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Importance of estuarine mangroves to juvenile banana prawns

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ABSTRACT

Offshore catches of banana prawns, *Penaeus merguiensis*, are correlated with the extent of mangrove forests. However, recent evaluation has questioned whether the apparent relationship between juvenile penaeids and mangroves reflects specific utilisation of mangroves or just the use of shallow, organically rich, muddy habitats. We investigated this by focussing on juvenile *P. merguiensis* within 30 mangrove estuaries spanning 650 km of the coast of north-eastern Australia. We investigated a range of hierarchically clustered spatial scales and within-estuary spatial resolutions, as well as variables representing a variety of estuary structural factors, anthropogenic impacts, and particular hypotheses about the ways in which mangroves could influence *P. merguiensis* catch per unit effort (CPUE). Estuary to estuary differences, rather than climatic zone or the proximity of other estuaries, was the major large scale spatial influence on CPUE. At the among-estuaries scale mangrove extent appeared to influence CPUE but was extensively confounded with the effects of two non-mangrove variables; intertidal extent and substrate type. The fact that 3 alternative measures of connectivity with mangrove forests were not influential, points to the importance of the non-mangrove variables rather than mangrove extent. At the within-estuary scale, *P. merguiensis* CPUE was correlated with the extent of shallow water but not with mangrove variables. The spatial and temporal extent of sampling support a strong conclusion that factors associated with mangroves alone do not drive abundances of juvenile prawns. Nevertheless, despite being the dominant habitat, mangroves are only one of a mosaic of interacting habitats occurring in the tropical estuaries inhabited by juvenile penaeids (Sheaves, 2009), so causal relationships are complex and difficult to define unambiguously.

1. Introduction

Although coastal wetlands are recognised as important nursery grounds for fish and crustaceans (Robertson and Duke, 1990; Vance et al., 2002; Minello et al., 2008), the exact provision of this nursery value is poorly understood. One group that seems to have a particularly strong affinity for coastal wetlands is penaeid shrimps. Peak catches often correlate with the proximity of major wetlands (Rozas and Minello, 1998; Zimmerman et al., 2000), river mouths (Dalzell et al., 1996), seagrass beds (Coles et al., 1993), or mangroves (Subramaniam, 1990; Manson et al., 2005), reflecting the high nursery value of these habitats (Sheaves et al., 2007; Minello et al., 2008). Not only are coastal wetlands vitally important to penaeids, but penaeids themselves are critical links in the complex food webs supporting biological function in these ecosystems (Abrantes and Sheaves, 2009). Penaeids occupy low trophic levels feeding on phytodetritus (Abrantes and Sheaves, 2009) and micro invertebrates (Kieckbusch et al., 2004; Karani et al., 2005), and are in turn prey for important predatory fish (Robertson and Duke, 1990; Salini et al., 1998). Additionally, many penaeids have life-cycle migrations in which estuarine juveniles are the biological vehicles for translocating nutrient subsidies across ecosystem boundaries (Deegan, 1993; Sheaves, 2009). Consequently, the health and integrity of coastal nurseries, and the manner in which penaeids utilise them, are critical to both the functioning of coastal ecosystems and to the offshore fisheries they support (Barbier and Strand, 1997; de Graaf and Xuan, 1998).

The banana prawn, *Penaeus merguiensis*, is an important target for commercial and subsistence fisheries from Pakistan east to Taiwan and Indonesia, and south to Papua New Guinea and tropical Australia (Holthuis, 1980). *P. merguiensis* exhibits a typical penaeid life cycle (Dall et al., 1990), with adults occupying and spawning in

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near- and off-shore waters (Crocos and Kerr, 1983; Rothlisberg et al., 1985), and larvae migrating to estuarine nurseries (Rothlisberg and Jackson, 1987).

Mangroves are the primary nurseries of *Penaeus merguiensis* (Staples et al., 1985; Staples and Vance, 1985; Primavera, 1998), and offshore catches often correlate with the presence of estuarine and coastal mangroves (Manson et al., 2005; Meynecke et al., 2008). However, our understanding of the exact relationship between *P. merguiensis* and mangroves is patchy, incomplete and restricted in its breadth of spatial representation. Relationships based on offshore catches are often difficult to interpret because of the coarse resolution of available data. For example, the data used for large scale analyses of Manson et al. (2005) and Meynecke et al. (2008) were reported on a 30 nautical mile grid (1/2° of latitude). Determining the relationship between *P. merguiensis* and mangroves is further complicated by correlations with other factors (e.g. the presence of river mouths (Dalzell et al., 1996)), analytical difficulties (Lee, 2004), considerable spatio-temporal variability, and uncertainty about migration patterns (Loneragan et al., 2005). For instance, on Australia's northwest shelf the offshore fishery for the closely related *P. indicus* is hundreds of kilometres from their mangrove nursery grounds (Kenyon et al., 2004). Such issues, and the realisation that environmental variation that regulates offshore prawn catches actually acts on early life-history stages during residence in estuary nursery areas (Staples and Vance, 1986; Vance et al., 1998), have prompted calls for studies that address the relationship between *P. merguiensis* and mangroves more directly by focussing on the mangrove systems themselves (Manson et al., 2005). This need is strengthened by analysis suggesting that factors such as tidal amplitude may have a stronger influence on penaeid abundance than the extent of mangroves themselves (Ahmad Adnan et al., 2002; Lee, 2004).

While a number of studies have investigated *Penaeus merguiensis* at smaller, within-nursery scales, most have only considered a limited number of estuaries in just a few geographical areas, or used large scale sampling gear such as beam trawls (e.g. Staples, 1979) that focus on the main body of the estuary and do not allow the effect of small-scale habitat differences to be investigated. Consequently, we have incomplete understanding of the spatial and temporal consistency of utilisation of estuarine nurseries by juvenile *P. merguiensis*, the relationship of *P. merguiensis* to small-scale habitat variations, and thus of the precise relationship of *P. merguiensis* with mangroves. We know that *P. merguiensis* favours areas of estuaries with muddy rather than sandy substrates (Vance et al., 1990; Kenyon et al., 2004), shallow rather than deep banks (Johnston and Sheaves, 2007), and turbid over clear areas (Johnston et al., 2007). Furthermore, the few studies that have sampled within mangrove forests have shown that *P. merguiensis* juveniles enter mangroves at high tide (Vance et al., 1996, 2002). However, it is unclear if this reflects specific utilisation of mangroves or just the use of shallow, organically rich, muddy habitats (Lee, 2004) in tropical estuaries that are almost invariably mangrove lined.

Given the uncertainty about the relationship of penaeids to mangroves raised by Lee (2004) and the lack of estuary scale evaluation identified by Manson et al. (2005) it is relevant to focus on the relationship between *Penaeus merguiensis* and mangroves at the level of estuarine nursery grounds themselves. If the established correlations between offshore fisheries catches and estuarine wetland nursery habitat characteristics (Manson et al., 2005; Meynecke et al., 2008) reflect important population regulating processes acting on juvenile life stages, then juvenile populations should respond to differences in the relative extent of mangroves among estuaries, and specific mangrove habitat characteristics within the estuaries themselves. We sampled juvenile *P. merguiensis* (1–25 mm carapace length) extensively along the lengths of 30 mangrove estuaries spanning 650 km of northeast coastline of north-eastern Australia, incorporating a range of hierarchically clustered spatial scales and within-estuary levels of spatial resolution. The primary aims were (i) to determine the spatial and temporal consistency of utilisation of estuarine nurseries by juvenile *P. merguiensis*, and (ii) to investigate the among- and within-estuary relationships of *P. merguiensis* juveniles to spatial and biological factors (especially mangroves) and anthropogenic factors.

2. Methods

2.1. Sampling

This study, focussed on *Penaeus merguiensis*, is part of a broader investigation examining spatial and temporal dynamics of estuarine nekton among a large number of tropical estuaries in north-eastern Queensland, Australia (Fig. 1), with previously published work concentrating on juvenile fish. The study includes two components, and additional site maps and detailed descriptions of the sampling designs can be found in the papers describing patterns in the fish assemblage; Sheaves and Johnston (2009, 2010) and Sheaves et al. (2010).

In the "among-estuaries" component, 21 estuaries spanning 650 km of the coastline of northeast Australia, from Saltwater Creek in Trinity Bay, to Constant Creek in the Hillsborough Channel, were sampled over 4 consecutive spring tidal cycles during the environmentally stable late dry season between August and October 2007 (Online appendix table 1) (Sheaves and Johnston, 2009). The late dry season provides strong interannual consistency in nekton assemblage structure (Sheaves, 2006) and is the season when habitat preferences are likely to be most well defined. Estuaries in northern Australia feature substantial wet-season flooding, likely to produce fluctuating catches, leading to noisy results. Additionally, greatly increased numbers of juvenile nekton in the high recruitment wet and immediate post-wet seasons (Sheaves, 2006) lead to the possibility of spill over effects masking habitat preferences. The

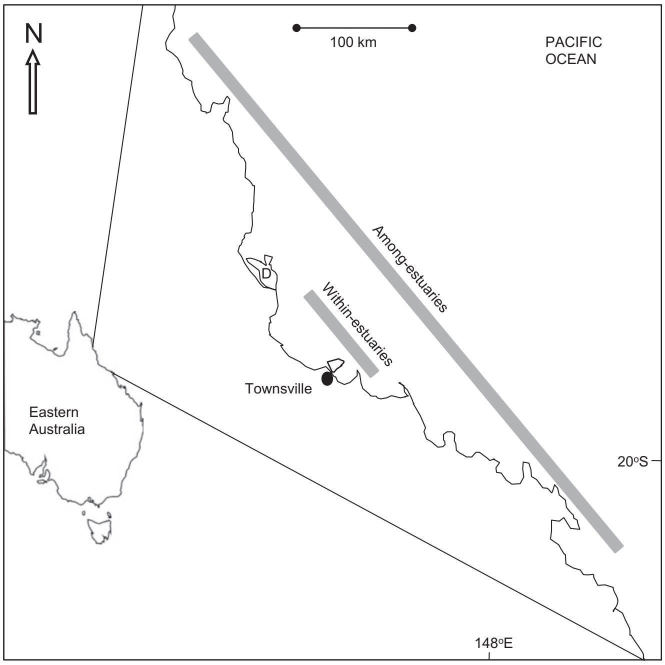

Fig. 1. Location map showing location and coastline spanned by each of the studies from which data were obtained.

Table 1
Explanatory variables for 21 estuaries in “among-estuaries” analysis. Mean sea level (MSL) is defined as the boundary between mangrove forest and open water (Duke, 2006). Open water includes subtidal area plus intertidal area that is lower than forest margins, i.e. below MSL.

	Name	Description	Purpose
Spatial variables	Estuary	Estuary name	Allow determination of critical spatial scale at which variability is focussed
	Zone	Northern wet, dry, southern wet tropics	
	Region	Discrete sections of coast separated by headlands	
	Reach	Lower, mid, upper	
Estuary Structure variables	Estuary classification	Defined Tables 2 and 3 Sheaves and Johnston (2009)	Allow assessment of the geomorphological form of the estuary
	Entrance structure		
	Influence at entrance		
	Tidal range		
	Estuary length		
	Sinuosity		
	Subtidal area		
	Intertidal area		
	Sediment type		
	Shape of system	Intertidal perimeter (m)/open water area (m^2)	
	Relative intertidal extent	Total intertidal area (m^2)/area submerged at MSL (m^2)	To represent the influence of the extent of intertidal above MSL relative to open water habitat below MSL (proxy for potential holding capacity of system)
Mangrove variables	Mangrove forest shape	Mangrove area (m^2)/mangrove perimeter (m)	To represent the influence of compact verses linear shapes
	Relative mangrove extent	Mangrove area (m^2)/area submerged at MSL (m^2)	To represent the influence of the extent of mangroves relative to area of aquatic habitat when mangrove forests are not flooded
	Mangrove-water interface	Mangrove forest interface with subtidal (m)/area submerged at MSL (m^2)	To represent the influence of the amount of edge for connectivity with the mangrove forest relative to aquatic habitat at MSL
	Relative mangrove edge extent	Mangrove forest interface with open water (m)/total intertidal perimeter (m)	To represent the influence of the proportion of the system edge providing connectivity with the mangrove forest
	Mangrove forest access	Mangrove forest interface with open water (m)/mangrove area (m^2)	To represent the influence of the extent of forest access from open water relative to the extent of the mangrove forest i.e. distinguishes between systems with extensive forests and those with narrow mangrove fringes
Impact variables	Total anthropogenic development	Total % of perimeter developed	Measure of the total extent of development around the system
	Urban/industrial proportion	% Perimeter with adjacent urban or industrial development	Measure of the extent of urban/industrial development around the system
	Aquaculture proportion	% Perimeter with adjacent aquaculture	Measure of the extent of aquaculture development around the system
	Agriculture proportion	% Perimeter with adjacent agriculture	Measure of the extent of agricultural development around the system
	Pasture proportion	%Perimeter with adjacent pasture	Measure of the extent of pastoral development around the system

number of estuaries included prohibited the repeated sampling of each estuary through time; however 5 were repeat-sampled to evaluate temporal consistency of prawn densities. The sampling design allowed for spatial dynamics to be examined across a range of hierarchically clustered spatial scales. The 21 estuaries spanned *3 climatic zones* (northern wet tropics, dry tropics, and southern wet tropics) (BOM, 2011), comprising *7 regions* (discrete sections of coast or coastal waterways separated by headlands or capes), with *3 estuaries* per region. Each estuary was divided into *reaches* (lower, mid, and upper), with *3 sites* per reach (Sheaves and Johnston, 2009; Online appendix Table 1). *10 random replicate* samples were collected per site, to ensure that catch data were representative of the sites. Spatial and non-spatial explanatory variables (Table 1) were recorded in field or developed to aid interpretations.

The “within-estuary” component focussed on the dry tropics, the region with the highest abundance and occurrence of *Penaeus merguiensis* in the among-estuaries study. Nine small (<8 km navigable length) natural estuaries were sampled. These spanned 225 km of the dry tropics coast centred on Townsville, from Insulator Creek in the north, to Hell Hole Creek in the south (Sheaves and Johnston, 2010). The estuaries were sampled monthly to bi-monthly between November 2007 and January 2009 (Online appendix Table 1) (Sheaves et al., 2010). Flooding during Jan/Feb 2008 and Jan 2009 prevented sampling at some sites (see Table 2 in Sheaves et al., 2010). Small estuaries were chosen for the within-estuary study so that sampling could effectively cover the entire estuary and so prevent any within-estuary migrations from confounding apparent temporal trends. Two artificial estuaries included in the study of Sheaves et al. (2010) were excluded from the present study since penaeid shrimps rarely occurred in samples from those systems. Estuaries were divided into reaches (lower and upper for most, with the addition of mid for the larger estuaries), with initially 60 (November, December 2007), and subsequently 46 samples distributed evenly among reaches within each estuary on each sampling occasion except for Bluewater and Healy Creeks where 30 samples were collected on all occasions (Sheaves and Johnston, 2010). To assist with explanations, a number of site-specific habitat variables were also recorded (Table 2).

All estuaries sampled had mangrove forests in their lower reaches and at least a narrow mangrove fringe (<5 m wide) along the majority of their tidal extents. The dry tropics estuaries usually had

Table 2
Spatial explanatory variables and variables collected for each net in the "within-estuaries" analysis.

	Name	Description	Purpose
Spatial variables	Trip	March, April, May, July, September, October, November, December 2008, January 2009	Allow assessment of temporal and spatial change at the estuary-to-estuary level
	Estuary	Insulator, Bluewater, Healy, Sandfly, Cocoa, Doughboy, Crab, Mud, Hell Hole Cks	
	Reach	Downstream (all estuaries), Mid (all except Bluewater & Healy), Upstream (all except Bluewater)	
Net-level variables	Substrate[a]	Mud (>75% mud sized particles), mud_s (75–50% mud sized particles), sand_m (50–25% mud sized particles), sand (<25% mud sized particles)	To represent the influence of substrate type
	Hydrodynamics[a]	Eddy, pressure point, still water - measures determined from surface flow patterns Low current flow, moderate flow, high flow – measures determined from extent of net deflection in water column	To represent the influence of hydrodynamics
	Bank angle[a]	Mean of 3 measurements; top of bank, waters edge, half way between	A proxy for the extent of shallow water throughout the tide
	Canopy overhang[b]	Presence or absence of overhanging canopy at sampling site	To represent the influence of vegetation shading
	Structure[b]	Presence or absence of roots or other timber at the perimeter of the sampling site	To represent the influence of complex structure
	Dominant vegetation[b]	Bare, mangrove single species (named), mixed mangroves, salt marsh/mangroves, salt couch (*Sporobolus virginicus*), salt marsh succulents, terrestrial vegetation	To represent the influence of vegetation type
	Mangrove pres/abs[b]	Presence or absence of mangroves	Two approaches to representing the influence of the occurrence of mangroves
	Mangrove dominant[b]	Mangroves dominant plant or not	

[a] Small-scale measures representing the immediate area that each net sampled.
[b] Meso-scale measures representing the area within 10 m of each net sample.

extensive saltpan and saltmarsh adjacent to their mid and upper reaches, and along the inland fringes of their mangrove forests. In contrast, wet tropics estuaries were mangrove lined for most of their tidal lengths, usually with rainforest or farmland along their inland fringes. Tidal ranges increased from north to south with the smallest range, 3.36 m, in the north and greatest range, 6.13 m, in the south. All estuaries were relatively short (maximum tidal incursions between 2 and 25.6 km) and narrow (maximum width < 200 m), with depths at low tide mainly 3 m or less.

All samples were collected with a 2.4 m radius monofilament draw-string cast net with 5 mm mesh. This approach allowed much more specific focus on individual habitat types than previous studies using gear such as beam trawls (Staples, 1979). Cast nets allow much higher replication in a given time than alternative sampling approaches (Johnston and Sheaves, 2007), can be deployed equivalently in habitats unsuited to use of seine or trawl nets (Stevens et al., 2006; Johnston and Sheaves, 2008) and provide consistent efficiency when collecting crustaceans (Baker and Minello, 2011). Cast nets sample shrimps effectively (Johnston et al., 2007) because shrimp escape response is triggered by tactile rather than visual signals (Watson et al., 1992) and escape direction is random (Watson et al., 1992; Xiao and Greenwood, 1993). To minimise sampling variability, one operator collected all samples for both studies. Theoretical sampling area of nets was 18.1 m^2 but in practice sample area is approximately 50% of theoretical maximum, around 9 m^2, with low variability for an experienced operator (Johnston and Sheaves, 2008; Baker and Minello, 2011). Samples were collected from a 4.3 m boat fitted with an electric motor to minimise disturbance, and followed the protocols of Sheaves et al. (2007). Samples were collected in daylight when *Penaeus merguiensis* burying behaviour is uncommon (Meager et al., 2005) and over low tide periods when mangrove forests were drained. Samples were collected along the banks of the estuaries since these habitats contain the bulk of small nekton, including penaeid shrimps (Meager et al., 2003; Johnston and Sheaves, 2007). This sampling design resulted in a total of 2030 individual replicate cast net samples for the among-estuaries study, and 3469 replicate samples for the within-estuary study.

2.2. Statistical analyses

2.2.1. Among-estuaries component

Penaeus merguiensis among-estuaries catch data were analysed using univariate Classification and Regression trees (CARTs) (De'ath & Fabricius, 2000). Site was the focal sampling unit so the 10 replicate nets per site were used to calculate the dependent variable, mean CPUE per net for each site. There were zeros in the final data set so the CPUE data were scaled to means per 100 nets to allow a ln $(\times + 1)$ transformation (which produced the most symmetrical distribution of residuals) to be used without the addition of 1 unit biasing the data where mean catches were low. As well as the 4 spatial variables (Zone, Region, Estuary, Reach), 21 non-spatial predictors were defined at the estuary level; 11 estuary structure variables, 5 mangrove variables, and 5 impact variables (Table 1). These included both redefined variables featured in the OzEstuaries data base (Anon, 2008) and newly defined variables. Definition and quantification of the variables were accomplished by using freely available remote imagery (Google Earth) and aerial photographic images, which were supported by detailed ground truthing (at least 1 d in each estuary system). Distances and areas were calculated from digitised images using SigmaScan Pro. There has been little quantification of human impacts on estuaries in the study area. Consequently, a set of variables was defined based on the perceived potential for human impact, which was estimated from the percentage of the estuaries' upper intertidal perimeters with potential anthropogenic stressors adjacent to them (derived from remote imagery). These predictors were constructed to allow evaluation of the importance of specific, potentially influential factors and processes (Table 1). Selection of the final CART model was conducted using 10-fold cross validation, with the 1-SE tree (the smallest tree with cross validation error within 1 SE of that of the tree with the minimum cross validation error) selected as the final tree model, a procedure that produces valid, biologically interpretable trees (Breiman et al., 1984; De'ath and Fabricius, 2000). The impact of each variable on model structure was evaluated by its occurrence in the final 1-SE tree. Additionally, the "relative importance" of variables was assessed to ensure variables that had high overall importance, but were not the best predictors for particular splits, were not overlooked. Importance is determined by using each variable at each branching of the final tree, with the best overall classifier given a relative importance of 100%.

2.2.2. Within-estuary component

Penaeus merguiensis within-estuary study data were again analysed using CARTs. The dependent variable was mean CPUE per 100 nets to allow a log (× + 1) transformation, which produced the most symmetrical distribution of residuals. This analysis focussed at small-scale (net-to-net level) differences. As well as Trip, Location and Reach, 8 predictor variables (Table 2) recorded for each net sample were used to investigate small scale correlates of *P. merguiensis* distribution.

3. Results

3.1. Among-estuaries component

Penaeus merguiensis juveniles were present in all 21 mangrove estuaries. The CART model (43% variability explained) was dominated by the spatial factors Estuary and Reach (Fig. 2). Estuary-to-estuary spatial differences form 4 of the 6 splits in the final model and had the highest relative importance. Notably neither Zone nor Bay was an influential predictor, and all major estuary groupings are comprised of estuaries from a mixture of Zones and Bays. Reach formed 2 splits in the CART model but overall had a low relative importance (26% that of Estuary). It had its principal effect in lower CPUE estuaries, where CPUE values were higher downstream than in mid and upstream reaches (Fig. 2a). Although

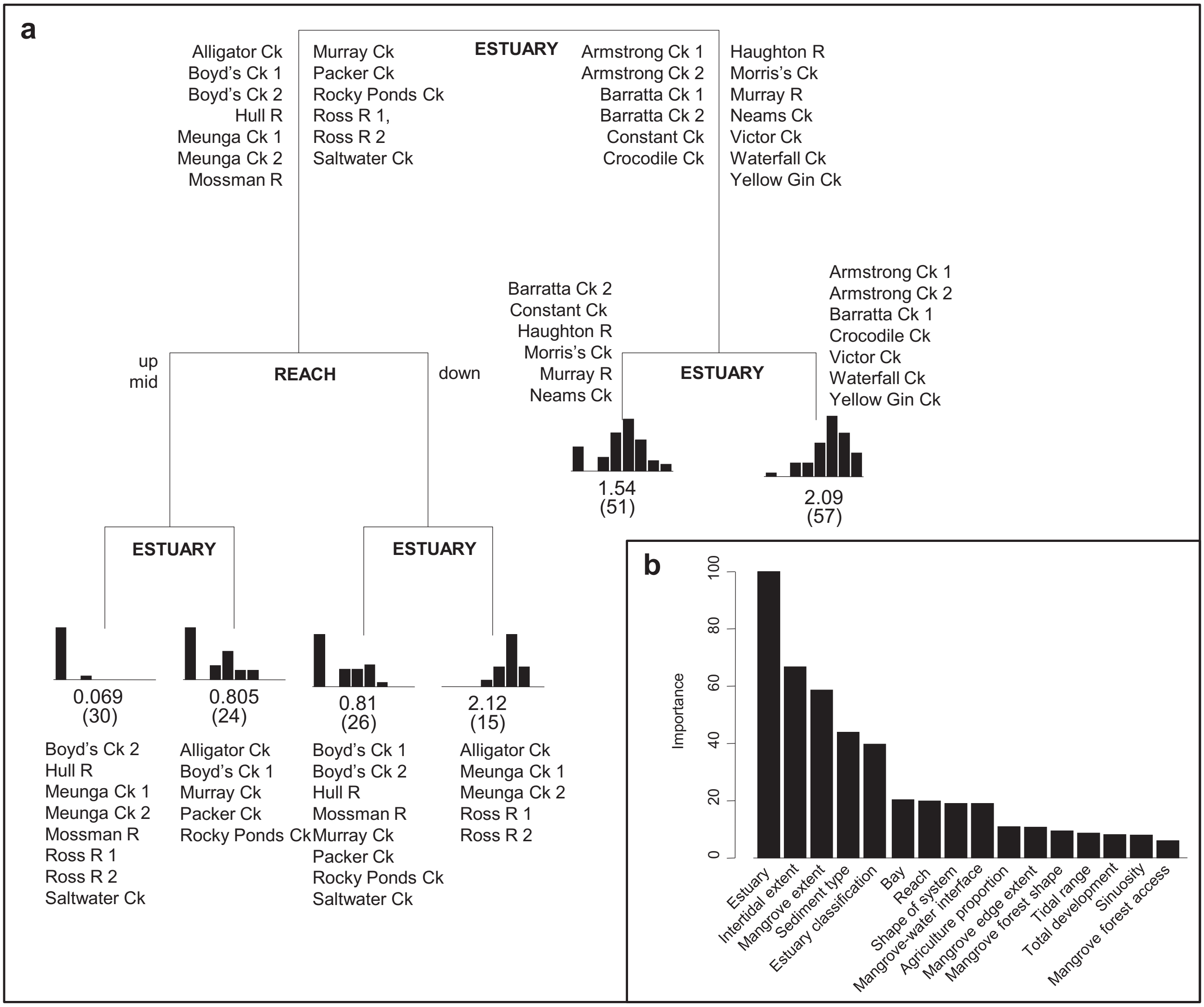

Fig. 2. CART analysis of *P. merguiensis* CPUE for the "among estuaries" data with all predictor variables included. (a) 6 leaf CART tree. Capitalised titles indicate the factor forming each split, text next to the branches indicates the composition of each branch, bar graphs below each terminal branch show distributions of log transformed CPUE for each terminal group, numbers below the bar graphs indicate the mean value for each branch, numbers in brackets indicate numbers of sites (groups of 10 replicate nets) represented by each node. (b) Relative importance of the variables providing the best overall classification for the CART tree.

non-spatial factors did not feature in the CART model, Intertidal Extent (intertidal area relative to sub-tidal area) and Mangrove Extent (mangrove area relative to sub-tidal area) had the second (65%) and third (60%) highest relative importances respectively (Fig. 2b), indicating that, although not in the predictor set for the final CART model, they possessed considerable explanatory power and potentially explained much of the spatial difference. Other predictors had relative importances below 50%. We examined the influence of structural and biological variables in more detail by using CART analysis again but this time omitting spatial variables. The best CART tree had a primary split on Mangrove Extent (Fig. 3a) and there were very high overall relative importances for both Intertidal Extent and Mangrove Extent (Fig. 3b), for a tree that explained almost as much variability (41%) as the one that included spatial factors. Moreover, both Mangrove Extent and Intertidal Extent have clear positive correlations with *P. merguiensis* CPUE (Fig. 4). Sediment Type also had high relative importance between those of Intertidal Extent and Mangrove Extent (Fig. 3b), indicating that this could also be an influential factor.

Repeat samples from individual estuaries (Armstrong Ck., Baratta Ck., Boyd's Ck., Meunga Ck., Ross R.) showed very similar CPUEs indicating consistency within sites over the sampling period (Fig. 4).

3.2. Within-estuary component

Juvenile *Penaeus merguiensis* were present throughout the study, with even the smallest size classes (<5 mm carapace length) found in most estuaries in all months sampled. When within-estuary factors are considered across 9 estuaries over time, estuary level temporal and spatial explanatory variables dominate the CART (Fig. 4a). *P. merguiensis* juveniles were present in all mangrove estuaries throughout the year but there was a strong primary temporal split with highest CPUEs in the post-wet season (March to May), and lower catches in the dry, pre-wet and wet seasons, although the actual details of the temporal pattern were quite variable (Fig. 6). Mud and Sandfly Cks had the highest CPUEs in all seasons, while Cocoa Ck was in the high CPUE group in the post-wet but not in the dry, pre-wet or wet seasons. The opposite was true of Hell Hole Ck, which was notable for having low *P. merguiensis* CPUEs in the post-wet compared to other seasons (Fig. 6f). There were substantial differences in CPUEs among the 4 primary tree groups, with estimates for the high CPUE post-wet estuaries more than 5 times greater than for low CPUE post-wet season estuaries and all estuaries in the dry, pre-wet and wet seasons (Fig. 5b).

Despite the domination of the CART by temporal and spatial factors, a number of site-specific factors (substrate, hydrodynamics,

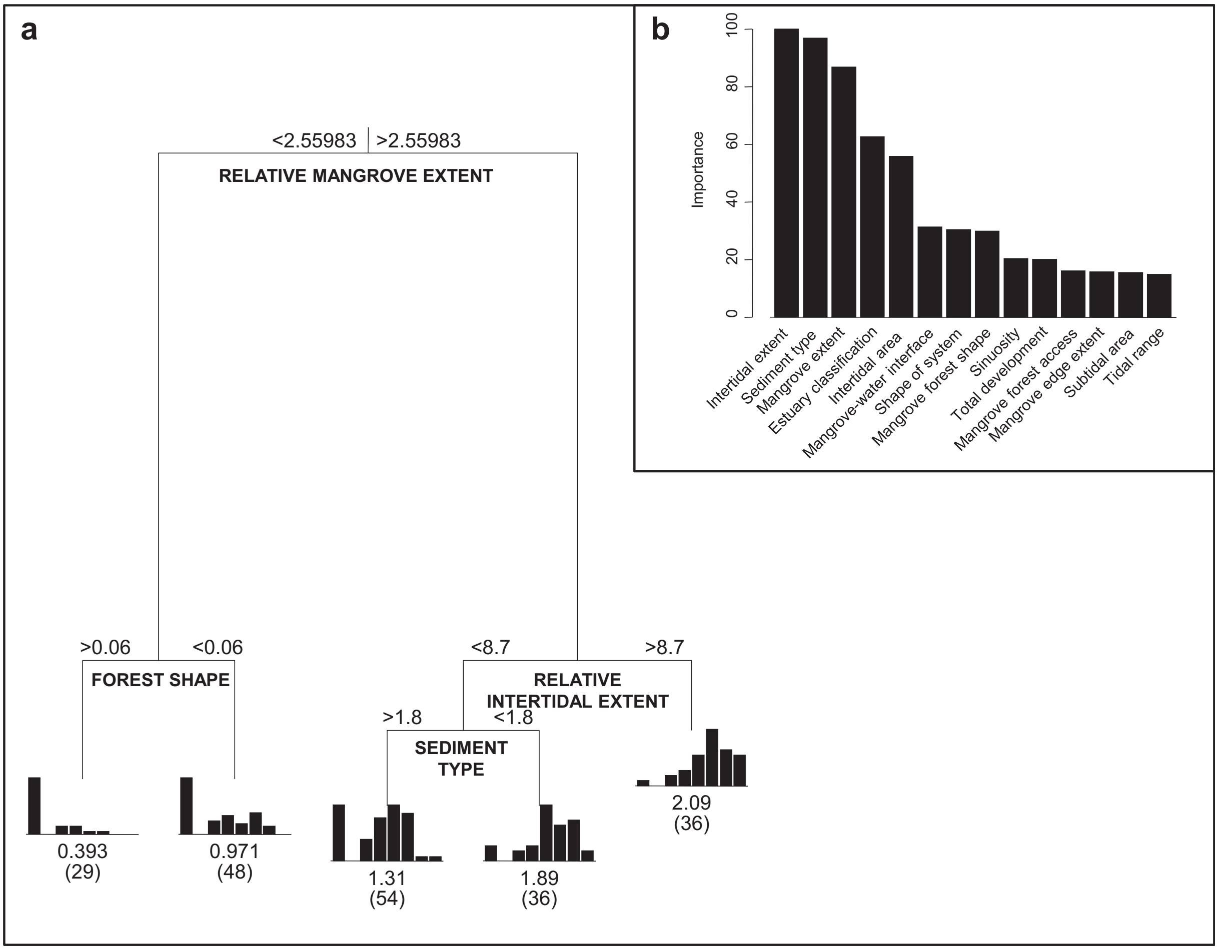

Fig. 3. CART analysis of *P. merguiensis* CPUE for the "among estuaries" data with spatial predictor variables excluded. (a) 5 leaf CART tree. Capitalised titles indicate the factor forming each split, text above branch nodes indicates the values defining each branch, bar graphs below each terminal branch show the distribution of CPUE, numbers below the bar graphs indicate the mean response for each branch, numbers in brackets indicate sample sizes at each node. (b) Relative importance of the variables providing the best overall classification for the CART tree.

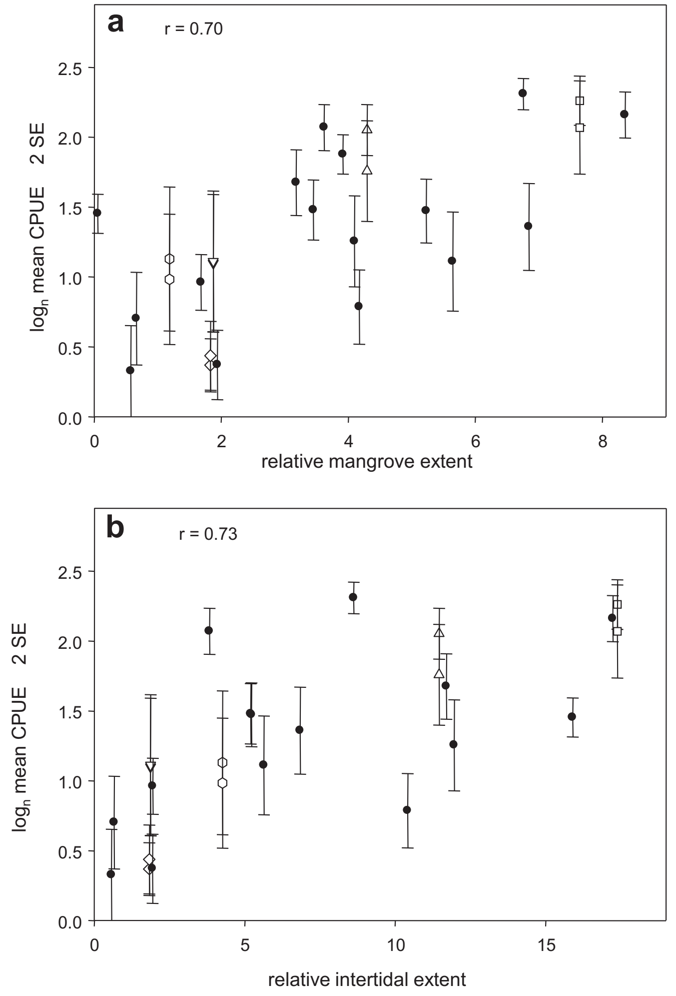

Fig. 4. Relationship between *P. merguiensis* CPUE and (a) Mangrove extent, and (b) Intertidal extent for the "among estuaries" data. CPUE data are ln transformed means per 100 nets across sites and reaches. Because this figure focuses on overall relationships rather than estuary-to-estuary comparisons, individual estuaries are not identified; except in the case of those that were repeat sampled. These are identified to allow evaluation of consistency of the repeat samples. White symbols indicate repeat samples: squares = Armstrong Ck, triangle up = Barratta Ck., diamonds = Boyd's Ck., triangles down = Meunga Ck., circles = Ross R. Note mangrove extent and intertidal extent are ratios of areas and so unitless.

bank angle, dominant vegetation) were important within particular spatio-temporal combinations (Fig. 5a). Notably, dominant vegetation type (the only vegetation related explanatory variable to be influential) only played a minor role in explaining small differences in restricted parts of the data set and had only moderate relative importance (59%) (Fig. 5c). In contrast, bank angle was influential in many parts of the tree, with high CPUEs invariably associated with lower bank angles, thus more extensive shallow water edges. Bank angle had the second highest predictor relative importance (93%) after location, indicating strong influence in explaining the pattern of variability. When the data are considered trip by trip, bank angle remains very influential, forming the second most primary tree splits, equal most total splits and second most occurrences among variables with relative importance >50% (Table 3).

Although CPUE was highest for most estuaries during the post-wet (March–May) (Figs. 4a, 5a–i), with catches much lower through the rest of the year, the pattern was quite variable among estuaries. This was not reflected in the pattern of change of prawn size, however, since the relationship between *Penaeus merguiensis* CPUE and mean biomass per *P. merguiensis* varied substantially among sites (Fig. 7), and there was no clear negative relationship that would be expected if high CPUEs were driven by high numbers of small individuals.

4. Discussion

4.1. Spatio-temporal consistency of utilisation of estuarine nurseries

In contrast to what might be expected, there were no indications of similarities in CPUE due to proximity (i.e. estuaries in the same Bay) or climatic zone. Rather the overriding scale of spatial variation in *Penaeus merguiensis* CPUE was at the estuary to estuary level. This indicates that, as with fish (Sheaves, 2006; Sheaves and Johnston, 2009), the particular characteristics of individual estuaries are more important than large scale physical variation among regions in determining patterns of distribution and abundance of *P. merguiensis*, and that within-estuary factors need to be investigated to understand the drivers of spatial patterns.

Within-estuary analysis showed that, although *Penaeus merguiensis* catches tended to peak in the post wet season, the pattern was quite variable among estuaries. This matches with estuaries of Australia's Gulf of Carpentaria (GoC), where the majority of *P. merguiensis* research has been conducted, that show peak abundances varying among estuaries (Staples, 1979). The relationship between *P. merguiensis* CPUE and mean biomass per *P. merguiensis* varied substantially among sites, with the lack of consistent negative relationships between CPUE and mean biomass per prawn. This inconsistent relationship is not surprising given a suite of studies from the GoC that show considerable spatio-temporal variation in recruitment (Staples et al., 1995), abundance (Staples, 1979; Vance et al., 1998) and mean carapace length (Staples and Vance, 1987) of juvenile *P. merguiensis*. Consequently, the variable patterns in CPUE and its relationship with mean biomass could reflect inconsistent timing and/or success of recruitment among estuaries, or differences in the period of residence, growth and mortality rates, and/or timing of emigration among estuaries. For instance, changes in size of *P. merguiensis* in the GoC are influenced both by changes in emigration triggered by rainfall variation (Vance et al., 1998) and by the presence or absence of overwintering individuals (Staples and Vance, 1987). The influence of rainfall and salinity (Browder et al., 2002; DeLancey et al., 2008), and other large-scale factors (Arreguin-Sanchez et al., 2008) such as water temperature (Rasolofo, 2007; Moeller et al., 2009; Viegas et al., 2012) and hydrodynamics (Wang et al., 2003), on movements of juvenile shrimps between estuaries and other habitats has been widely reported as responsible for among-estuary, seasonal and interannual variability in juvenile abundances. Inconsistency in recruitment, period of residence, growth, mortality or timing of emigration among estuaries could mask or add considerable noise to relationships between CPUE and the explanatory variables.

4.2. Among- and within-estuary relationships to predictor variables

The among-estuaries CART model structure was based entirely on spatial factors, with the focus of variation at the among-estuaries level indicating that key ecological processes operate at that scale (Holling, 1992; Levin, 1992; Hamid et al., 1999). However, a number of explanatory variables had strong predictive power in explaining the among-estuaries CART model structure; they had high relative importances in the model and became dominant explanatory factors when the spatial variables were excluded.

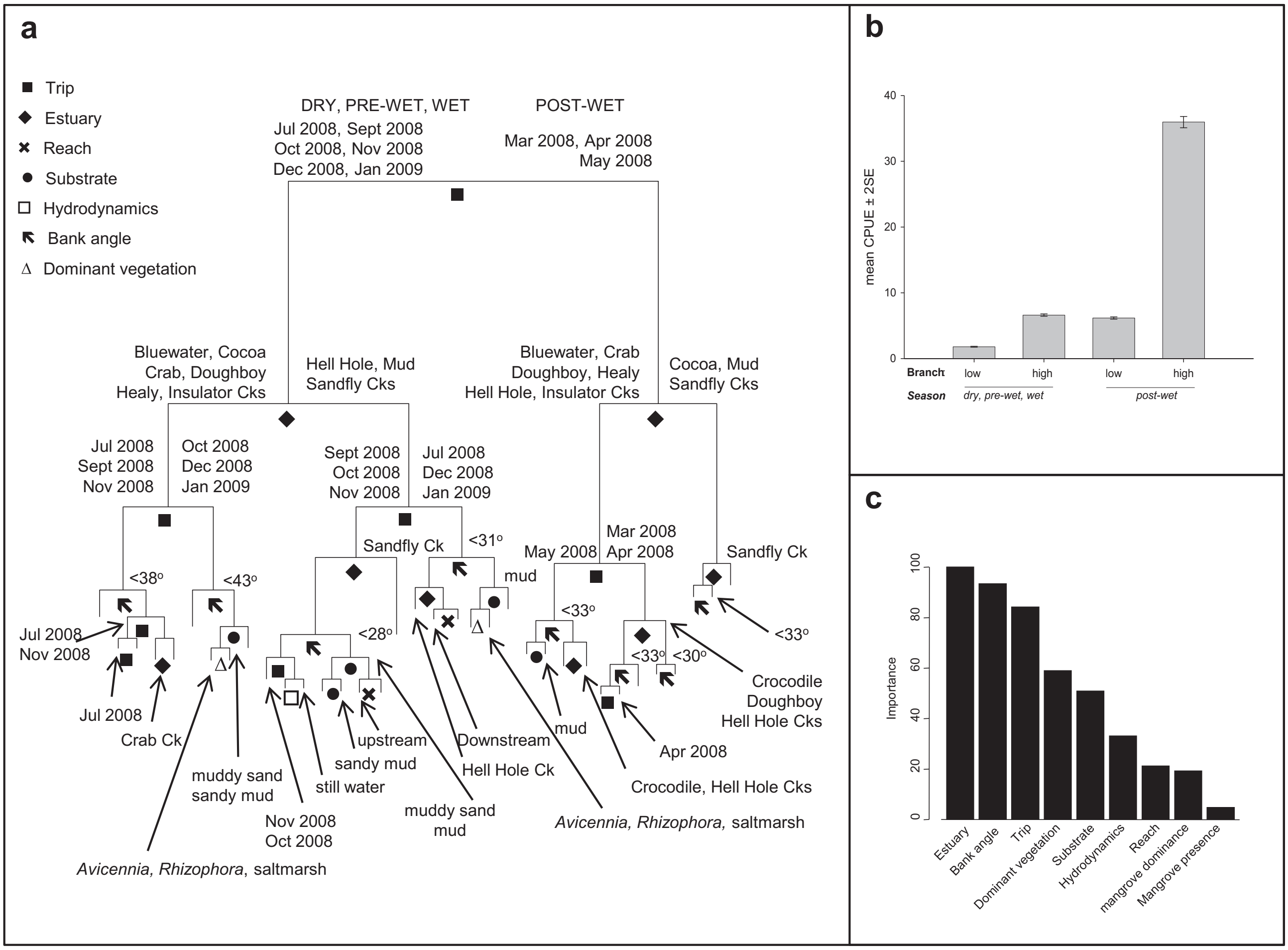

Fig. 5. CART analysis of *P. merguiensis* CPUE for the "within estuary" data. (a) 35 leaf CART tree. Symbols indicate the factor forming each split, for uppermost splits text above branches indicates the composition of each branch, for lower splits only one split value is indicated above the branch or via arrows from labels. (b) Estimated CPUE (in transformed means per 100 nets) for the 4 primary tree groups. (c) Relative importance of the variables providing the best overall classification for the CART tree.

Mangrove Extent (mangrove area relative to sub-tidal area) was an important predictor of differences in *Penaeus merguiensis* CPUE among estuaries, while other estuary structure, vegetation and impact variables (Table 1) were not. This accords with studies showing correlations between offshore catches of *P. merguiensis* and mangrove area (Manson et al., 2005; Meynecke et al., 2008), and is consistent with the idea that mangroves are key nursery grounds for *P. merguiensis* (Staples et al., 1985; Staples and Vance, 1985; Primavera, 1998). However, Intertidal Extent and Substrate Type were also strong predictors, which aligns with the results of Lee (2004), who suggested that factors that are correlated with the occurrence of mangroves may actually exert the primary influence on penaeid abundance. More importantly, this result and the results of previous studies (e.g. Lee, 2004; Manson et al., 2005) emphasise the difficulty of determining the importance of mangroves to penaeids like *P. merguiensis*; mangroves are a consistent feature of intertidal margins of tropical estuaries (Duke, 1992), so the effect of mangroves are confounded with a range of other intertidal variables. Some clarification comes from stable isotope studies, a number of which have concluded that mangroves in northern Australia provide limited nutritional support to *P. merguiensis* juveniles (e.g. Loneragan et al., 1997; Sheaves et al., 2007; Abrantes and Sheaves, 2009) (but see Chong et al. (2001) for an alternative view for Malaysian mangroves). If mangroves themselves are important to juvenile *P. merguiensis* it appears likely to be for a reason other than nutritional support. A second line of evidence comes from *P. merguiensis* catch data from the Pacific, where catches are associated with large estuarine mangrove systems rather than coastal mangroves (Dalzell et al., 1996). This implies that it is estuaries rather than mangroves that are important to *P. merguiensis*, although it may simply be that estuaries harbour the largest areas of mangrove and associated complex structure. *P. merguiensis* selected structured habitats such as mangrove pneumatophores and mangrove debris in preference to less structured alternative habitats (Meager et al., 2005). This suggests presence of mangrove structure may influences *P. merguiensis* distribution however field observations don't support this idea (Meager et al., 2003). Considering the assumptions underpinning the among-estuaries mangrove predictors that were not influential in the among-estuaries model (Table 1) provides further support for the proposition of Lee (2004). The variables Mangrove–Water Interface, Mangrove Edge Extent and Mangrove Forest Access (three alternative measures of the importance of connectivity with the mangrove forests) all had very low predictive power in both the CART model including all predictors (Fig. 2b), and the model with only non-spatial variables (Fig. 3b). From this it appears that the amount of access to mangroves in an estuary is not a critical factor determining *P. merguiensis* distribution at the estuary to estuary scale. This supports the idea that a factor such as the area of the intertidal or the type of substrate is

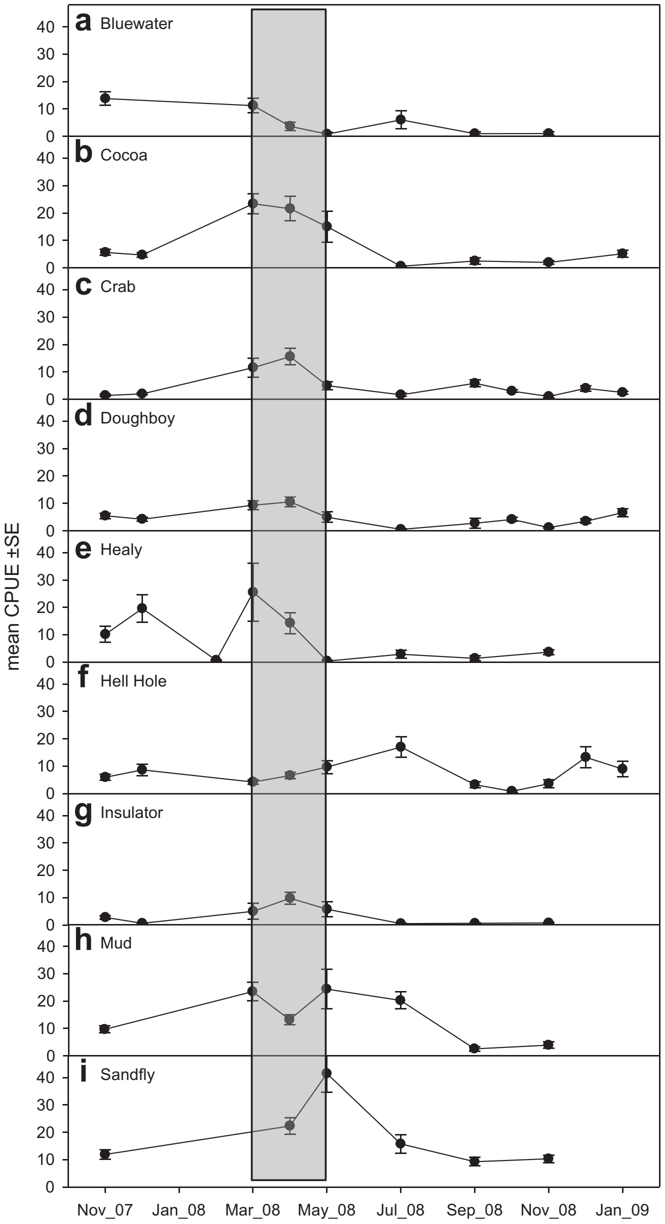

Fig. 6. Details of *P. merguiensis* CPUEs over time for the "within estuary" data. The grey box indicates the post wet season period (March to May).

more likely to be the actual determinant of *P. merguiensis* distribution than the extent of mangroves.

When viewed at a within-estuary scale *Penaeus merguiensis* CPUE did not correlate with any of the mangrove variables (Table 3), rather, high CPUEs correlated with low bank angles, used as a proxy for the occurrence of shallow water through extended periods of the tidal cycle. This aligns with the importance of Intertidal Area in the among estuary scale study, reinforcing the idea that *P. merguiensis* CPUE is more likely to be determined by the presence of extensive areas of shallow water than the presence of mangroves per se (Lee, 2004), with shrimps probably utilising a range of resources from different parts of the mosaic of habitats that comprise tropical estuaries (Sheaves, 2005, 2009).

Table 3
Percentage of months in which main factors had high explanatory power in classification and regression trees for "within-estuaries" analysis.

	1st split	Any split	Surrogate >50%
Location	78	89	100
Bank angle	22	89	78
Dominant veg.	0	56	44
Reach	0	11	56
Substrate	0	44	33
Hydrodynamics	0	11	11
Mangrove dominance	0	0	0

5. Conclusion

The extensive correlations between the presence of mangroves and other features of tropical estuaries make definitive determination of the importance of mangroves to *Penaeus merguiensis*, and other penaeids, extremely challenging. If juvenile *P. merguiensis* use tropical estuaries for reasons not directly related to the presence or extent of mangroves, why do they occur predominantly in mangrove systems? The classical concept is that mangroves provide juvenile nekton with food, low numbers of predators and/or structural refuge from predation (Robertson and Blaber, 1992; Laegdsgaard and Johnson, 2001). Nutritional explanations are attractive but difficult to validate. The complex habitat mosaics that comprise tropical estuaries (Sheaves, 2009) do provide rich and diverse sources of nutrients to juvenile nekton (Bouillon et al., 2007; Abrantes and Sheaves, 2008, 2010), but there seems to be no research that would explain why *P. merguiensis* preferentially use mangrove habitats for nutrient acquisition if it is not to access mangrove carbon. Similarly, the idea that mangrove systems have low numbers of nekton predators (Blaber, 1980) has been shown not to apply to tropical Australian estuaries, where both specialist shallow water predators (Baker and Sheaves, 2006) and small predatory nekton (Baker and Sheaves, 2009) are abundant. The proposition that estuaries provide a refuge from predation appears to have more substance. *P. merguiensis* responds strongly to turbidity, showing much higher abundances in turbid compared to adjacent less turbid water (Johnston et al., 2007), although there are a number of possible explanations for this other than refuge from predation.

Definitive understanding of the actual importance of mangroves to *Penaeus merguiensis*, and other penaeids, will require determination of the specific benefits gained from using particular estuarine habitats. It is possible that the complexity of the interaction might make unambiguous understanding impossible, consequently focussing on individual habitats may be less informative than understanding how synergies among habitats function to secure species persistence. Whatever the situation, the apparent lack of direct relationship between *P. merguiensis* and mangroves should not be taken as an indication that mangroves are not important. On the contrary, mangroves play critical roles in stabilising shorelines and facilitating the accumulation of organic peat (Gedan et al., 2011), so the very presence of mangroves is critical to the development and maintenance of the muddy, shallow water habitats that *P. merguiensis* rely on. Moreover, mangroves are critical components of the complex ecosystem mosaic supporting nekton that spend part of their life histories in tropical estuaries (Sheaves, 2009). The importance of maintaining the integrity of this mosaic is emphasised by our increasing understanding of connectivity (Sheaves, 2005; Nagelkerken, 2007) that covers the spectrum of biological processes ranging from enabling complex trophic dynamics (Bouillon et al., 2007, 2008) to critical support for offshore ecosystem resilience (Mumby et al., 2004).

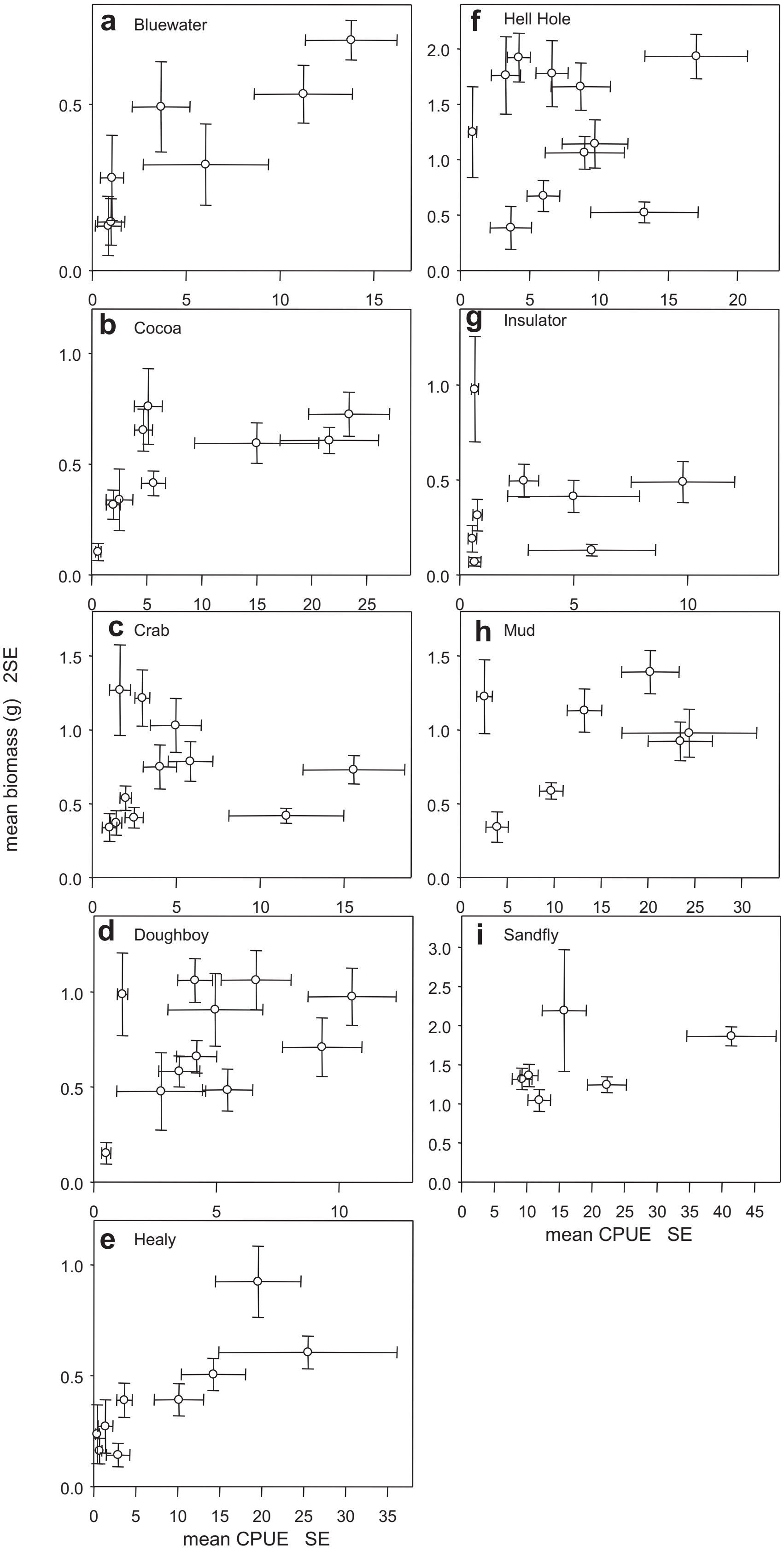

Fig. 7. Relationship between *P. merguiensis* mean CPUEs and mean biomass for the “within estuary” data.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ecss.2012.09.018.

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