Seascape and metacommunity processes regulate fish assemblage structure in coastal wetlands

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ABSTRACT: Faunal complexity is an impediment to understanding the function of fragmented 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. We assessed the role of local vs. regional factors on the 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 2 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 because of 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.

KEY WORDS: Nursery grounds · Estuary · Salt marsh · Tidal wetland · Connectivity · Spatial dynamics

INTRODUCTION

Considering habitat units as a component of a broader landscape/seascape is essential for understanding the range of processes driving assemblage compositions. Patches of fragmented habitats (e.g. lakes embedded in a terrestrial matrix) do not function as isolated entities, but faunal communities within patches are linked by the dispersal of species or subjected to a common source of colonists. Consequently, faunal assemblages in fragmented habitats operate as an interconnected group of communities, or a '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, and 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) and have provided greater insights into the 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 because of 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 (Rozas 1995, Rountree & Able 2007). Although similar multi-scale landscape principles have recently been applied to components of coastal ecosystems, such as mangroves and seagrass meadows (Pittman et al. 2004, Boström et al. 2011), 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 of different habitat types providing complementary resources for fish (Olds et al.

2012, Nagelkerken et al. 2013). Pools scattered across intertidal zones 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 (Davies et al. in press). These characteristics of tidal pools, coupled with being 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 the community dynamics of these systems.

Tidal pools are an important component of the coastal seascape (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 and coastal marine waters, and from freshwater reaches during wet season flows (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') (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 (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 that 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, several potential pathways must be considered when defining patch connectivity, beyond the simple inter-patch distances considered in studies of other wetland systems (Astorga et al. 2012, 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, and 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. Variation in the 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, and types and extent of fringing vegetation. However, the relative influence of these factors on patterns of fish community structure and dynamics is 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, we sampled 20 tidal pools scattered across a tropical salt marsh system over 3 annual cycles. We examined the extent to which assemblages differed between pools and then considered the 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 we 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.

MATERIALS AND METHODS

Study site

The study was conducted in Annandale Wetland (19.19° S, 146.44° E) (Fig. 1), a 0.4 km^2 *Sporobolus virginicus* salt marsh 8 km upstream of the mouth of the Ross River. Interspersed across the wetland are 20 discrete permanent pools ranging in area from 80 to 2500 m^2 and in low tide depth from 30 to 130 cm. The pools generally lack aquatic vegetation or woody debris. They encompass a range of substrates, varying from fine mud to coarse rubble.

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 of tidal connectivity a pool receives is largely governed by its position along the intertidal gradient from the estuary channel to the terrestrial-aquatic ecotone. However, tidal connectivity is modified by topographic heterogeneity within the gradient. Many pools are connected by narrow channels of different lengths and depths, providing regular but
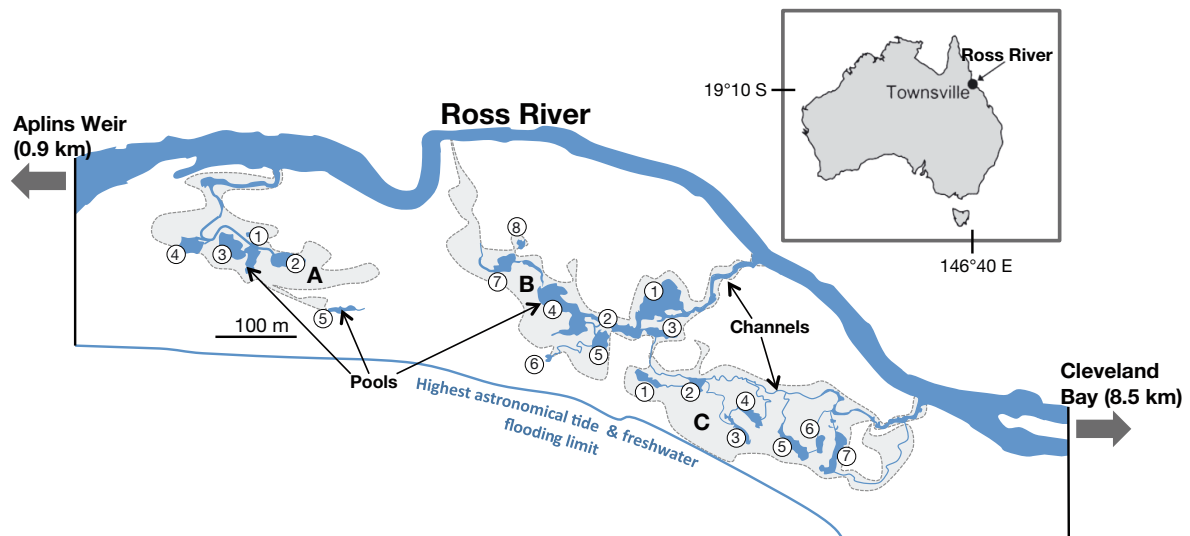

Fig. 1. Annandale Wetland containing the 20 wetland pools adjacent to the Ross River, Australia. The wetland extends from the subtidal channel of the Ross River south to the uppermost tidal limits (highest astronomical tide ~4 m; occurring during January and February), indicated by the blue boundary 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 to 3.8 m; occurring for a few days during 1 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 have been assigned unique numbers, such that each pool on the wetland can be referred to by a unique alphanumeric code

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 to March), Aplins Weir (located ~0.9 km upstream) overflows, blanketing the wetland in a sheet of fresh water. 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.

Fish sampling

Fish were sampled from all 20 pools following drawdown of floodwaters in March 2010. Sampling then continued through the year on a monthly basis until the re-commencement of flooding in December. An annual replicate was collected in 2011, including monthly sampling in the first 3 months following drawdown (April to June), followed by bi-monthly sampling until the end of the year. Another annual replicate was collected in April 2012. 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. All samples were collected at the bottom quarter of the tide (i.e. around low tide) during the new moon phase to ensure consistent tidal regimes for each sampling occasion throughout the study. Sampling occurred during the spring tide period of the lunar tidal cycle, when hydrological connectivity and hence the potential for fish exchange is greatest.

Sampling was conducted using a seine net (12 m long, 2 m deep, 6 mm mesh), with an effective sampling width of 8 m. Some pools could be comprehensively sampled in a single seine haul. However, in larger pools where 1 net haul covered less than ~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 differ-

ent taxa. Fish numbers and size classes (in 10 mm increments) in each haul were quickly recorded and 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. After recording, the catch was immediately returned to the water alive, with the exception of the noxious pest species *Oreochromis mossambicus*, which was euthanized onsite in accordance with government regulation. Since the exchange rate of individuals and species in and out of the wetland system was unknown, the return of catch was important to minimize mortalities, which could have potentially modified catches in subsequent months. To control for possible recaptures of the same individuals in pools requiring multiple hauls on a single sampling occasion, for each taxon only the count from the haul with maximum abundance was used to represent their contribution to the pool's assemblage for that 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 to December over 2 annual cycles (and a third annual cycle for April).

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 local patch variables, which included pool morphology and physicochemical variables (Table 1). Because of the multi-faceted 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 among variables.

Data analysis

The 22 most abundant taxa which together comprised >95% of the total catch were selected for assemblage-level analysis. Two taxa (*Oreochromis mossambicus* and *Elops hawaiensis*) showed strong bimodal size structure, with each mode representing

Table 1. Description of the explanatory variables for 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	Units	Method	Underlying ecological/biological hypothesis
Connectivity				
Freshwater overbank distance	Shortest linear distance from the 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 fresh water
Tidal overbank distance	Shortest path from the 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 the Ross River to a pool via channelised connections; channels were defined as water courses connecting pools to the Ross River or other pools; for 2 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 the Ross River	m above lowest astronomical tide	Pool depths were continuously logged over a tidal sequence; depth fluctuations were plotted against realised tide data (courtesy of Townsville Port Authority); 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).	3 network categories defined: *A, B, C*	GIS + ground truthing	Differences in assemblage between pool clusters are greater than differences between individual pools within clusters because of upstream/stochastic disparities in colonisation followed by little connectivity between the 3 networks

Table 1 (continued)

Variable	Description	Units	Method	Underlying ecological/biological hypothesis
Connectivity				
Pool order	Number of intermediate pools an individual would need to pass through to colonise the destination pool from the Ross River	Number of pools	GIS	Colonisation of a pool may be reduced by the number of intermediate pools between a given pool and the 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	Adjacent pools may act as sources for recruitment, in turn modifying the assemblage of a neighbouring pool
Pool morphology				
Maximum depth	–	cm	Measuring staff	Fish may only settle in a pool if it exceeds a critical depth
Surface area	Low tide surface area	m²	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 settle in pools with appropriate substrate
Mangrove fringe	Proportion of pool perimeter fringed by mangrove	m	GIS	Certain species may settle 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	m²	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 pools within tolerable range
Visibility	–	cm	Secchi disc	Fish limited to pools within tolerable range
Temperature	–	°C	Thermometer	Fish limited to pools within tolerable range

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 to 90 mm) and adult (>200 mm) stages, and *E. hawaiensis* was split into small juvenile (0 to 110 mm) and large juvenile (150 to 300 mm) stages. Although many other species on the wetland occurred 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 downweight the influence of highly abundant taxa, favouring a more assemblage-orientated analysis (Clarke 1993).

Assemblage structure (CPUE × pool × month) was analysed with a multivariate classification and regression tree (mCART) (De'ath 2002) based on Bray-Curtis dissimilarities, using the R 'mvpart' package. Final tree models were selected based on a scree plot of explained variance, with tree size pruned at the point where the proportion of variance explained began to noticeably tail off. mCART analysis is accepted as a simple and robust technique for modelling ecological data (De'ath & Fabricius 2000) and has been used previously to explain nekton assemblage structure (Sheaves et al. 2010). Initially, a tree was constructed using pool codes (consisting of network and pool number; see Fig. 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, including the temporal variables 'month' and 'year' 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 over time.

The mCART model was then re-run with pool codes replaced by the explanatory variables (see Table 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 a univariate CART, 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.

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*, *Herklotsichthys castelnaui*, *Gerres filamentosus*, and *Stolephorus* spp. together constituted >85% of the assemblage.

Assemblage composition

General patterns in assemblage structure

Assemblages varied considerably among pools. The dominant split in the mCART formed at the 'pool' level (Fig. 2), suggesting spatial organisation of fish on the wetland explained more assemblage variability than any temporal change (i.e. 'month' and 'year') and showed that spatial patterns were consis-
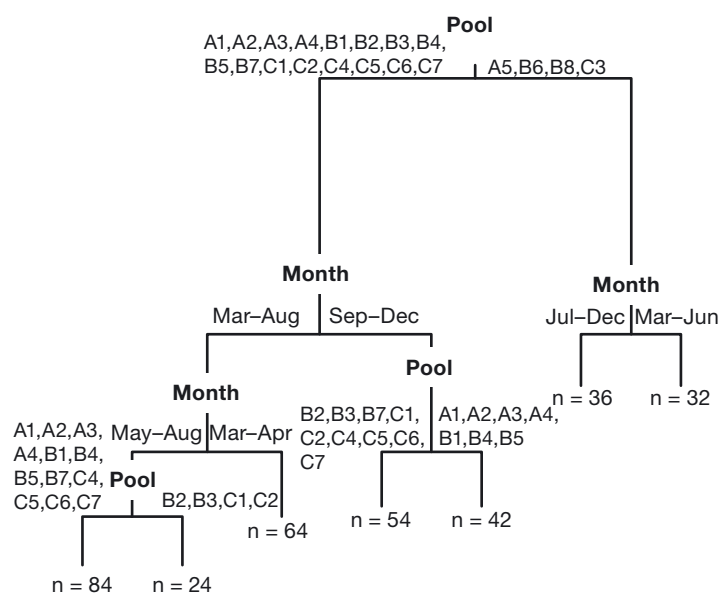

Fig. 2. Multivariate classification and regression tree (mCART) of catch per unit effort [$\log(CPUE + 1)$] based on pool codes (network and pool number), month, and year, explaining 21% of the variation in assemblage structure. Factors responsible for splits are indicated in bold above branch points. Codes above branches indicate levels of factors split in each direction. n represents the number of pool × month × year cases grouped in each terminal branch

tent. This split was characterised by a minority of pools (A5, B6, B8, C3) consistently harbouring a different assemblage to the rest of the wetland.

Explaining patterns

Explanatory variables fed into the mCART (see Table 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, and 20% explained variability for the 'explanatory' model). The mCART output suggested that a connectivity metric 'critical tidal connection' was the key structuring variable (Fig. 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 by 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 during tides <2.8 m (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. 3a) indicated the presence of 2 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 *Leiognathus equulus*, *Ambassis vachelli*, *Gerres filamentosus*, *Stolephorus* spp., *Herklotsichthys castelnaui*, adult *Oreochromis 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*, *Nematalosa erebi*, *Pseudomugil signifer*, juvenile *O. mossambicus*, small juvenile mugilids, and small juvenile *Elops 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. 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 phenome-

non similar to '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 2 additional pools in Network C (Fig. 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. 3a), the 2 additional 'terminal' pools in Network C harboured an intermediate assemblage (Fig. 3b). This intermediate assemblage was characterised by high abundances of taxa typical of both higher elevation pools (juvenile *Oreochromis mossambicus*, *Hypseleotris compressa, Pseudomugil signifer*, small juvenile mugilids, and small juvenile *Elops hawaiensis*) and lower elevation pools (including *Acanthopagrus* spp. and *Ambassis vachelli*) (Fig. 3b) but also the diminished abundances of other lower elevation taxa (*Leiognathus equulus*, *Stolephorus* spp., and *Herklotsichthys castelnaui*). It is also worth noting that these terminal pools in Network C are the 2 shallowest pools on the wetland (maximum depths <60 cm).

Both model outputs displayed similar secondary splits that reflected seasonal dynamics (Fig. 3a,b). Seasonal assemblage shifts occurred in both more isolated (higher elevation/terminal) and better connected (lower elevation/mid-stream) pools. These shifts were partially caused by the high abundances of freshwater-spawned *Nematalosa erebi* across the whole wetland early in the year (Fig. 3a,b). In more isolated pools, seasonal assemblage shifts were also caused by higher abundances of juvenile *Oreochromis mossambicus* during post-wet season months (March to May/June) (Fig. 3a,b). Meanwhile, in better connected pools, seasonal assemblage shifts were also caused by the influx of *Acanthopagrus* spp., *Stolephorus* spp., *Thryssa hamiltonii*, and *Herklotsichthys castelnaui* to the wetland later in the year (September to December). These late-year recruits consistently occupied Network A in higher abundance than Network C, illustrated by the tertiary network split (Fig. 3a,b), indicative of finer scale structuring among better connected pools.

Individual species distribution

Univariate CART analysis 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

Fig. 3. Multivariate classification and regression tree (mCART) of catch per unit effort [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. n represents the number of pool × month × year cases grouped in each terminal branch. Species profiles below represent species CPUEs corresponding to each of the terminal branches. See Table 2 for full species names
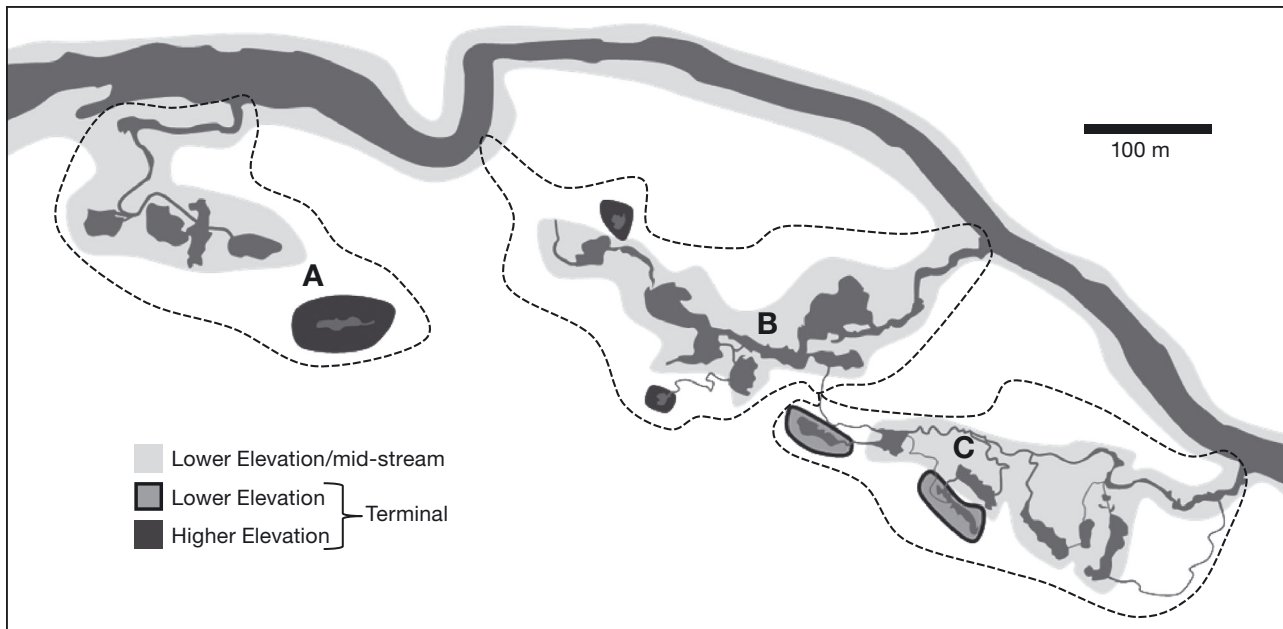
Fig. 4. Heterogeneity in fish assemblages, derived from pool groupings in Fig. 3a,b. Light grey indicates an assemblage which mirrors that of the estuary channel, including the 'lower elevation pools'. Dark grey indicates a unique 'higher elevation' assemblage, connected to the Ross River at tides >2.8 m. Light grey with black margins indicates an intermediate assemblage occurring in the 2 shallowest pools (<60 cm maximum depth), which also represent the upstream 'terminals' of Network C. The dark grey pools are also terminal pools in their respective networks. The network boundaries are shown with a dotted black line

distributed independently of assemblage level patterns (Table 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, *Glossogobius 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). *Chanos chanos* also responded to an alternative connectivity metric, occurring in higher abundances in pools located further from the Ross River (freshwater overbank distance >210 m) during post-wet season and early dry season months. *Penaeus merguiensis*, on the other hand, occurred in greatest abundance in pools connected to the 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 *Leiognathus equulus* and *Oreochromis mossambicus* were most abundant, they were primarily found over mud or muddy sand rather than coarser sandy or rubble substrates.

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 (Davis et al. 2012).This pronounced spatial variability indicates the operation of key ecological processes.

Connectivity-based processes took primacy over local processes in regulating these spatial patterns, although 2 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 an assemblage distinct from the rest of the wetland, which generally connected to the Ross River on neap

Table 2. Results from univariate classification and regression trees (CART) of catch per unit effort [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 (+ branch)	Secondary split (− branch)
Ambassis vachelli	Critical tidal connection − (2.8 m)		
Gerres filamentosus	Critical tidal connection − (2.8 m)		
Megalops cyprinoides	Critical tidal connection + (2.4 m)		Year (2011)
Hypseleotris compressa	Terminals	Maximum depth + (85 cm)	
Lates calcarifer	Mid-stream	Channel length + (290 m)	
Oreochromis mossambicus (adult)	Mid-stream	Substrate (mud/muddy sand)	
Leiognathus equulus	Mid-stream	Substrate (mud/muddy sand)	Tidal overbank − (180 m)
Mugilid (small juvenile)	Terminals	Month (July to December)	
O. mossambicus (juvenile)	Terminals		
Gobiid sp. 1	Tidal overbank − (210 m)	Critical tidal connection − (2.2 m)	
Acanthopagrus spp.	Month (September to December, March)	Critical tidal connection − (2.8 m)	
Chanos chanos	Month (March to July, September)	Freshwater overbank distance + (210 m)	
Elops hawaiensis (small juvenile)	Month (November to December)	Terminals	
Herklotsichthys castelnaui	Month (November to December)	Network (A & B)	
Metapenaeus bennettae	Month (June, August to November)	Year (2011)	
Nematalosa erebi	Month (March to April)	Year (2011)	
Pseudomugil signifer	Month (June to October)	Network (B) & maximum depth (<60 cm)	Critical tidal connection + (2.68 m)
Glossogobius circumspectus	Nearest neighbour − (17 m)	Month (June, August to December)	
Stolephorus spp.	Network (A)	Critical tidal connection − (>2.8)	
Penaeus merguiensis	Tidal overbank − (150 m)	Month (June to September, December)	
E. hawaiensis (large juvenile)	No viable model		
Liza subviridis	No viable model		
Selenotoca multifasciata	No viable model		
Thryssa hamiltonii	No viable model		
Moolgarda seheli	No viable model		

high tides. Assemblages in these higher elevation pools were dominated by *Hypseleotris compressa*, juvenile *Oreochromis mossambicus*, small juvenile mugilids and *Elops hawaiensis*, *Pseudomugil signifer*, *Nematalosa erebi*, and *Megalops 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 (*Ambassis vachelli*, *Leiognathus equulus*, *Gerres filamentosus*, *Herklotsichthys castelnaui*, and *Stolephorus* spp.) comprise a subset of typical estuary channel fauna (Robertson & Duke 1990, 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 2 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. 5a), which predict patterns of assemblage attenuation along gradients of isolation.

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 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 *Pseudomugil signifer* and *Hypseleotris compressa* actively use the tropical marsh surface (Connolly et al. 1997), advancing with the leading edge of water at high tide (M. Sheaves unpubl. 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. The purpose of this upstream migration may be for 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 fresh water is denied. It seems reasonable that freshwater species (including *Nematalosa erebi* and juvenile *Oreochromis mossambicus*) would move in pursuit of lower salinities as conditions become more marine after the wet season, while some marine-spawned taxa (including *Megalops cyprinoides*, *Chanos chanos,* and mugilids) are known to move into freshwater reaches to varying extents as young juveniles (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, Elops hawaiensis*, and mugilids 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 (Russell & Garrett 1983, Stevens et al. 2007, Sheaves & Johnston 2008). However, despite these general trends, species-specific dispersal capabilities, resource requirements, and life history strategies meant that some species were structured independently of assemblage patterns in the present study. For instance, the distribution of 2 species of Gobiidae were best explained by distance-based variables (tidal overbank distance and nearest neighbour), possibly because of brood spawning and small home ranges common to this family (Ray & Lynda 2001). Similarly, *Penaeus merguiensis* was largely restricted to 2 pools close 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 particular 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 *Nematalosa erebi.* Only one species, *Chanos chanos,* appeared to respond to freshwater overbank distance to access more upstream habitats during wet season floods. This suggests that fresh-

water floods are not as important in structuring assemblages of tidal wetlands or that tidally mediated processes rapidly overcome the effects of flooding.

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 5b). The biggest split among lower elevation pools was because of certain taxa colonising particular networks in higher abundance during the late dry to 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 (*Herklotsichthys castelnaui*, *Stolephorus* spp., and *Thryssa hamiltonii*).

Many species appeared to avoid particularly shallow pools (<60 cm maximum depth), including *Leiognathus equulus*, *Stolephorus* spp., and *Herklotsichthys castelnaui*, while *Megalops cyprinoides* was biased towards particularly deep pools (>85 cm maximum depth), in accordance 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.

Within-pool substrate type may have also been important for some species; *Leiognathus equulus* and *Oreochromis mossambicus* were rarely found over coarser sand or rubble substrates. A preference for finer substrates has been observed previously for *L. equulus* in Australian tropical estuaries (Johnston & Sheaves 2007). This behaviour may relate to selective foraging for benthic invertebrates, which form a considerable proportion of their diet (Wilson &
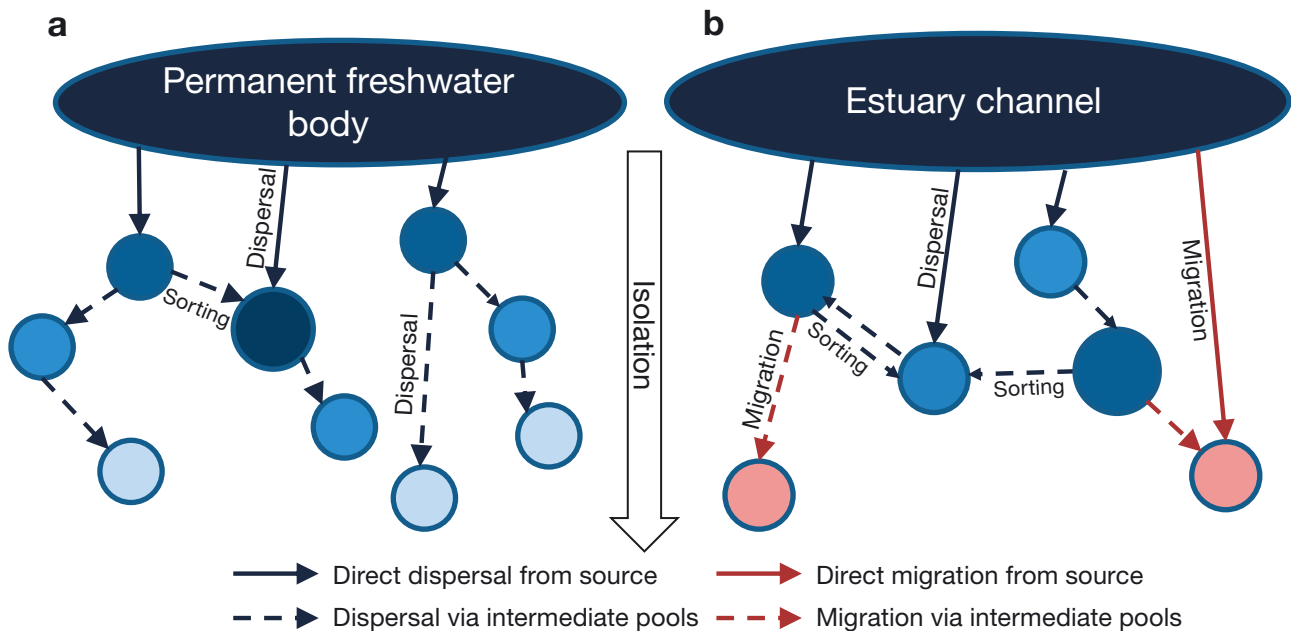

Fig. 5. Conceptual models illustrating how assemblages are structured in (a) freshwater mainland-island type metacommunities, based on trends reported in the literature (Snodgrass et al. 1996, Taylor 1997, Magnuson et al. 1998) and (b) in tidal systems of similar topological configuration based on results 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 the red circles)

Sheaves 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, rather, the avoidance of high flow velocities (Whitfield & Blaber 1979) that result in coarser substrates.

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. 5) due to the contrasting responses to hydrological connectivity of 2 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. 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 (Pittman & McAlpine 2003, Boström et al. 2011). 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.

Conclusions

The clear assemblage distinction among higher and lower elevation pools illustrates how otherwise similar patches of coastal wetland habitat may per-

form very different functions because of 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. 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.

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