consistent with the core principle of landscape ecology, that heterogeneity in physical structure at a range of scales shapes distribution and abundances of species (Allen & Starr 1982). While such simplification of complexity may tempt the use of landscape structure as a surrogate for pattern (Ward et al. 1999, Whaley et al. 2007), we must exercise caution when doing so. It is clear that tropical estuarine systems are dynamic places where both physical and biological variables interact with landscape structure at multiple scales to generate various faunal outcomes within a single system over time. In other words, the patterns described in the chapters are liable to deviation. This complexity is further exaggerated by the range of species responses to the same physical, biological, and ecological processes (Ch. 2-5). Consequently, we must consider how landscape utilisation and function for the assemblage may shift through time, both intra-annually (Ch. 3 & 4) and inter-annually.

6.3.1 Intra-annual shifts in landscape use

For much of the year assemblages will be hierarchically organised in a relatively predictable fashion, according to landscape structure and associated processes (i.e. reach > mosaic > complex > patch), with an undercurrent of programmatic nursery-driven changes (i.e. cycles of recruitment, life-history migrations, and ontogenetic shifts). However, species-landscape associations may periodically shift or decouple in response to cyclical and sporadic shifts in environmental condition. As environmental variables fluctuate, the relative influence of different levels of process detailed in the previous section (Fig 6.1) will be variously emphasised, prompting shifts in assemblage structure.

Species responses to environmental shifts are likely to be mostly reactive, reflecting trade-offs between energetic expenditure, feeding efficiency, and predation vulnerability as environmental variables change. However, environmental changes may also prompt more programmatic life-history movements for certain species. Two main types of environmental variable drive shifts in landscape use in Australian tropical estuaries: freshwater inflow and prey dynamics.

Freshwater inflow

Rainfall patterns driven by seasonal monsoons means that freshwater inflows into dry-tropical and sub-tropical estuaries are episodic, typically concentrated around 2-3 months each year. This intense pulse of freshwater is the agent for multifaceted shifts in ecosystem function, triggering changes in assemblage structure across multiple spatial and temporal scales through a range of mechanisms.

Freshwater inflows can result in abrupt and severe salinity drops, accompanied by concomitant shifts in other physico-chemical variables that inevitably prompt ecosystem-level changes (Robins et al. 2005, Whitfield 2005). In response to these shifting conditions, priorities of many fish species will shift from foraging-refuge oscillations, staged at the complex and mosaic level, to seeking physiological refuge or tracking shifting resource dynamics (e.g. the Interrupted Persistence group in Chapter 3) (Sakabe & Lyle 2010). Freshwater discharges simultaneously serve to enhance connectivity across the landscape. Stream flows act as two-way corridors of conveyance, delivering freshwater fish to upstream reaches of estuaries (Chapter 3), whilst concurrently enabling upstream migration of diadromous species (such as tarpon and barramundi) in the opposite direction (Kowarsky & Ross 1981). Meanwhile, floods resulting from discharges facilitate the flux of individuals in and out of isolated floodplain habitats (Sheaves & Johnston 2008). The seasonal inundation of these floodplains also provide habitat *per se* (Winemiller & Jepsen 1998, Jardine et al. 2012), and can be perceived as an intermittently available component of the estuary habitat mosaic (Fig 6.4), which seemingly provide crucial early-life history nurseries for particular species (Russell & Garrett 1983, Jardine et al. 2012) (including the 'Delayed Recruits' in Chapter 3). Less obvious effects of freshwater discharges, such as provision of allochthonous inputs from both river systems and floodplains are also likely to spread their influence throughout the estuary system, subsidising fish production, and subsequently influencing assemblage structure in the estuary through the remainder of the year (Abrantes et al. 2013).

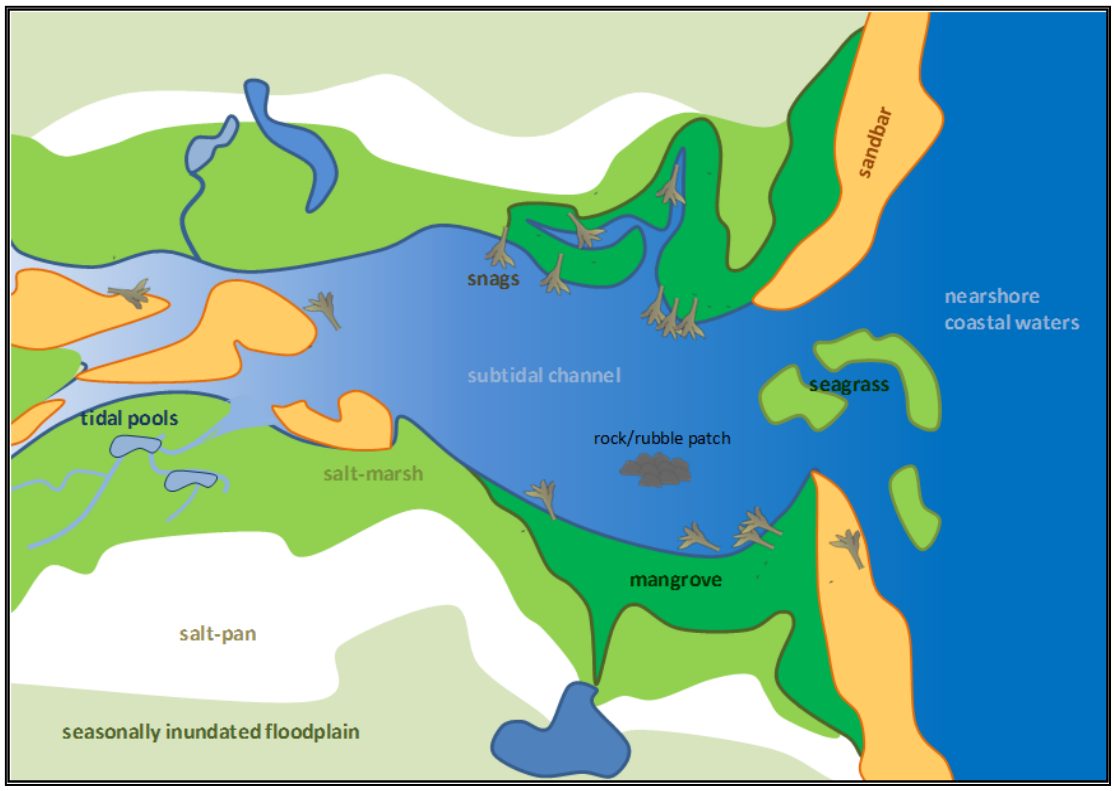

Figure 6.4: Common components of the tropical estuary habitat mosaic

Prey availability

Shifts in prey dynamics can alter assemblage structure across multiple scales. In the present study, optimal-foraging processes and associated bottom-up controls exerted influence over metacommunity dynamics at the habitat complex level (Ch. 5). Alterations in prey distribution among patches will therefore have knock-on effects for fish distribution. During pulses of high prey availability in the estuary, optimal-foraging processes are likely to 'scale-up', as fish abandon fine-scale structuring controls to take advantage of high feeding efficiencies elsewhere. For example, many species of fish within tropical estuaries, although not typically piscivorous, turn to feed on new recruits during windows of high larval recruitment (Baker & Sheaves 2008, 2009a).These species would benefit by congregating around the bottlenecks (e.g. the estuary mouth) as recruiting fish run the gauntlet into estuary mouths, to optimally exploit this transient resource (Limburg 2001, Sheaves 2009). Such a response would effectively override finer-scale species-landscape associations, temporarily causing shifts in the way fish assemblages are spatially structured. In a similar way, King George Whiting (*Sillaginodes punctata*) abandons favoured seagrass habitats when prey is particularly abundant in adjacent bare substrate (Connolly 1994, Jenkins & Hamer 2001).

6.3.2 Inter-annual regime shifts

Wet vs. dry years

Multi-year climatic cycles driven by the El Niño Southern Oscillation (ENSO) mean freshwater inflows into dry-tropical and sub-tropical estuaries are highly variable from year-to-year (Sheaves et al. 2007b). Although the present study was conducted through a relatively wet period of the cycle, it was clear that freshwater inflow played a central role in shaping faunal pattern through the year, suggesting extended drought conditions could impose distinct phase-shifts in patterns of landscape use (Sheaves et al. 2007b). Although droughts will ultimately affect all components of the estuary assemblage, either directly or indirectly, species with life-history strategies closely intertwined with freshwater flows will be most profoundly affected.

For example, the complex life-history schedule of barramundi (*Lates calcarifer*) predisposes it to great inter-annual variability in patterns of abundance and distribution. Barramundi synchronise spawning aggregations with river inflow events (Moore 1982, Russell 1985), thus the time of spawning and subsequent recruitment varies relative to timing of freshwater inflow. The size of the spawning stock is also modified by the extent of flows/floods by promoting downstream transport of mature barramundi to coastal spawning aggregations, and facilitating passage for landlocked barramundi in off-stream wetlands (Robins et al. 2005). River discharges simultaneously inundate estuarine floodplains that larval barramundi are suspected to primarily recruit to (Russell & Garrett 1983), enabling rapid growth and high survival rates (Davis 1984), and modifying timing and levels of subsequent recruitment to permanent habitats (Ch. 3). Freshwater flows also donate substantial nutrient loads to estuarine wetlands (Robins et al. 2005), promoting productivity through the post-wet season, and providing a fertile ecosystem in which barramundi can thrive as apex-predators after floods draw down. However, during drought periods when floods do not occur, barramundi populations suffer (Staunton-Smith et al. 2004). The few barramundi recruiting to estuaries during these periods will be forced to use the estuary seascape in a different manner to wet years, as recruiting barramundi will be restricted to potentially sub-optimal habitats within the confines of the estuary channel and associated tidal wetlands (Fig 6.4). For instance, patches of fine-scale habitat with suitably sized interstitial niches (e.g. algal clumps, rubble patches, seagrass beds, or fine woody debris (Dahlgren & Eggleston 2000, Caddy 2008)), may become paramount to survivorship by providing surrogate settlement sites and early nurseries.

Stochastic recruitment variability

Levels of recruitment can be highly variable among years due to a mixture of physical and biological processes (Kraus & Secor 2005). For instance, variable coastal currents and vagaries of other oceanographic processes can alter patterns of larval supply (Roughan et al. 2011). Meanwhile, the extent to which recruiting populations are regulated by biological control at the estuary mouth is also likely to vary substantially across years (Sheaves 2009). An obvious implication of varying recruitment success is inter-annual variability in estuary-level assemblage composition. At finer scales, large variability in recruitment could potentially influence patterns of landscape use within the estuary (Bacheler et al. 2013), perhaps in terms of meta-community structure at the habitat complex level if structuring processes are density-dependant (e.g. in accordance with ideal free distribution) (Hansson et al. 1995, Eggleston et al. 1998).

CONCLUSION

The hierarchy of processes presented above, or modified forms of this, are also likely to structure assemblages across estuarine and coastal seascape systems around the world. Depending on the type of system in question however, different levels of process within the hierarchy will vary in their specific nature and relative influence. For instance, in coastal seascape systems of the Caribbean, broad-scale variation in faunal pattern will largely result from the orientation of nursery grounds relative to spawning aggregations on fringing coastal reefs (Huijbers et al. 2013). At meso-scales, assemblages within these systems are largely structured relative to the spatial arrangements of habitat types across the seascape (Nagelkerken et al. 2001, Pittman et al. 2007a), while gradients in depth may further structure the assemblage (Pittman et al. 2007b). In the salt-marsh systems of the Gulf of Mexico however, fish assemblages are likely to be broadly structured relative to position along extensive gradients of salinity (Rakocinski et al. 1992), and also distance to the ocean pass where recruits primarily colonise the system from (Whaley et al. 2007). Meanwhile, at meso-scales, the level of reticulation of marsh vegetation and resultant ‘edge’ area is likely to strongly influence densities (Rozas & Zimmerman 2000, Minello & Rozas 2002), perhaps with less emphasis on configuration of different habitat types .

A hierarchically organised complexity is a common feature across ecosystems in general. As such, similar conceptual and operational frameworks that incorporate scale and landscape structure into models of understanding are increasingly being applied to a range of system types, including dendritic river systems (Poff 1997), floodplain river systems

(Winemiller & Jepsen 1998, Arthington et al. 2005), coral reefs (MacNeil et al. 2009, Pittman & Brown 2011), seagrass meadows (Turner et al. 1999, Jackson et al. 2006a, Jackson et al. 2006b), and terrestrial forests (Urban et al. 1987). Embracing the hierarchical nature of ecosystems will ultimately foster improved mechanistic understandings of faunal structure to complement and feed back into more conventional correlative approaches. This does not necessarily mean quantifying and partitioning the influence of processes at each scale, as even a mere consideration of the hierarchy can safeguard against misinterpretation, by promoting caution in attributing correlations exclusively to measured variables.

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Appendix A

Selected images of Annandale Wetland

Figure 1: Annandale Wetland at low tide, looking across the wetland from the aquatic-terrestrial ecotone towards the Ross River. At low tide during post-wet, dry, and pre-wet season months, pools are discrete units embedded in a *Sporobolous* salt-marsh matrix.

Figure 2: Neap high tide channel connection between pool B1 and B2.

Figure 3: Medium spring high tide channel connection between pool C2 and B3. The channel is lined by the mangrove shrub *Aegiceras corniculatum*.

Figure 4: High spring tide flooding, connecting pools over the *Sporobolous* marsh surface.

Figure 5: Annandale Wetland, looking towards the Ross River during a wet season freshwater flood. Only the highest parts of the wetland and tops of *Avicennia marina* trees are visible.

Figure 6: A seine net haul in pool A1.

Appendix B

Catch summary from Annandale Wetland

Table 1: Summary of catch - raw abundance across all 20 pools summed over the complete sampling period, featuring taxa collectively constituting 99% of the total catch. Pools which required 2 net hauls per sampling occasion are marked '*', and pools which required 3 net hauls per sampling occasion are marked '**'.

Family	Species	Pool																		
		A1*	A2*	A3*	A4	A5	B1**	B2*	B3*	B4**	B5**	B6*	B7*	B8*	C1*	C2*	C3*	C4*	C5*	C6**	C7*
Ambassidae	*Ambassis vachelli*	2284	2170	916	849	39	2057	802	2207	1837	5278	153	3359	353	2198	3923	1141	4823	2169	2330	4304
Apogonidae	*Glossamia aprion*	8	3	1	3	1	3		4	1	9		4	17	2		1			3	
Atherinidae	*Craterocephalus stercusmuscarem*	62	24	41	32	50	3	14	21	7	19	5	3		7		1				
Belonidae	*Stongylura kreffti*	9	5	15	15		11	6	8	4	5		4		5	1	1	2	1		2
Centropomidae	*Lates calcarifer*	21	78	76	26	1	22	8	5	35	75	13	26	7	23	56	5	30	30	3	8
Chanidae	*Chanos chanos*	20	23	10	9	45	1	4	20	18	11	7	6	7	95	24	24	13	17	10	10
Cichlidae	*Oreochromis mossambicus*	35	125	142	67	76	69	6	30	86	161	149	46	147	132	101	169	75	48	105	104
Clupeidae	*Herklotsitchthys castelnaui*	453	221	392	169	4	466	28	60	1018	214	3	138	6	14	18	5	41	50	35	23
	Nematalosa erebi	401	810	750	828	934	156	86	182	246	877	1164	700	280	1082	681	275	350	152	467	184
Eleotridae	*Butis butis*	7	2		3	1	8	4	6	9	4		4			4	2	2	4	3	10
	Hypseleotris compressa	149	186	116	40	1447	151	245	60	189	79	809	58	425	158	90	514	6	11		17
Elopidae	*Elops hawaiensis*	14	18	14	5	12	5		3	7	15	26	7	3	12	3	6	2	3	4	3
Engraulidae	*Stolephorus* spp.	251	481	693	469		229	10	26	404	228		29	2	25	6		43	9	48	30
	Thryssa hamiltonii	28	71	108	25	1	1	1	1	10	12			1				10		21	10
Gerreidae	*Gerres erythrourus*	37			1	1	20	4	7	9	9		7	1	3	16		1		1	1
	Gerres filamentosus	183	211	276	114	15	484	159	258	222	195	2	96	20	159	141	43	82	73	138	278
Gobiidae	Gobiidae sp. 1	95	48	83	38		28	1	14	100	44		17	48	1	3	1	8	29	96	131
	Glossogobius circumspectus	49	13	9	9	1	164	107	48	112	82		8	3	4	17	2	9	24	44	53

	Favinogobius reichei	14	1	25			8	12	9	15	11	2	3	10	4		15		1	1		
Hemiramphidae	*Zenarchopterus buffonis*	1				1		5	1		2							14	17	1	26	
Leiognathidae	*Gazza minuta*			15			31			63			2					15		1	16	
	Leiognathus equulus	335	358	622	298		1324	51	244	1483	1534	5	562	9	40	167		405	409	243	420	
	Secutor ruconius	8	12	14			10		11	14	26		8					11		3	8	
Lutjanidae	*Lutjanus argentimaculatus*				1		11	5	3	2	1				5	2	1	7	3	4	14	
Megalopidae	*Megalops cyprinoides*	1	38	47	15	21	2				2	23	5	1	8	11	4	3	4	7	21	
Monodactylidae	*Monodactylus argenteus*						3	4	24						4	1		2	16		3	
Mugilidae	*Liza subvirids*	15	5	16	3	3	8	13	15	8	26	22	10	21	42	21	53	14	7	29	37	
	mugilid juv.	16	8			14	1		1	1	15	154	1	82	42	2	102	1	2	10	24	
	Valamugil seheli	3	2		5	4	7	2	17	13	19	2	7	10	12	21	17	8	3	10	5	
Platycephalidae	*Platycephalus* juv.	12	8	8	11	1	2	6	6	18	16		1		1		2	2	1		7	
Pseudomugilidae	*Pseudomugil signifer*	8	4	1	1	3	46	47	209	37	101	142	19	87	226	7	54	1	1	1	16	
Scatophagidae	*Selenotoca multifasciata*	10	1	6	3	22	7	15	11	8	5	77	4	13	36	11	11	4	9	12	6	
Sparidae	*Acanthopagrus* spp.	92	20	12	14		204	54	42	192	77		74	10	19	91	13	25	21	55	51	
Tetraodontidae	*Arohtron reticularis*	1	1		3		7	5	21	9	4				1	4	1	17	3	1		
Toxotidae	*Toxotes chatareus*	4				3	5	7	15	3	3				5	1	3	3	1	3	14	

Appendix C

Consistency in fish assemblage structure through the lunar cycle

INTRODUCTION

All sampling of fish assemblages occurred around low tide during the spring tide portion of the lunar cycle. Consequently, the spatial patterns interpreted in Chapter 4 were based on data collected from one half of the spring-neap-spring-neap lunar cycle. However, it is possible fish assemblages may respond to the shifting magnitude of tidal connection that occurs through the lunar cycle, and assemblage structure over the wetland may vary between neap and spring periods (Hampel et al. 2003, Krumme et al. 2004).

During neap tides, pools at higher elevations, or pools without channel connections, remain isolated, while better connected pools are restricted to relatively shallow channel connections. Consequently, during neap tides it is possible that conditions may become physically deleterious and perhaps fatal for less tolerant species due to low DO and high temperatures. As a result, certain fish may only utilise particular pools during spring tide sequences when conditions are more favourable and movement in and out of the pools is aided by high connectivities (Rountree & Able 2007). Furthermore, there are several other mechanisms and processes which could potentially skew assemblage structure among spring and neap periods, but which are not well understood, including endogenous lunar rhythms (Aschoff & Neumann 1981) and responses to cyclical prey dynamics (e.g. greater abundances of zooplankton may be conveyed to the wetland during spring tide periods).

To validate that sampling of fish assemblages during spring tide periods is representative of assemblages through the entire lunar cycle, I repetitively sampled four pools (representing a broad cross-section of connectivity regimes) 6 times through a semi-lunar cycle (bottom of neap tides to top of spring tides). This repetitive sampling also enabled me to examine pool colonisations by species or populations in response to particular connection events.

METHODS

Study site

Four pools in Annandale Wetland were sampled, representing a broad cross-section of connectivity regimes (Fig 1), and which were small enough to representatively sample in a single seine net haul. This included:

- a lower elevation pool, connected by a discrete channel, with little overbank connection (B3)
- a lower elevation pool with a small, poorly defined channel connection, but good overbank connection (C6)
- an intermediate elevation pool connected by a discrete channel, and with good overbank connection (A2)
- a higher elevation pool only connected by large spring tides overbank (A5)

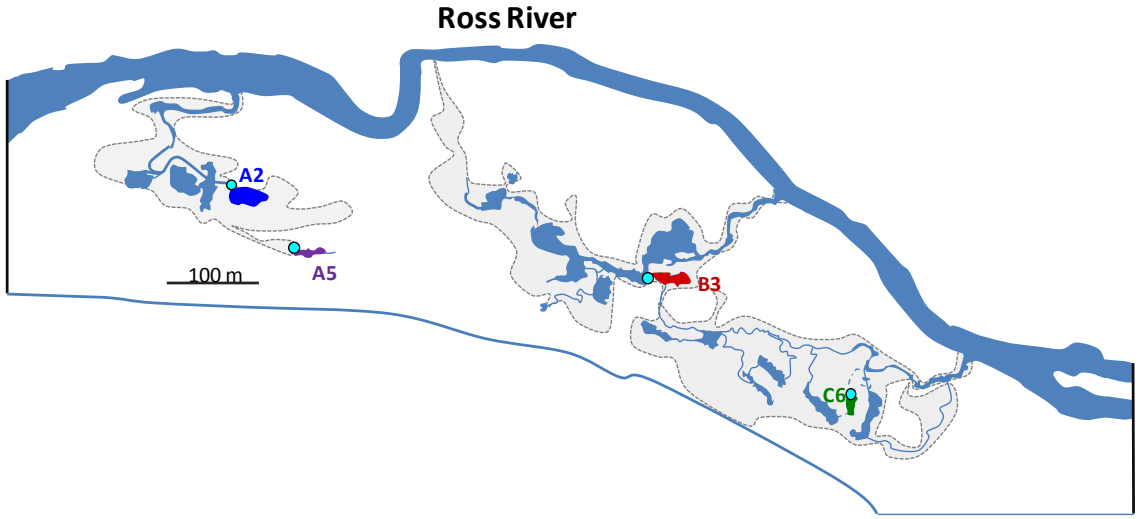

Figure 1: Site map of Annandale Wetland, with the four sampled pools displayed in red. Light grey shading represents the area of salt-marsh temporarily flooded by high spring tides (~3.6 m). Blue circles indicate the positioning of the pressure loggers installed to record connectivity regimes.

Sampling

Sampling of fish assemblages in the four pools occurred every 2 days between the 19th August and the 29th August 2011, totalling 6 sampling trips. For each pool the first two sampling trips served as a control, since no tidal connections were established between these two dates. For pool B3 and C6 connections were not established until after the 3rd sampling trip, and for pool A5 connection was only established after the 5th sampling trip. On each sampling trip all four pools were sampled with a single seine hauls (net dimensions: 12 m long, 2 m wide, 6 mm mesh size; details as per Chapter 4). The catch was quickly quantified, resolved to the lowest taxonomic level, before being promptly returned to the water alive.

Recording connectivity regimes

Throughout the study period regimes of tidal connection were measured in each pool, including both channel connections and connections over the salt-marsh surface, since these two types of connections may have different implications for fish movements (Rozas et al. 1988). Channel connections were recorded by fixing stationary pressure loggers where channels join a pool to more downstream pools (or the estuary channel). These data were calibrated against data from an atmospheric pressure logger, and converted to depth data. Depth readings were then cross-referenced against realised tide data (courtesy of Townsville Port Authority), enabling assessment of when tidal connections occurred and at what magnitude. Since only four pressure loggers were available, overbank connections were measured by recording connections depths with a chalked pole at a single known tide height. This 'tide height-overbank depth' relationship allowed overbank connection data to be extrapolated for the entire study period, by cross-referencing with realised data.

Data analysis

Fish assemblage shifts (and implicitly fish colonisations) in each pool over the semi-lunar cycle were analysed with nMDS ordinations of log(CPUE+1) data based on Bray-Curtis dissimilarities (details as per Chapter 5). Then, incorporating data from all four pools into a single nMDS ordination enabled assessment of lunar-period consistency in wetland-scale assemblage patterns.

RESULTS & DISCUSSION

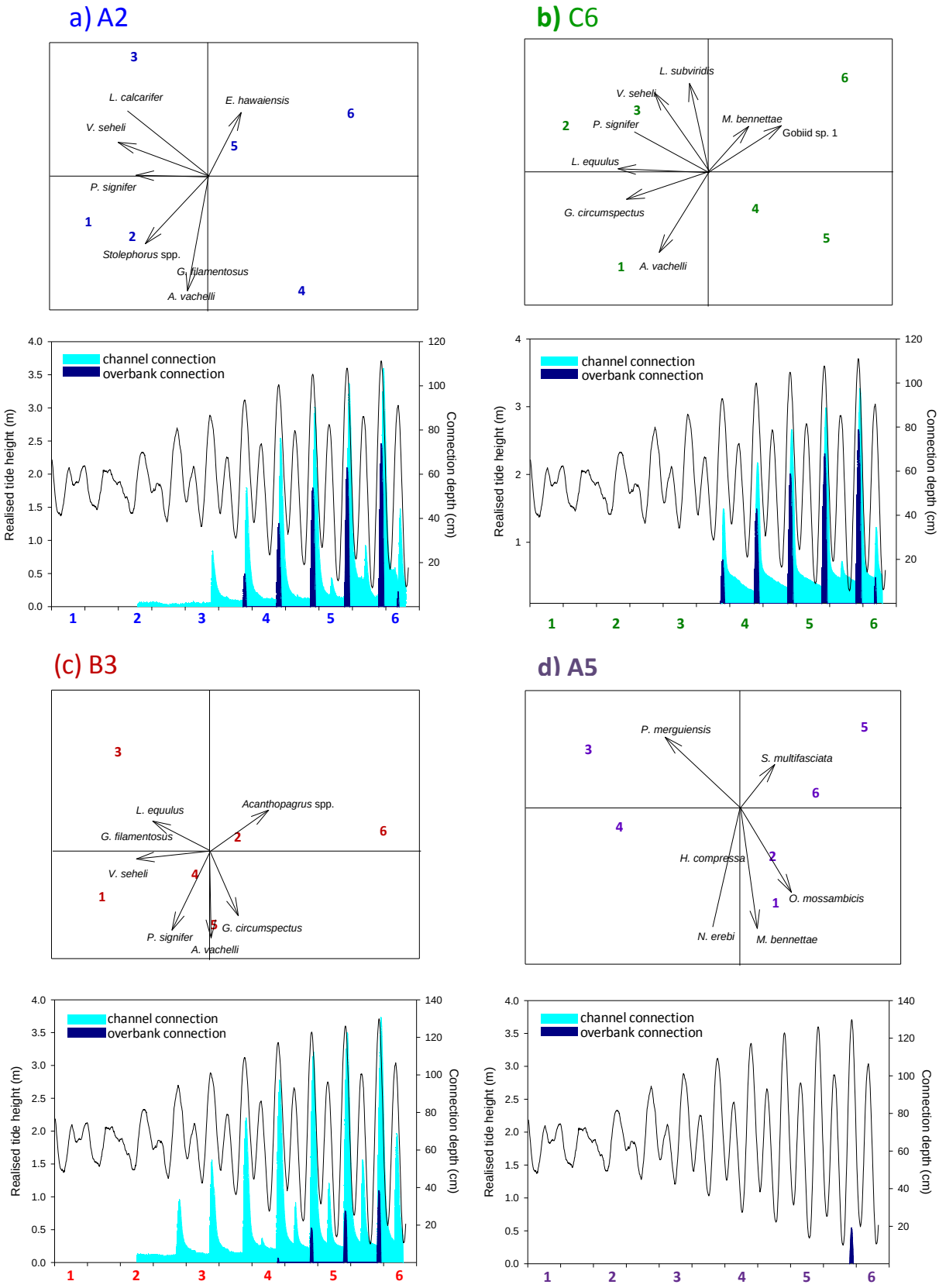

Figure 2: nMDS ordinations displaying shifts in assemblages of (a) pool A2 (b) pool C7 (c) pool B3 (d) pool A5, across 6 sampling trips through a semi-lunar cycle. Vectors radiating from the intersection of axes relate to species abundances most highly correlated with the ordination space. Arrows indicate the direction of greatest increase in abundance, with length proportional to R˙ Pool groupings basedon relative positions in the ordination. The regime of tidal connections through the sampling period is also displayed on a separate panel below each pool's nMDS. The juncture of each sampling trip is displayed on the x-axis.

Movement of individuals of certain species in and out of pools was apparent through the study, but no unequivocal patterns emerged. Pool A2 and C6 appeared to experience a shift in assemblage from periods of isolation to periods of connection. Both pools were first connected after the 3rd sampling trip, and assemblages in trips 1-3 differed considerably from assemblages in trips 4-6, illustrated by their locations on opposite halves of the nMDS ordinations (Fig 2a & b). In pool A2 this assemblage shift seemed to primarily represent lower abundances of several species in trips 4-6, possibly due to emigration or motility induced by netting (Fig 2a). In pool C6 the assemblage shift seemed to result from a combination of emigration/mortality and also colonisation by populations of *Metapenaeus bennettae* and gobiid sp. 1 (Fig 2b). This implies an exchange in individuals between pools during tidal connections, but it is unclear whether this represents part of a systematic cyclical pattern or just random movements. In pool B3 and A5 there was no clear change in assemblage in response to tidal connections through the semi-lunar cycle (Fig 2c & d). Assemblages in these pools did not shift in response to connection events any more than between control samples (i.e. between sampling trips with no connections) (Fig 2c & d). This suggests any change in assemblage through the study was not discernible from sampling variability in the pools.

Despite some drift in assemblages within pools through the semi-lunar cycle, assemblages between the four pools remained discrete through the study period, with no overlap in pool assemblages (Fig 3). This indicates that there is no interaction between wetland assemblage structure and lunar period, and that sampling during the spring tide period is representative of the entire lunar cycle.

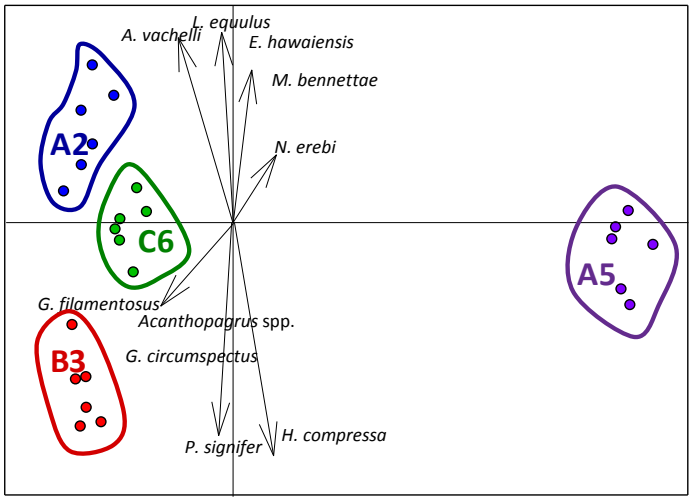

Figure 3: nMDS ordination displaying the consistency of assemblage structure across Annandale Wetland through a semi-lunar cycle. Vectors radiating from the intersection of axes relate to species abundances most highly correlated with the ordination space. Arrows indicate the direction of greatest increase in abundance, with length proportional to R. Pool groupings based on relative positions in the ordination. The regime of tidal connections through the sampling period is also displayed for each pool, and the juncture of sampling trips displayed on the x-axis.

Appendix D

Site-fidelity and movement patterns of large-bodied fish species in Annandale Wetland

INTRODUCTION

To determine whether the spatio-temporally consistent patterns of fish distribution described in Chapter 4 and 5 reflected a regular flux of individuals in and out of pools, or relatively resident populations, a suite of larger-bodied fish were tagged with unique coded external tags. The nested organisational structure of Annandale wetland (Fig 1) allowed fidelity and movement of individuals to be loosely assessed across three scales – the scale of the entire wetland, the scale of networks of pools, and the scale of individual pools.

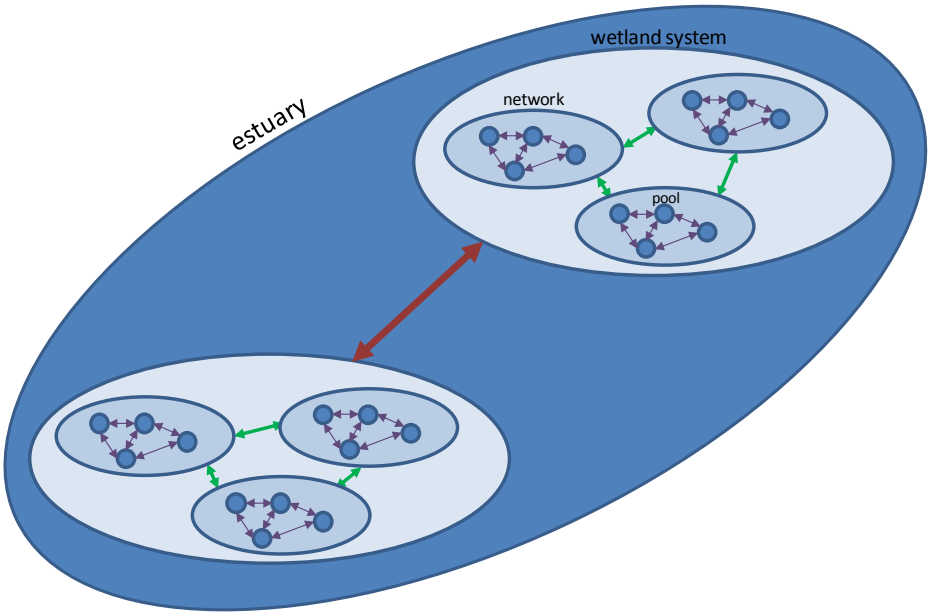

Figure 1: Conceptual model illustrating the three nested scales of landscape organisation at which fidelity and movement of individuals can be loosely examined in Annandale Wetland.

The two alternate hypotheses have different implications for the mechanisms shaping assemblage structure. A regular turnover of individuals in and out of pools would suggest that different individuals of a species consistently find there way into the same pools, due to certain connectivity criteria or environmental cues. On the other hand, a relatively resident population would suggest that individuals are selecting and remaining in particular pools based on preferred environmental conditions.

METHODS

Continually throughout the 2010 and 2011 monthly/bi-monthly sampling regime in Annandale Wetland (described in Ch. 2), individuals from five large (>150 mm FL) species of fish, including barramundi (*Lates calcarifer*), tarpon (*Megalops cyprinoides*), milkfish (*Chanos chanos*), giant herring (*Elops hawaiensis*), and greenback mullet (*Liza subviridis*), were tagged upon capture with external unique-coded T-bar anchor tags (4cm long, 1cm T-bar width) before being returned to the water alive. Tags were punched into the dorsal musculature with a handheld tagging gun, and rotated 90 degrees, to lock the T-bar behind the pterygiophores. The pool and date of capture were recorded, as well as the unique tag code. Upon recapture, the unique code, pool and date of recapture were recorded.

Data analysis

For each species the recapture rate (recaptured individuals as a percentage of those tagged) was calculated. This was used as a loose proxy for fidelity at the scale of the wetland system, whilst acknowledging that species net evasion capabilities may bias these estimates. For each species, the duration between first and last capture of individuals was also calculated, and used to assess the relative wetland residence time of different species.

For species with sufficient recaptures, patterns of movement and fidelity within the wetland were analysed. This involved calculating the rate of movement between networks, between pools, and also the amount of individuals that were exclusively recaptured in the pool of origin. The spatial patterns of movement and fidelity were qualitatively examined to assess whether individuals were faithful to particular pools, or whether there were specific trends of movement between pools.

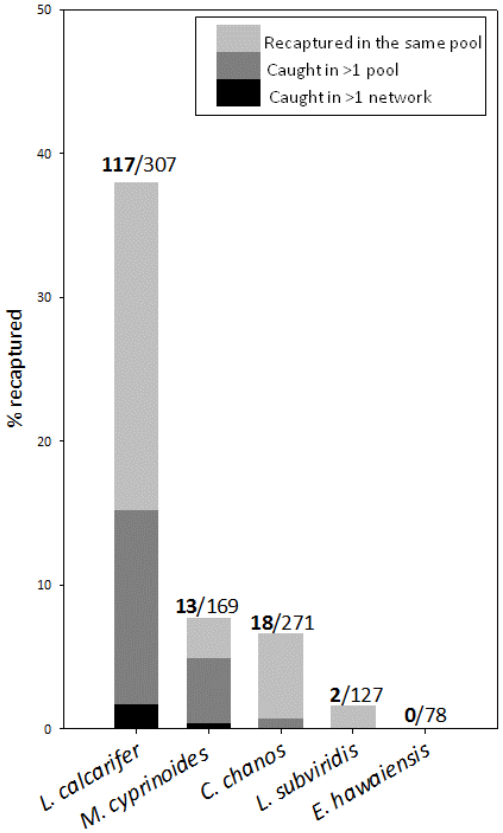

Figure 2: Bar chart showing the rate of recapture of the five tagged species, and the proportion of recaptures that: (1) were exclusively recaptured in the pool of origin, (2) were recaptured in a different pool in the same network, or (3) were recaptured in a pool in a different network.

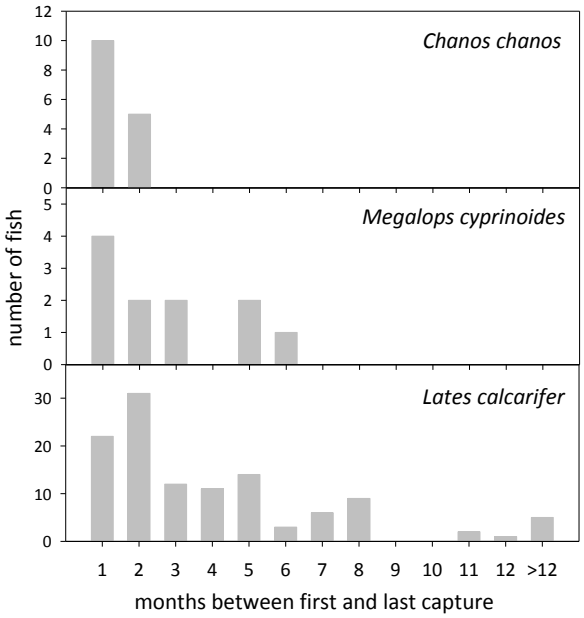

Figure 3: Histogram showing the duration between first and last capture for recaptured individuals of *L. calcarifer, M. cyprinoides, and C. chanos*.

L. calcarifer was the most of abundant of the 5 large fish species in Annandale Wetland, and also the most faithful to the wetland, with 117/307 tagged individuals recaptured (38% recapture rate) (Fig 2). This was approximately 5 times higher than the recapture rate of the next most faithful sepcies, *M. cyprinoides*, of which 13/169 individuals were recaptured (8% recapture rate). Only 18/271 (7% recapture rate) *C. chanos* individuals were recaptured, while 2/127 *L. subviridis* individuals were recaptured, and 0/78 *E. hawaiensis* individuals were recaptured. The high recapture rate of *L. calcarifer* is still likely to be an underestimate of true wetland residence, as it is likely that several tagged individuals evaded subsequent recapture in the wetland, while mortality can also not be controlled for.

Recaptured *L. calcarifer* were also generally resident in Annandale Wetland for relatively long periods, with approximately 50% of individuals remaining in the wetland for at least 3 months, while a few individuals were resident for >11 months (Fig 3). Of the 13 *M. cyprinoides* recaptures, individuals were moderately resident, with over 50% resident for at least 2 months. This suggests the low recapture rate of this species may have been a function

of net evasion capabilities. By contrast, none of the 18 recaptured *C. chanos* individuals were recaptured after 2 months at large, which is consistent with patterns of brief wetland residence identified in Chapter 3.

Based on the number of individuals recaptured in Annandale Wetland it was only deemed viable to further analyse movement patterns of *L.calcarifer* individuals. Approximately 60% of *L. calcarifer* individuals were recaptured exclusively in the pool of origin (Fig 2). Very few individuals moved between networks (only 2% were recaptured in a different network), but many individuals moved into neighbouring pools (38% were recaptured in a different pool within the same network). This suggests that individual *L. calcarifer* exhibit fidelity at relatively small scales, with strong fidelity exhibited at the wetland, network, and pool scale.

The relatively long residence times of individual *L. calcarifer* in Annandale Wetland, and fidelity at small spatial scales, is consistent with the settle and stay hypothesis. Although barramundi may move between neighbouring pools to some extent, individuals generally settle and remain in particular pools. Furthermore, spatial patterns of CPUE and recaptures (Fig 4) suggest that individuals aggregate within certain pools, and exhibit greater fidelity to those with higher CPUE. Individuals presumably 'sample' pools during connection events, and remain within those of favourable environmental condition, which become 'hotspots'.

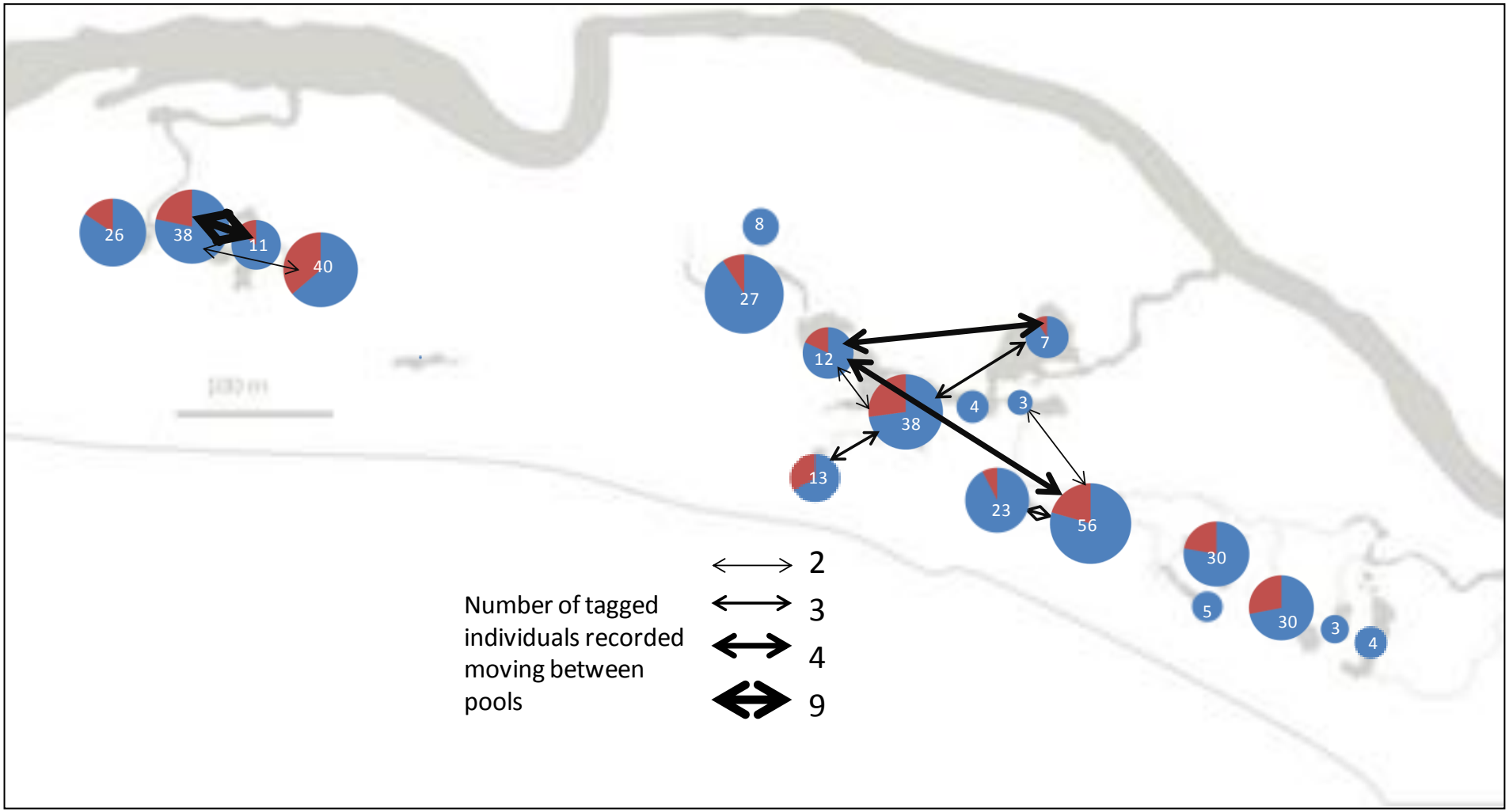

Figure 4: Map of Annandale Wetland illustrating the nature of individual *L. calcarifer* (barramundi) movements between pools, and the fidelity exhibited for each pool as a function of CPUE. The circles have been scaled to represent log(CPUE) of barramundi within each pool, while the total number of barramundi captured in each pools over the 2 year sampling period (standardised by netting effort) is written within each circle. The red segment of each circle represents the proportion of tagged individuals that were resident (i.e. recaptured exclusively in the pool of origin) to a pool. Black arrows represent recorded movements of individuals between pools. To simplify visual representation, pathways of movement made only by a single individual have not been shown on the map.

Appendix E

List of publications arising from this thesis

Davis B, Johnston R, Baker R, Sheaves M (2012) Fish utilisation of wetland nurseries with complex hydrological connectivity. PLoS ONE 7(11): e49107. doi:10.1371/journal.pone.0049107

Davis B, Baker R, Sheaves M (2014) Seascape and metacommunity processes regulate fish assemblage structure in coastal wetlands. Marine Ecology Progress Series 500:187-202

Davis B, Mattone C, Sheaves M (2014) Bottom-up control regulates patterns of fish connectivity and assemblage structure in coastal wetlands. Marine Ecology Progress Series 500:175-186