

Connectivity between seagrass and mangroves influences nekton assemblages using nearshore habitats

Greg A. Skilleter^{1,2,*}, Neil R. Loneragan², Andrew Olds¹, Yuri Zharikov¹,
Bronwyn Cameron¹

¹Marine and Estuarine Ecology Unit, School of Biological Sciences, University of Queensland, St Lucia, QLD 4072, Australia

²Centre for Fish and Fisheries Research, School of Veterinary and Life Sciences, Murdoch University, South Street, Murdoch, WA 6150, Australia

ABSTRACT: Fragmentation in landscapes may result in a reduction in connectivity among component patches as patch sizes decrease and/or the distance between different patches increases. The movement of nekton into wetlands and intertidal banks during high tide may be influenced by the habitats they traverse. Here, we examined whether the proximity between shallow seagrass beds and mangrove forests affected the utilisation of the seagrass beds by nekton at 2 levels of habitat complexity (dense and sparse seagrass). Fish and epibenthic invertebrates were sampled on multiple occasions in 2 different regions in subtropical Moreton Bay, Queensland, Australia. The nekton assemblages varied considerably with distance between the seagrass and mangroves, although specific effects varied between the 2 regions of the bay. Overwhelmingly, larger numbers of individuals and more species were associated with seagrass beds that were close to the mangroves than those further away. Generally, proximity also had strong effects on the abundance of individual species, but these varied as a function of seagrass complexity and also resulted in some species being more abundant close to mangroves, while others showed the opposite pattern. For many species, the influence of potential connectivity between seagrass and mangroves, i.e. distance of seagrass from mangroves, had a greater influence on nekton than structural complexity of the habitat.

KEY WORDS: Estuarine · Landscape ecology · Habitat fragmentation · Moreton Bay · Subtropical

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INTRODUCTION

Habitat loss and changes to habitat quality and extent have marked impacts on estuarine and coastal systems globally (Lotze et al. 2006), with implications for fisheries (Loneragan et al. 2005, 2013), biodiversity and ecosystem services (Jackson et al. 2001, Danielsen et al. 2005). Fragmentation and disturbance change the structure and configuration of coastal landscapes (Valiela et al. 2001, Valiela & Cole 2002, Manson et al. 2003, Adger et al. 2005), potentially decreasing the extent to which they can

support plants and animals (Saunders et al. 1991, Fahrig 2003).

Fragmentation may decrease patch size and/or increase the distance between different types of patch, leading to a decrease in the connectivity within the landscape (Goodwin & Fahrig 2002, Hock & Mumby 2015). A loss of connectivity among habitats may affect the capacity for animals to move through and take advantage of resources within the landscape (Taylor et al. 1993, Goodwin & Fahrig 2002). Maximising connectivity among different patches of habitat is important to maintain biodiversity (e.g.

*Corresponding author: g.skilleter@uq.edu.au

Pyke 2005) because of its influence on the persistence of populations and assemblages.

Estuarine tidal banks and wetlands (mangroves/saltmarshes) support diverse and abundant assemblages of nekton, a function of abundant food and refuges from predation (reviewed by Manson et al. 2005, Sheaves 2005). Access to these areas by nekton is often restricted to high tides, when the amount of shallow water habitat is greatly increased, especially for small fish (McIvor & Odum 1988) but also prawns (Sheaves et al. 2012). Nekton move from subtidal refuge habitats into mangroves and intertidal seagrass areas (Kneib & Wagner 1994, Irlandi & Crawford 1997, Nagelkerken et al. 2015) but may have to traverse patches of habitat, such as bare sediment or sparse seagrass (Skilleter et al. 2005, Zharikov et al. 2005), that provide less protection from predators (Coen et al. 1981, Heck & Thoman 1981, Skilleter 1994, Sheaves 2009).

An increase in the distance between patches of habitat where the intervening area provides less refuge will decrease connectivity through increased rates of predation (Dunning et al. 1992, Puth & Wilson 2001) and/or greater avoidance of riskier habitats (Taylor et al. 1993, Keyser et al. 1998, Olden et al. 2004). Goodwin & Fahrig (2002) showed that inter-patch distance had the strongest and most consistent effect (negative) on landscape connectivity in terrestrial systems. In estuarine systems, the value of nursery habitats may also be reduced by declining connectivity between nearby patches, but direct measures of connectivity often require detailed measurements of individual movements or indirect measures of immigration/emigration rates (Goodwin & Fahrig 2002). Few data are available on movements by nekton in estuarine systems, though, as these data are difficult to obtain (see Beck et al. 2001, Gillanders et al. 2003, Nagelkerken et al. 2015).

Here, we examined whether the proximity between seagrass beds and mangrove forests affected the utilisation of intertidal seagrass beds by nekton, one important measure likely to influence connectivity among patches of habitat (Dunning et al. 1992, Taylor et al. 1993). The composition of different patches may affect connectivity (Goodwin & Fahrig 2002), so we simultaneously examined the effects of proximity at 2 levels of habitat complexity for the seagrass beds: dense and sparse seagrass. Dense seagrass generally supports more nekton species and individuals than sparse patches (e.g. Coen et al. 1981, Heck & Thoman 1981, Loneragan et al. 1998). Variation in landscape context (sensu Wiens 2002) (i.e. characteristics of the broader region surrounding

the landscape) may also influence connectivity, so we examined the effects of proximity to mangroves (and seagrass density) in 2 very different regions of a subtropical lower estuarine embayment: one surrounded by high human population density and associated urban setting and the other in a low human population density region with relatively little urban development and undisturbed mangroves.

MATERIALS AND METHODS

Study sites

Sampling was done in Moreton Bay, Queensland, a large subtropical embayment on the eastern coast of Australia (27° S, 153° E, Fig. 1) with extensive seagrass beds (Hyland et al. 1989) dominated by *Zostera capricorni* Ascherson. Moreton Bay has a semi-diurnal tidal pattern with a range of 1.5 to 2.0 m during a full monthly tidal cycle (Dennison & Abal 1999). Salinity ranges from 28 to 34‰, with little seasonal variation on the oceanic, eastern side of the embayment (Gabric et al. 1998), but salinities on the western side are more variable because of the influence of several major river systems (Young 1978, O'Brien 1994). Water temperatures in Moreton Bay range from approximately 19°C in September to 23°C in November, with only small differences in temperature between eastern and western Moreton Bay (Blaber & Blaber 1980).

Experimental design and sampling methods

Four different categories of seagrass bed were sampled: (1) dense seagrass beds proximal to mangroves, (2) dense seagrass beds distal to mangroves, (3) sparse seagrass beds proximal to mangroves and (4) sparse seagrass beds distal to mangroves. Initially, 3 sites in each type of bed were surveyed in the eastern and western regions of Moreton Bay (total 24 sites) (Table 1) to determine any influence of landscape context on the effects of connectivity between mangroves and seagrass. The distribution and extent of the 4 categories of seagrass bed varied within the 2 regions (see Zharikov et al. 2005), so beds belonging to the different categories were as spatially interspersed as possible (Fig. 1) to reduce spatial confounding of comparisons among treatments. Measures of proximity and density varied between the 2 regions. Proximal patches were categorised as those from 0 to 20 m from adjacent mangrove forests in the western bay

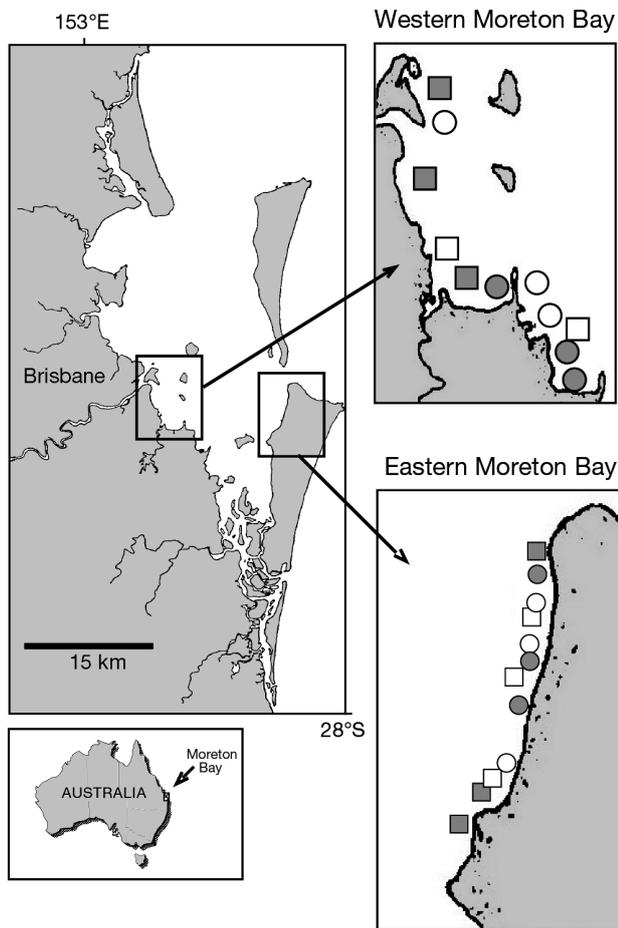


Fig. 1. Sampling locations in western and eastern Moreton Bay, Australia, showing the 4 seagrass categories: (1) dense seagrass beds proximal to mangroves (■), (2) dense seagrass beds distal to mangroves (●), (3) sparse seagrass beds proximal to mangroves (□) and (4) sparse seagrass beds distal to mangroves (○) (modified from Skilleter et al. 2005)

and 0 to 40 m in the eastern bay. Distal beds were separated from adjacent mangroves by 90 to 150 m of unvegetated sediment in the western bay and 150 to 350 m in the eastern bay. Sparse sites had 30 to 40% seagrass coverage in the western bay and 20 to 30% cover in the eastern bay. Dense sites had 70 to 90% seagrass coverage in the western bay and 60 to 70% cover in the eastern bay (see also Skilleter et al. 2005). Other details on seagrass percent coverage, blade length, shoot density and biomass are provided in Skilleter et al. (2005), which dealt specifically with the penaeid prawns from this broader study.

Sampling of the different sites was randomised through time, except that sites in western Moreton Bay (September–October 2002) were all sampled before those in eastern Moreton Bay (October–November 2002). Two sites could be sampled on any

Table 1. Number of sites and seine net samples (in parentheses) taken in each category of seagrass for western and eastern Moreton Bay, Australia, in (a) the austral spring of 2002 and (b) 2 different time periods. Period 1: January 2003; Period 2: February 2003

Category of seagrass	Western bay (Sep–Oct)	Eastern bay (Oct–Nov)
(a) Austral spring 2002		
Dense	6 (24)	6 (24)
Proximal	3 (12)	3 (12)
Distal	3 (12)	3 (12)
Sparse	6 (24)	6 (24)
Proximal	3 (12)	3 (12)
Distal	3 (12)	3 (12)
Total	12 (48)	12 (48)
	Period 1	Period 2
(b) Different time periods		
Dense	4 (24)	4 (24)
Proximal	2 (12)	2 (12)
Distal	2 (12)	2 (12)
Sparse	4 (24)	4 (24)
Proximal	2 (12)	2 (12)
Distal	2 (12)	2 (12)
Total	8 (48)	8 (48)

day, so a set of 12 sites (3 sites in each of the 4 categories of seagrass) required 6 d of sampling (Table 1). Sampling of the 12 sites was organised so that any effect of short-term (daily) variation in abundance was randomised across all treatments, avoiding confounding of comparisons among treatments.

Sampling was done using a small seine net (6 m long, 1 mm mesh with 2 m drop) hauled for 25 m along a pre-designated path marked by buoys, parallel to the shore, with a constant mouth width of 4 m, sampling an area of 100 m² for each haul. At each site, 4 replicate hauls were positioned on a transect along the shoreline, each haul separated by a distance of 10 m. Sampling was done within 2 h either side of the daytime high tide during the 6 d spanning either the full or new moon and at a relatively constant water depth (0.7 to 1.0 m). Samples were frozen until they could be examined in the laboratory, where individuals were identified to species and counted.

Analyses of the data from this first set of samples indicated marked effects of proximity and density on nekton (see 'Results; Community composition: regional comparisons'), so 2 sites from each of the 4 categories of seagrass bed in western Moreton Bay were sampled more intensively to determine whether these patterns were consistent through time. These 8 sites were sampled in 2 blocks between 30 January and 2 February 2003 and then again between 7 and

10 February 2003. Samples were collected by seine nets as described above, except 6 replicate samples were collected at each site (Table 1b). Two sites, selected at random, were sampled on each day in each sampling block. Samples were frozen until they could be examined in the laboratory, where individuals were identified to species and counted. The physical characteristics of the vegetation and sediments within each category of seagrass bed are described in Skilleter et al. (2005).

Statistical analyses

The composition of the nekton assemblage in seagrass beds was compared using ANOSIM on untransformed data using the Bray-Curtis similarity measure (Clarke 1993), indicating highly significant differences between the 2 regions of Moreton Bay (see 'Results; Community composition: regional composition'). On this basis, subsequent analyses comparing the different categories of seagrass bed were done separately for each region.

In each region, the 4 categories of seagrass bed were analysed with a single-factor ANOSIM. Pairwise tests within ANOSIM, on all possible combinations of the 4 categories of seagrass bed, were done to determine the specific differences among the bed types in the composition of the nekton assemblage. Examination of the values for the R-statistic from pairwise tests and the ordination plots was used to infer the presence of any interactions between the effects of proximity and density of seagrass bed. Differences in composition of the nekton assemblage were also examined graphically using non-metric multidimensional scaling (ordination) using the Bray-Curtis similarity measure on untransformed data (Clarke 1993). The contributions of different taxa to the variation in the composition of the nekton among the 4 categories of seagrass bed were examined using SIMPER.

The abundances of species selected as diagnostic by SIMPER were analysed with 3-factor univariate ANOVAs, with proximity (proximal, distal) and complexity (dense, sparse) treated as fixed factors and sites as a random factor (i.e. sites nested within proximity \times complexity). Because of bad weather, sampling at 1 site in the dense distal seagrass category in western Moreton Bay was disrupted. Catches at this site were dominated by large amounts of seagrass and algal debris, and it was not clear whether the efficiency of the seine net was similar to that at the other sites. Data from this site were excluded from

analyses, leaving an unbalanced design for the western bay. Data from the eastern bay were analysed with the same ANOVA design, except analyses were completely balanced. Data were log transformed before ANOVA to meet the assumptions of homoscedasticity of variances after Cochran's test (Underwood 1981).

Data from the more intensive sampling in western Moreton Bay were analysed similarly, except univariate ANOVAs included an additional factor of period. Period was considered a fixed factor in these analyses, as (1) sampling on both these occasions was specifically done during summer to allow valid comparisons with the previous sampling, also done during the austral spring–summer period; and (2) the 2 periods were separated by only a short amount of time to increase the likelihood that the same populations of nekton would be sampled as they accessed the intertidal seagrass beds from subtidal refuge areas, without substantial recruitment from the plankton.

Data on community composition were analysed with a 3-way PERMANOVA (Anderson 2001, 2005, McArdle & Anderson 2001), using fixed factors of period, proximity and complexity. We pooled the data from the 2 sites as there were insufficient data/permutations to provide reliable pseudo- F values for the nested spatial component (sites nested within proximity \times complexity). Initial analysis of the data indicated very little variation in community composition between the 2 sites in any combinations of factors. There were heterogeneous multivariate dispersions in these temporal data, with the nekton community in one category of seagrass being significantly more variable than the other categories. PERMANOVA is, however, extremely robust to heterogeneous multivariate dispersions with balanced designs (Anderson & Walsh 2013), so we considered the multivariate analyses to provide a reliable test of our hypotheses.

Overall, for each variable analysed, the sampling programmes provided potentially up to 4 independent tests of whether proximity had a significant effect on the abundance of epibenthic nekton: 1 sampling period in eastern Moreton Bay and 3 in western Moreton Bay (see Table 5). We calculated the probability that the abundance of any species was greater in proximal than distal beds more often than would be expected by chance using a binomial test on the results from these 4 independent sets of data. If the abundance of a species was greater in the proximal than the distal beds, then the probability of obtaining that result is 0.0613:

$$\left(\text{Prob}(r) = \frac{n!}{r!(n-r)!} p^r (1-p)^{(n-r)} \right) =$$

$$\left(\text{Prob}(r) = \frac{4!}{0!(4)!} 0.5^0 (1-0.5)^{(4)} = 0.0613 \right)$$

where n = number of trials, r = number of successes and p = probability (0.05).

Given that only 4 tests are possible, a probability of $p = 0.06$ was interpreted as indicating a significant departure from the chance occurrence of a greater abundance of animals occurring in proximal than distal beds. We determined the probability of obtaining this result separately for dense and sparse seagrass, given the large number of cases where there was a significant interaction between the effects of seagrass density and proximity when examining the abundance of individual taxa on each occasion.

RESULTS

Environmental characteristics

The mean aboveground biomass of the dense seagrass beds (200–220 g m⁻²) was greater and the mean leaf length (13–17 cm) longer than those of the sparse

seagrass beds (35–61 g m⁻² and 7–10 cm) (see Table 3 of Skilleter et al. 2005). The mean percent gravel content was smaller in dense (≈ 3.6 – 9.2%) than in sparse seagrass (≈ 21 – 23%). These differences in the structure of sparse and dense seagrass beds were far greater than those between different distances to mangroves for seagrass beds with the same level of structure. The water temperature was ≈ 20 to 23°C during the spring of 2002 and ≈ 23 to 25°C during the summer of 2003.

Community composition: regional comparisons

The 15 most abundant species of nekton caught on both sides of Moreton Bay comprised 8 species of invertebrate (2 penaeids, 5 carids, 1 cephalopod) and 7 species of fish (Table 2). Some clear distinctions in the distribution of these species were found, especially for the gobies. Two species, *Arenigobius frenatus* and *Favonigobius exquisitus*, were abundant on the western side of the bay but rare on the eastern side. In contrast, *F. lentiginosus* and *A. leftwichi* were abundant on the eastern side and rare on the western side (Table 2). Several of the invertebrates also showed differences in abundance between western

Table 2. Total catch (no. of ind.) of the 20 most abundant species of nekton caught in the seagrass beds in western and eastern Moreton Bay using seine nets. Samples in western Moreton Bay (September–October 2002) were all collected before those in eastern Moreton Bay (October–November 2002). I: invertebrate; F: fish

Species	Common name	Total	West	East
<i>Penaeus plebejus</i> (I)	Eastern king prawn	3990	862	3128
<i>Arenigobius frenatus</i> (F)	Half-bridled goby	2296	2259	37
<i>Favonigobius lentiginosus</i> (F)	Eastern longfin goby	1511	3	1508
<i>Urocampus carinirostris</i> (F)	Hairy pipefish	1164	289	875
<i>Pelates sexlineatus</i> (F)	Six-lined grunter	1061	674	387
<i>Palaemon debilis</i> (I)	Feeble shrimp	987	542	445
<i>Centropogon australis</i> (F)	Fortescue	925	624	301
<i>Metapenaeus bennettiae</i> (I)	Greasyback prawn	586	586	0
<i>Latreutes porcinus</i> (I)	Big-nosed shrimp	492	469	23
<i>Idiosepius notoides</i> (I)	Southern pygmy squid	413	133	280
<i>Latreutes pygmaeus</i> (I)	Hump backed shrimp	410	405	5
<i>Arenigobius leftwichi</i> (F)	Oyster goby	370	12	358
<i>Palaemon serenus</i> (I)	Rock-pool prawn	362	51	311
<i>Gerres subfasciatus</i> (F)	Common silverbidy	231	226	5
<i>Hippolyte</i> sp. (I)	Broken-back shrimp	213	67	146
<i>Favonigobius exquisitus</i> (F)	Exquisite goby	203	189	14
<i>Tetraodon hamiltoni</i> (F)	Common toadfish	183	147	36
<i>Petroscirtes lupus</i> (F)	Sabretooth blenny	133	40	93
<i>Acanthopagrus australis</i> (F)	Yellowfin bream	124	99	25
<i>Gnatholepis gymnocara</i> (F)	Sand goby	81	81	0
Total of 20 species		15735	7758	7977
Total of all species		16476	8286	8190
Number of species		67	58	42

Table 3. Results of SIMPER analysis showing the contributions to differences in composition for the nekton assemblage caught in dense and sparse intertidal seagrass beds in eastern Moreton Bay, proximal and distal from mangroves, during the day in September to November 2002. The average abundance for each species and percent contribution of each species to the separation of the nekton assemblages in each category are shown. Only those species contributing up to ~80% between the 2 regions are shown. Comparisons are shown for the interaction between proximity and complexity. Data are the number of animals caught in 100 m² of seagrass (n = 12 seine net samples pooled across 2 sites in each of 4 categories of seagrass bed) (see 'Materials and methods; Experimental design and sampling methods' for further details)

Species	Proximity to mangroves		Contribution (%)
	Proximal \bar{X} abundance	Distal \bar{X} abundance	
Dense seagrass			
<i>Penaeus plebejus</i>	183.42	30.83	41.86
<i>Favonigobius lentiginosus</i>	46.75	29.42	14.24
<i>Urocampus carinirostris</i>	27.50	13.42	6.91
<i>Palaemon debilis</i>	3.25	10.92	5.45
<i>Arenigobius leftwichi</i>	24.42	2.83	3.90
<i>Idiosepius notoides</i>	5.75	12.25	3.78
<i>Centropogon australis</i>	8.58	5.50	2.44
<i>Pelates sexlineatus</i>	4.67	4.75	2.43
Sparse seagrass			
<i>Penaeus plebejus</i>	38.08	8.33	24.32
<i>Palaemon serenus</i>	24.25	1.25	15.09
<i>Favonigobius lentiginosus</i>	7.83	23.83	13.96
<i>Palaemon debilis</i>	20.75	2.17	12.20
<i>Urocampus carinirostris</i>	17.33	14.67	10.10
<i>Pelates sexlineatus</i>	8.33	3.00	4.82
<i>Centropogon australis</i>	7.08	3.92	4.29
<i>Hippolyte</i> sp.	2.33	5.17	3.96

and eastern sides of the bay: *Metapenaeus bennettiae* (absent in the east), *Latreutes porcinus* and *L. pygmaeus* (rare in the east but abundant in the west) and *Palaemon serenus* and *Hippolyte* sp. (more abundant in the east than the west) (Table 2).

These distinctive distributions for many common species resulted in the eastern and western regions of Moreton Bay supporting distinct nekton assemblages (ANOSIM, $p < 0.001$). Seven species of invertebrates and 5 species of fish contributed 80% to the separation of the 2 assemblages, with 1 species, the eastern king prawn *Penaeus (=Melicertus) plebejus*, contributing >18% to the distinction between the 2 regions (SIMPER analysis, Table 3). Additionally, 10 species were only sampled from eastern Moreton Bay, and 2 species were restricted to western Moreton Bay (Skilleter & Loneragan 2007). On the basis of these large differences in the overall composition of the assemblages in the 2 regions, all further analyses to assess any interactive effects of proximity (between seagrass and mangroves) and complexity (of seagrass) were done separately for each region.

Community composition: effects of proximity and seagrass complexity

In eastern Moreton Bay, the composition of the nekton in both dense and sparse seagrass was affected by distance between seagrass and mangroves, i.e.

proximity of mangroves (ANOSIM, $p < 0.001$; pairwise comparisons: $p < 0.001$ to 0.003). Some overlap was found in samples from the distal and proximal beds in dense seagrass but not in sparse seagrass, suggesting an interaction between proximity and

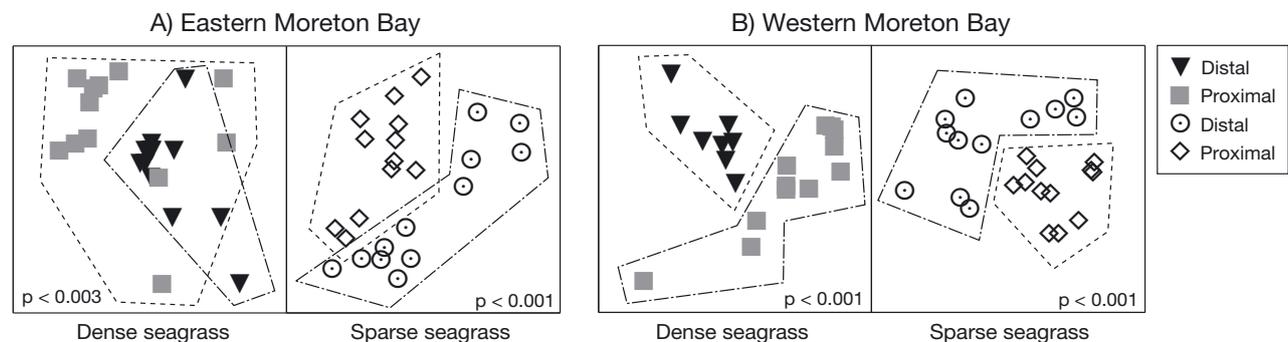


Fig. 2. Non-metric multidimensional scaling ordinations of untransformed data on the composition of the nekton assemblage (fish, decapods and cephalopods) utilising intertidal seagrass beds in (A) eastern Moreton Bay and (B) western Moreton Bay. Comparisons are shown separately for dense and sparse seagrass, contrasting proximal and distal beds, for ease of viewing but are based on a single analysis. n = 48 samples from eastern and western Moreton Bay, pooled across sites in each of 4 different categories of seagrass bed (see 'Materials and methods; Experimental design and sampling methods' for further details).

Dashed lines represent significantly different groups in ANOSIM. p-values are from pairwise tests after ANOSIM

density (Fig. 2A). This was supported by the differences in the R-statistic for pairwise comparisons, with a larger value for the proximity comparison in sparse than in dense seagrass (proximal vs. distal: $R_{\text{sparse}} = 0.52$; $R_{\text{dense}} = 0.39$).

In dense seagrass, 8 species contributed ~80% to the separation of the assemblages in proximal and distal beds (Table 3), with eastern king prawns *Penaeus plebejus* contributing >40%, with greater abundances in beds close to mangroves than those further away. Fish were generally more abundant in the proximal beds, except for *Pelates sexlineatus*, the six-lined trumpeter, where abundance was slightly greater in distal beds. Both the carid shrimp *Palaemon debilis* and the southern pygmy squid *Idiosepius notoides* were more abundant in distal seagrass beds. In the sparse seagrass beds, *Penaeus plebejus* again made the largest contribution to the separation of the assemblages (>24%) in proximal and distal beds. Five species each contributed >10% to the separation of proximal and distal beds in sparse seagrass, compared with only 2 species in dense seagrass (Table 3).

In western Moreton Bay, the assemblages of nekton using the seagrass beds separated completely

by proximity from mangroves (Fig. 2B), but here, the separation was evident for both dense and sparse patches (ANOSIM, $p < 0.001$; pairwise comparisons: $p < 0.001$ to 0.003). There was no indication of an interaction between the effects of proximity and density, and the values of the R-statistic for the pairwise comparisons were similar in dense and sparse grass (proximal vs. distal: $R_{\text{sparse}} = 0.48$; $R_{\text{dense}} = 0.49$).

In western Moreton Bay, a larger number of species contributed to the separation of the proximal and distal beds in both dense and sparse seagrass (11 species in dense seagrass, 9 species in sparse seagrass) than in the eastern bay. In dense seagrass, the half-bridled goby *A. frenatus* contributed the greatest amount to the separation of the assemblages in proximal and distal beds, with 100 times more animals occurring in the dense beds close to the mangroves than those further away (Table 4). In dense seagrass, 8 of the 11 species contributing to the differences in the nekton assemblage between proximal and distal beds were more abundant in the former (Table 4). In the sparse seagrass beds, 6 of 9 species were more abundant in the proximal beds than those further away (Table 4).

Table 4. Results of SIMPER analysis showing the contributions to differences in composition for the nekton assemblage caught in 4 different categories of intertidal seagrass bed in western Moreton Bay during the day in September to November 2002. Other details as in Table 3

Species	Proximity to mangroves		Contribution (%)
	Proximal \bar{X} abundance	Distal \bar{X} abundance	
Dense seagrass			
<i>Arenigobius frenatus</i>	166.84	1.38	31.30
<i>Metapenaeus bennettiae</i>	34.08	2.00	8.74
<i>Latreutes porcinus</i>	22.00	22.50	7.17
<i>Penaeus plebejus</i>	38.08	9.63	6.79
<i>Centropogon australis</i>	36.25	10.13	6.73
<i>Pelates sexlineatus</i>	26.42	13.75	6.59
<i>Latreutes pygmaeus</i>	15.25	6.13	3.74
<i>Favonigobius exquisitus</i>	6.67	7.50	3.13
<i>Urocampus carinirostris</i>	16.17	5.13	3.10
<i>Gnatholepis gymnocara</i>	3.67	4.50	2.67
<i>Palaemon debilis</i>	14.33	2.75	2.65
Sparse seagrass			
<i>Lucifer hansenii</i>	28.00	6.83	16.88
<i>Penaeus plebejus</i>	23.58	3.33	14.35
<i>Arenigobius frenatus</i>	16.42	2.17	10.82
<i>Palaemon debilis</i>	12.42	16.67	10.47
<i>Metapenaeus bennettiae</i>	12.92	0.50	7.77
<i>Pelates sexlineatus</i>	10.42	7.75	6.03
<i>Latreutes pygmaeus</i>	0.58	13.83	5.84
<i>Centropogon australis</i>	6.00	3.00	4.28
<i>Idiosepius notoides</i>	2.08	6.33	3.22

Abundance: effects of proximity and seagrass complexity

In eastern Moreton Bay, similar numbers of fish used sparse proximal and distal seagrass beds, but there were almost twice as many fish caught in the dense seagrass close to the mangroves than further away (ANOVA; significant interaction for proximity \times complexity, Table 5; Fig. 3A). The number of species of fish was, however, only marginally greater in the dense than in the sparse beds, and there was no significant interaction between proximity and density nor any effect of proximity as a main effect (Table 4; Fig. 3B). Of the 9 species with sufficient catches to analyse individually, 3 were significantly more abundant in dense seagrass beds close to mangroves than those further away: *A. leftwichii* (Fig. 3E), *F. lentiginosus* (Fig. 3F), *Tetractenos hamiltoni* (Fig. 3G) (Table 5). *Centropogon australis* showed a similar pattern, with a 3-fold greater density in the dense proximal beds than those fur-

Table 5. Significance levels (p-values are shown) from nested 3-way ANOVAs comparing the abundance (per 100 m²) of fish and invertebrates (decapods and cephalopods) sampled in seagrass beds of different complexity (dense versus sparse) and proximity to mangroves (proximal and distal) in eastern and western Moreton Bay during spring (September–November 2002). Data were transformed to $\log_e(x + 1)$ where indicated. n = 4 replicate samples from each of 3 sites per category of seagrass. Terms in the analyses that were interpreted and presented graphically are shown in *italics*. P: Proximity; C: Complexity; S: Site

Species	P	C	P × C	S (P × C)
Eastern Moreton Bay				
Individuals (fish) ^a	0.109	0.017	<i>0.032</i>	0.005
Species (fish)	0.930	0.070	1.000	0.005
<i>Arenigobius leftwichi</i> ^a	0.007	0.001	<i>0.006</i>	0.003
<i>Favonigobius lentiginosus</i> ^a	0.186	0.006	<i>0.010</i>	0.010
<i>Centropogon australis</i> ^a	0.174	0.244	0.970	0.001
<i>Pelates sexlineatus</i> ^a	0.577	0.364	0.368	0.005
<i>Urocampus carinirostris</i> ^b	0.329	0.599	0.545	0.001
<i>Penaeus plebejus</i> ^c	<i>0.032</i>	<i>0.026</i>	0.589	0.001
<i>Hippolyte</i> sp. ^a	0.344	0.371	0.559	0.001
<i>Palaemon debilis</i> ^a	0.168	0.126	<i>0.033</i>	0.001
<i>Idiosepius notoides</i>	<i>0.020</i>	<i>0.002</i>	0.108	0.202
Western Moreton Bay				
Individuals (fish) ^a	0.004	0.003	<i>0.008</i>	0.001
Species (fish)	<i>0.003</i>	<i>0.003</i>	0.194	0.001
<i>Arenigobius frenatus</i> ^a	0.001	0.007	<i>0.012</i>	0.013
<i>Favonigobius exquisitus</i> ^a	0.732	0.138	0.786	0.010
<i>Centropogon australis</i> ^a	0.008	0.002	<i>0.021</i>	0.016
<i>Pelates sexlineatus</i> ^a	0.922	0.456	0.974	0.001
<i>Urocampus carinirostris</i> ^b	<i>0.006</i>	<i>0.003</i>	0.474	0.431
<i>Penaeus plebejus</i> ^c	<i>0.047</i>	0.132	0.748	0.002
<i>Metapenaeus bennettiae</i> ^c	0.001	0.002	<i>0.012</i>	0.819
<i>Latreutes pygmaeus</i> ^a	0.417	0.589	0.683	0.001
<i>Latreutes porcinus</i> ^a	0.641	0.019	0.718	0.001
^a Data transformed				
^b Figure not shown				
^c Results reported in Skilleter et al. (2005)				

ther away, but this was not significant (Fig. 3D; Table 5). *Palaemon debilis* was more abundant in the sparse beds close to mangroves than those further away, but in dense beds, the pattern was reversed (Fig. 3H). In contrast, the shrimp *Palaemon serenus* was more abundant in sparse seagrass close to mangroves than in the sparse beds further away, but there was no difference in the numbers using the dense beds (Fig. 3I). The six-lined trumpeter *Pelates sexlineatus* showed a similar pattern to *Palaemon debilis*, but these differences were not significant (Fig. 3C). Another shrimp, *Hippolyte* sp., was 2.5 times more abundant in sparse seagrass away from the mangroves than in other patch types, but this difference was not significant (Fig. 3J). Finally, the squid *I. notoides* was significantly more abundant in distal than proximal grass beds and in dense than

sparse beds, and there was no significant interaction between these main effects (Fig. 3K; Table 5).

In western Moreton Bay, over 4 times as many fish individuals were caught in the dense beds close to the mangroves than in any of the other patch types (Fig. 4A). Slightly more species of fish were caught in the proximal than distal beds, but there was no difference in species richness between densities of seagrass and the proximity–density interaction was not significant (Fig. 4B; Table 5). Five species were more abundant in proximal than distal beds: *A. frenatus* (Fig. 4D) (dense and sparse beds), *C. australis* (Fig. 4E), *T. hamiltoni* (Fig. 4F), *Acanthopagrus australis* (Fig. 4G) (dense beds only) and *Urocampus carinirostris* (Fig. 4H) (proximal beds irrespective of density) (Table 5). *Pelates sexlineatus* was also more abundant in dense proximal beds than in patches further away, but this difference was not significant (Fig. 4C; Table 5). In dense seagrass, the shrimp *L. pygmaeus* was more abundant in beds close to the mangroves than those further away, but the opposite was true for sparse seagrass, with more shrimp in distal than proximal beds, although neither of these differences was significant despite the large effect sizes (Fig. 4I; Table 5). *F. exquisitus*, the exquisite goby, was more abundant in dense than sparse seagrass, but there was no effect of proximity on its abundance (Fig. 4J; Table 5). Finally, *L. porcinus* was more abundant in dense than sparse seagrass, but there was no effect of proximity as a main effect or an interaction with seagrass density (Fig. 4K; Table 5).

Temporal variation: western Moreton Bay

Consistent with the earlier sampling, in western Moreton Bay, clear differences were found in the nekton community among the 4 categories of seagrass on both occasions (January–February 2003) (Fig. 5), although these differences were complex (PERMANOVA, period × proximity × complexity interaction, $p < 0.012$). It was clear, though, that proximal beds supported nekton assemblages distinct from those in the beds further from the mangrove forests. As expected, dense and sparse seagrass beds also supported distinctive communities from each other (Fig. 5).

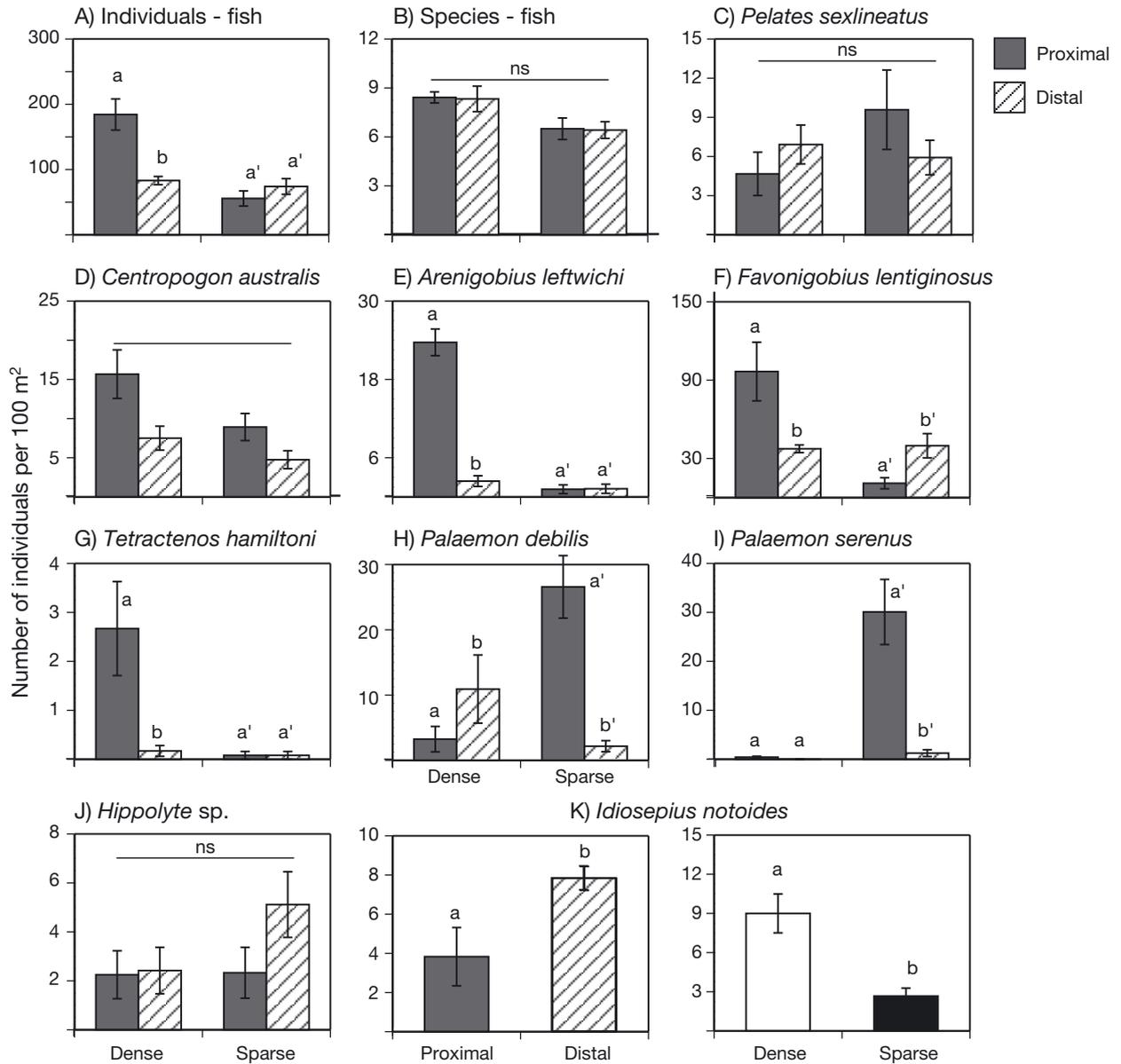


Fig. 3. Mean (\pm SE) number of (A) fish individuals, (B) fish species, (C) *Pelates sexlineatus*, (D) *Centropogon australis*, (E) *Arenigobius leftwichi*, (F) *Favonigobius lentiginosus*, (G) *Tetractenos hamiltoni*, (H) *Palaemon debilis*, (I) *Palaemon serenus*, (J) *Hippolyte* sp. and (K) *Idiosepius notooides* per 100 m² of intertidal seagrass in 4 categories: proximal dense, proximal sparse, distal dense and distal sparse in eastern Moreton Bay, sampled in October and November 2002. Results of Student-Newman-Keuls tests after ANOVA are shown: means topped by the same letter were not significantly different from each other ($p > 0.05$). A bar topping all means indicates no significant difference among treatments in ANOVA. Note the differences in the scale on the y-axes

Many of the patterns previously described in the abundance of different species between proximal and distal seagrass beds were now more pronounced. Total species richness (of fish and invertebrates) was greater in dense than sparse seagrass but did not differ significantly with proximity, either as a main effect or as an interaction with any other term (Table 6; Fig. 6A). In contrast, more species of fish occurred in the proximal than distal beds but only in

dense seagrass (Fig. 6B; Table 5). The total number of individuals of fish was significantly greater in the dense beds close to mangroves than those further away (Fig. 6C), with no effect of proximity on the number of fish in the sparse beds. This same pattern was seen for 5 individual species: *A. frenatus* (Fig. 6D), *F. exquisitus* (Fig. 6E), *Mugilogobius stigmaticus* (Fig. 6F), *C. australis* (Fig. 6G) and *T. hamiltoni* (Fig. 6H). In contrast, marginally more silver-

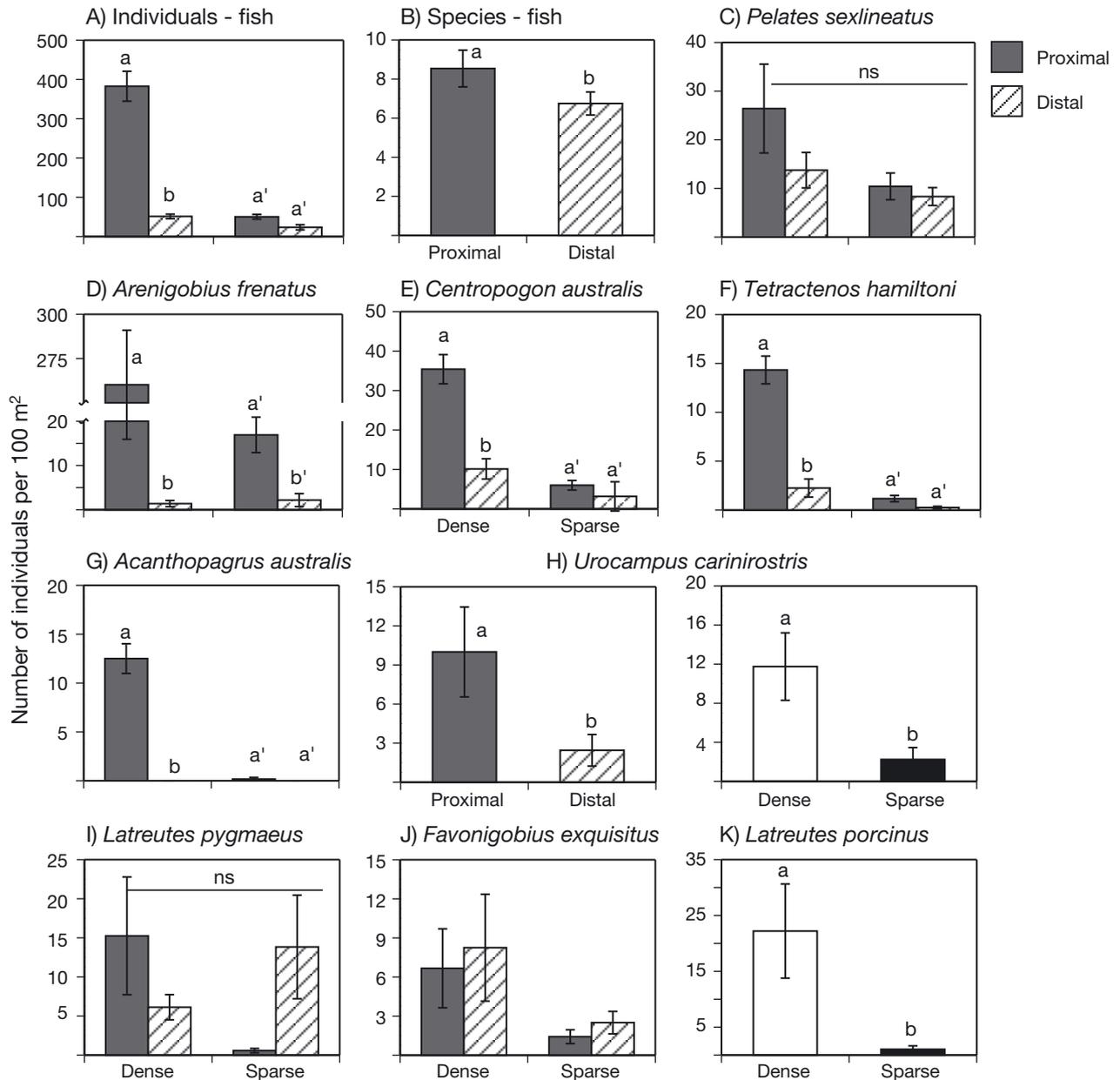


Fig. 4. Mean (\pm SE) number of (A) fish individuals, (B) fish species, (C) *Pelates sexlineatus*, (D) *Arenigobius frenatus*, (E) *Centropogon australis*, (F) *Tetractenos hamiltoni*, (G) *Acanthopagrus australis*, (H) *Urocampus carinirostris*, (I) *Latreutes pygmaeus*, (J) *Favonigobius exquisitus* and (K) *Latreutes porcinus* per 100 m² of intertidal seagrass in 4 categories: proximal dense, proximal sparse, distal dense and distal sparse in western Moreton Bay, sampled in October and November 2002. Other details as in Fig. 3

biddy *Gerres subfasciatus* (Fig. 6I) were caught in proximal than distal beds for both dense and sparse seagrass, but these differences were not significant, presumably because of significant small-scale spatial variation in abundance (Table 6). For other species of fish, significantly more were caught in proximal beds but only on 1 of the 2 occasions, e.g. *Pelates sexlineatus* (Fig. 6J), *Pseudogobius* sp., *U. carinirostris* (Fig. 6K). Finally, brown sabretoothed blennies *Pet-*

rosirtes lupus were always more abundant in the distal seagrass beds (Fig. 6L), although the magnitude of that difference varied between dense and sparse seagrass and between the 2 sampling periods (significant 3-way interaction, Table 6).

In contrast to the patterns for the majority of species of fish, the total number of epibenthic invertebrates was greater in the distal than proximal seagrass beds. There was a 10-fold increase in the abundance of

Palaemon debilis (Fig. 7A) in the distal beds compared with the proximal ones, with no effect of seagrass density, either as a main effect or as an interaction (Table 6). *L. pygmaeus* was also more abundant in distal than proximal beds for both dense and sparse

seagrass, although only the former was significant (Fig. 7B). *L. porcinus* was significantly more abundant in distal than proximal dense seagrass beds, but proximity was not significant in the sparse seagrass (Fig. 7C). Finally, *I. notoides* was generally more abundant in distal than proximal beds, but this was only significant in dense seagrass on one occasion.

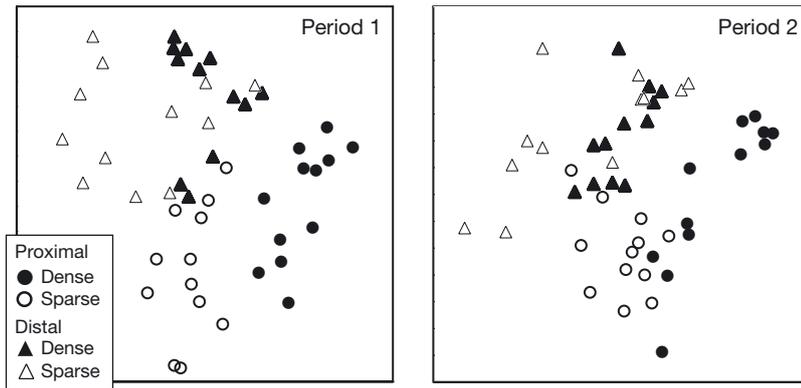


Fig. 5. Non-metric multidimensional scaling ordinations of untransformed data on the composition of the nekton assemblage (fish, decapods and cephalopods) utilising intertidal seagrass beds in western Moreton Bay, sampled in January (Period 1) and February (Period 2) 2003, contrasting the 4 categories of seagrass bed for ease of viewing, but based on a single analysis. n = 48 samples in each period, pooled across sites in each of 4 different categories of seagrass bed

Overall effects of proximity

From the 4 comparisons of densities of organisms in the nekton community (total number of fish, total number of species) and individual taxa, on most occasions abundances were greater in proximal beds, even though those differences were not always significant in post hoc tests. A total of 18 cases had sufficient data (i.e. from all 4 independent tests) to calculate whether the probability that the abundance of any species was

Table 6. Significance levels from 3-way ANOVAs comparing the abundance (per 100 m²) of fish and invertebrates sampled in seagrass beds of different complexity (dense versus sparse) and proximity to mangroves (proximal and distal) in western Moreton Bay during 2 periods in summer (January and February 2003). n = 6 replicate samples from each of 2 sites per category of seagrass. Other details as in Table 5. P: Period; Pr: Proximity; C: Complexity; S: Site. Significant values are in **bold**

Species	P	Pr	C	P × Pr	P × C	Pr × C	P × Pr × C	S (P × C)	P × S (P × C)
Species (fish + invertebrates)	0.017	0.470	0.001^c	0.496	0.130	0.513	0.496	0.163	0.152
Species (fish only)	0.002	0.402	0.001	0.452	0.050	0.001^c	1.000	0.275	0.589
Individuals (fish) ^a	0.556	0.118	0.001	0.791	0.709	0.001^c	0.956	0.275	0.204
<i>Arenigobius frenatus</i> ^a	0.148	0.060	0.001	0.583	0.824	0.001^c	0.769	0.182	0.145
<i>Favonigobius exquisitus</i>	0.710	0.110	0.510	0.280	0.040	0.003^c	0.750	0.120	0.130
<i>Gnatholepis gymnocara</i> ^a	0.220	0.162	0.614	0.847	0.367	0.438	0.159	0.070	0.003
<i>Pseudogobius</i> sp.	0.015	0.028	0.028	0.015	0.015	0.028	0.015	0.317	0.205
<i>Centropogon australis</i> ^a	0.304	0.019	0.008	0.242	0.331	0.010	0.874	0.282	0.002
<i>Gerres subfasciatus</i>	0.584	0.332	0.897	0.944	0.177	0.682	0.459	0.040	0.538
<i>Mugilogobius stigmaticus</i> ^a	0.308	0.388	0.361	0.469	0.308	0.388	0.469	0.002	0.370
<i>Pelates sexlineatus</i>	0.009	0.381	0.040	0.045	0.117	0.048	0.015	0.174	0.840
<i>Petroscirtes lupus</i> ^a	0.250	0.107	0.726	0.445	0.890	0.630	0.046	0.071	0.257
<i>Tetractenus hamiltoni</i> ^a	0.709	0.001	0.001	0.902	0.144	0.001	0.737	0.757	0.020
<i>Urocampus carinirostris</i> ^a	0.147	0.698	0.409	0.475	0.717	0.077	0.021^d	0.396	0.000
<i>Penaeus plebejus</i> ^b	0.794	0.002	0.016	0.979	0.222	0.787	0.002	0.516	0.001
<i>Penaeus esculentus</i> ^b	0.380	0.098	0.836	0.323	0.733	0.918	0.023	0.001	0.008
<i>Metapenaeus bennettiae</i> ^b	0.923	0.004	0.030	0.502	0.847	0.576	0.040	0.001	0.001
<i>Metapenaeus ensis</i> ^b	0.908	0.520	0.167	0.073	0.312	0.516	0.060	0.001	0.001
<i>Latreutes porcinus</i> ^a	0.258	0.001	0.005	0.175	0.301	0.002	0.001^d	0.105	0.473
<i>Latreutes pygmaeus</i> ^a	0.673	0.217	0.819	0.713	0.400	0.550	0.932	0.025	0.193
<i>Palaemon debilis</i>	0.213	0.033	0.153	0.286	0.480	0.148	0.812	0.313	0.003
<i>Idiosepius notoides</i> ^a	0.619	0.004	0.784	0.019	0.010	0.798	0.002	0.337	0.356

^aData transformed; ^bResults reported in Skilleter et al. (2005); ^cTest using pooled term for P × S (P × C) + S (P × C) + error (with 88 df)
^dTest using pooled term for S (P × C) + error (with 84 df)

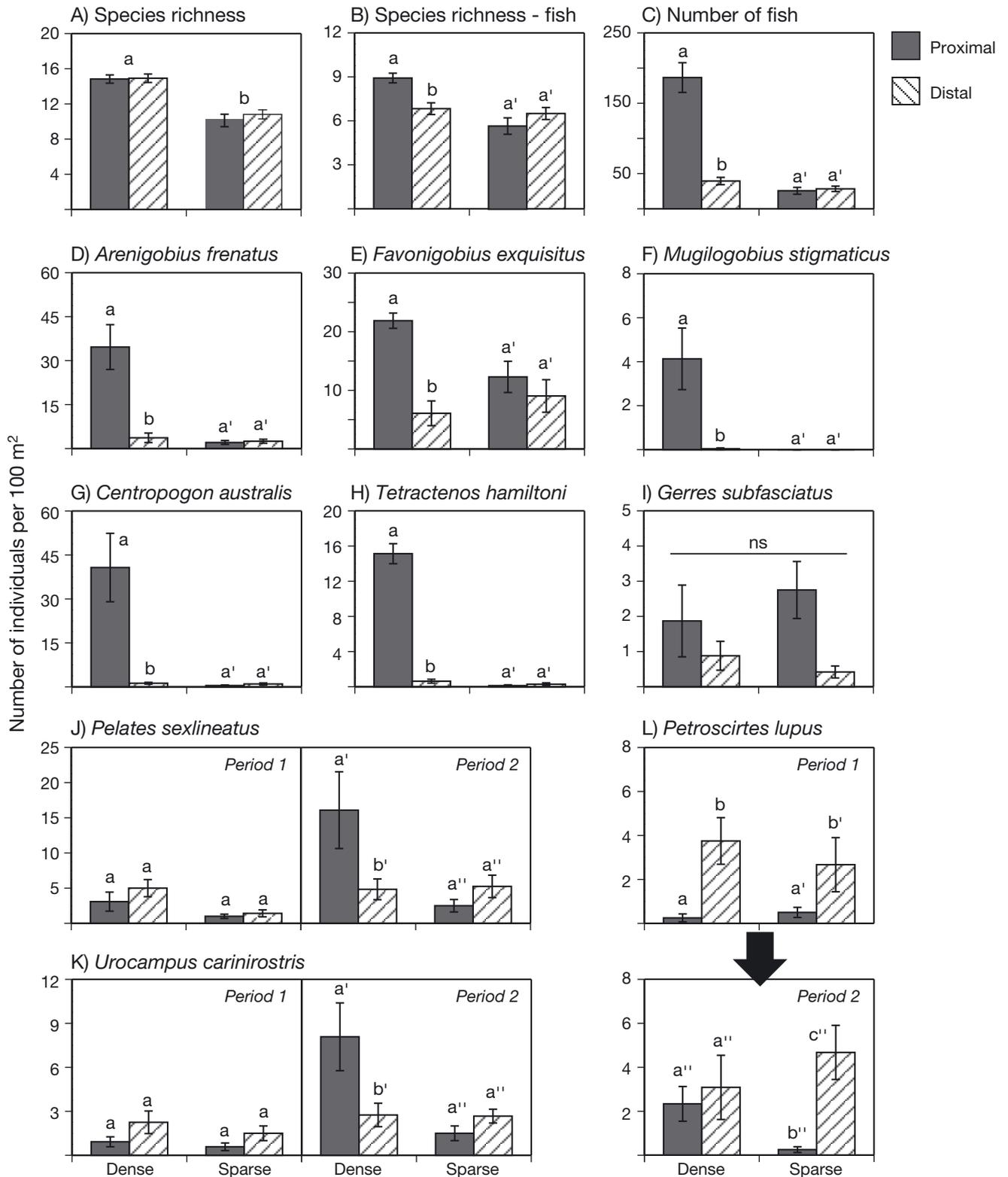


Fig. 6. Mean (\pm SE) number of (A) all species, (B) species of fish, (C) fish individuals, (D) *Arenigobius frenatus*, (E) *Favonigobius exquisitus*, (F) *Mugilogobius stigmaticus*, (G) *Centropogon australis*, (H) *Tetractenos hamiltoni*, (I) *Gerres subfasciatus*, (J) *Pelates sexlineatus*, (K) *Urocampus carinirostris* and (L) *Petroscirtes lupus* per 100 m² of intertidal seagrass in 4 categories: proximal dense, proximal sparse, distal dense and distal sparse in western Moreton Bay, sampled in January (Period 1) and February (Period 2) 2003. Other details as in Fig. 3

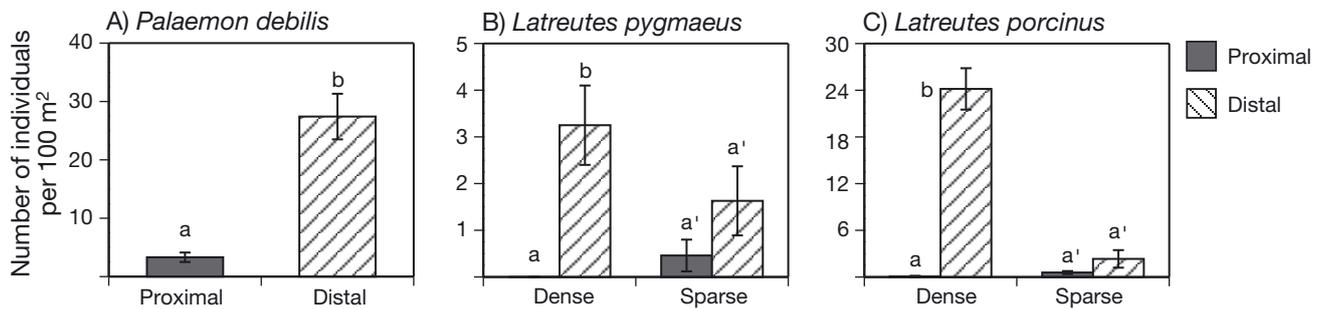


Fig. 7. Mean (\pm SE) number of (A) *Palaemon debilis*, (B) *Latreutes pygmaeus* and (C) *L. porcinus* per 100 m² of intertidal seagrass in 4 categories: proximal dense, proximal sparse, distal dense and distal sparse in western Moreton Bay, sampled in January and February 2003. Other details as in Fig. 3

greater in proximal than distal beds more often than would be expected by chance (Table 7). In 6 cases, the densities of animals or species were greater in proximal than distal seagrass beds (number of fish in dense beds, species richness of fish in dense beds, number of *T. hamiltoni* and *C. australis* in dense and sparse beds) in all 4 tests; the densities or numbers of species caught were greater for 4 other species in proximal than distal beds in 3 of the 4 tests (species richness of fish in sparse seagrass, number of invertebrates in dense and sparse seagrass, number of *U. carinirostris* in dense seagrass). In contrast, the number of individuals or species was greater in distal than in proximal beds in 5 cases (number of fish in sparse beds, species richness of invertebrates in dense and sparse beds, number of *Palaemon debilis* in dense and sparse beds) in all 4 tests. Two species of goby, *A. frenatus* and *F. frenatus*, only occurred in eastern Moreton Bay, so it was only possible to obtain 3 independent tests of the hypothesis. For both these species in dense seagrass, more individuals were found in the patches close to the mangroves than those further away on all 3 occasions (Table 7). *F. frenatus* was also more abundant in proximal than distal sparse seagrass on all 3 occasions it was sampled.

DISCUSSION AND CONCLUSIONS

Changes in the connectivity between patches of seagrass and mangroves had a marked effect on the composition and abundance of nekton using near-shore seagrass beds. Consistently, larger numbers of individuals and species used seagrass beds close to mangroves than those further away, an outcome consistent with previous studies on 4 species of subtropical penaeid prawns (Skilleter et al. 2005) and temperate fishes (Jelbart et al. 2007). For many species, this pattern was repeated in dense and sparse sea-

grass beds, indicating that the potential connectivity between the 2 types of habitat (i.e. seagrass and mangroves) had a greater influence than structural complexity of the habitat. For other species, the effect of proximity was pronounced in dense seagrass but not in sparse patches, or the pattern was reversed and more animals were present in the distal than proximal patches. Clearly, though, how patches of habitat are used by nekton in these systems is influenced by the surrounding landscape, and individual patches or types of habitat are not independent of the surrounding matrix. Such interactions among and between habitats have been well described in terrestrial systems (e.g. Kareiva 1990, Dunning et al. 1992), but there is less information for marine and estuarine communities (but see Irlandi & Crawford 1997, Eggleston et al. 1998, Micheli & Peterson 1999, Hovel & Lipcius 2001, 2002 for exceptions). The significance of seascapes and the influence of the spatial arrangement of habitats on fish communities were recognised in a review by Nagelkerken et al. (2015), who defined the term seascape nurseries, which conceptualised a nursery as a spatially explicit seascape comprising multiple mosaics of functionally connected habitats.

Most of the species caught in the intertidal seagrass beds must have moved there from subtidal areas on the rising tide (Skilleter & Loneragan 2003, Sheaves 2005, Sheaves et al. 2015). Very few species remain in the intertidal seagrass during low tide, except penaeid prawns and portunid crabs (Vance et al. 1994, Kenyon et al. 1995, Loneragan et al. 1998, Skilleter & Loneragan 2007). The subtidal habitat downshore from the areas sampled was primarily seagrass *Zostera capricorni* (Zharikov et al. 2005), providing a structurally complex refuge into which nekton could retreat at low tide (Irlandi & Crawford 1997, Sheaves 2005). The intertidal seagrass was separated from the mangroves by a band of unvege-

Table 7. Differences in abundance (effect sizes) of nekton between proximal (P) and distal (D) seagrass beds for each of the dense and sparse categories on each occasion that sampling was done. On the first occasion, both eastern and western Moreton Bay were sampled (Period 1). On the subsequent 2 occasions, only western Moreton Bay was sampled (Periods 2 and 3). Where the effect size was greater than 10%, the magnitude of the increase in abundance (%) is shown. On some occasions, some species were either not sampled or were in very small numbers, so effect sizes were not calculated. No. = number of times present; '-' species not present in that region of Moreton Bay or only in very small numbers, so data were not analysed; grey shading: effect size <10%, so details are not shown, but results were included in calculations of binomial tests

Measure of community or species	No.	Period 1		Period 2	Period 3	
		East	West	West	West	
Summary measure						
Number individuals (fish)	Dense	4	P > D: 122%	P > D: 647%	P > D: 351%	P > D: 396%
	Sparse	4	D > P: 33%	P > D: 113%	D > P: 42%	D > P
Number of species (fish)	Dense	4	P > D	P > D: 10%	P > D: 29%	P > D: 32%
	Sparse	4	P > D	P > D: 39%	D > P: 27%	P > D
Number of individuals (invertebrates)	Dense	4	P > D: 228%	P > D: 194%	D > P: 104%	P > D: 286%
	Sparse	4	P > D: 307%	P > D: 45%	P > D	D > P: 124%
Number of species (invertebrates)	Dense	4	D > P	P > D: 23%	D > P: 51%	D > P: 24%
	Sparse	4	P > D: 16%	D > P	D > P	D > P: 17%
Density of fish						
<i>Arenigobius leftwichi</i>	Dense	1	P > D: 878%	-	-	-
	Sparse	1	D > P	-	-	-
<i>Arenigobius frenatus</i>	Dense	3	-	P > D: 18753%	P > D: 444%	P > D: 1301%
	Sparse	3	-	P > D: 679%	P > D: 86%	D > P: 105%
<i>Favonigobius lentiginosus</i>	Dense	1	P > D: 158%	-	-	-
	Sparse	1	D > P: 261%	-	-	-
<i>Favonigobius exquisitus</i>	Dense	3	-	D > P: 24%	D > P: 132%	D > P: 938%
	Sparse	3	-	D > P: 76%	D > P	D > P: 63%
<i>Pseudogobius</i> sp.	Dense	1	-	-	P > D: 1116%	Not present ^a
	Sparse	0	-	-	Not present ^a	Not present ^a
<i>Mugilogobius stigmaticus</i>	Dense	1	-	-	P > D: 7086%	Not present ^a
	Sparse	0	-	-	Not present ^a	Not present ^a
<i>Gnatholepis gymnocara</i>	Dense	2	-	-	D > P: 12925%	D > P: 266%
	Sparse	2	-	-	D > P: 6988%	D > P: 42%
<i>Gerres subfasciatus</i>	Dense	2	-	-	P > D: 120%	P > D: 100%
	Sparse	2	-	-	P > D: 582%	P > D: 550%
<i>Tetractenos hamiltoni</i>	Dense	4	P > D: 1471%	P > D: 537%	P > D: 1567%	P > D: 5332%
	Sparse	4	P > D	P > D: 368%	P > D	P > D
<i>Centropogon australis</i>	Dense	4	P > D: 109%	P > D: 249%	P > D: 1246%	P > D: 4830%
	Sparse	4	P > D: 88%	P > D: 59%	P > D: 432%	P > D
<i>Pelates sexlineatus</i>	Dense	4	D > P: 48%	P > D: 92%	D > P: 62%	P > D: 233%
	Sparse	4	P > D: 62%	P > D: 25%	D > P: 42%	D > P: 110%
<i>Urocampus carinirostris</i>	Dense	4	P > D: 54%	P > D: 215%	D > P: 145%	P > D: 194%
	Sparse	4	P > D: 13%	P > D: 471%	D > P: 157%	D > P: 78%
<i>Petroscirtes lupus</i>	Dense	2	-	-	D > P: 1400%	D > P: 32%
	Sparse	2	-	-	D > P: 434%	D > P: 1768%
Density of invertebrates						
<i>Palaemon debilis</i>	Dense	4	D > P: 236%	P > D: 421%	D > P: 798%	D > P: 1790%
	Sparse	4	P > D: 1125%	D > P: 34%	D > P: 26%	D > P: 340%
<i>Palaemon serenus</i>	Dense	3	D > P	-	D > P: 628%	P > D: 756%
	Sparse	3	P > D: 2306%	-	D > P: 527%	D > P: 1193%
<i>Latreutes pygmaeus</i>	Dense	2	-	P > D: 149%	D > P	D > P
	Sparse	3	-	D > P: 2284%	D > P: 1363%	D > P: 151%
<i>Latreutes porcinus</i>	Dense	3	-	D > P	D > P: 30 113%	D > P: 25420%
	Sparse	3	-	D > P	D > P: 302%	D > P: 273%
<i>Idiosepius notoides</i>	Dense	3	D > P: 113%	-	D > P: 2381%	D > P: 3529%
	Sparse	3	D > P: 78%	-	D > P: 167%	D > P: 171%
<i>Penaeus plebejus</i>	Dense	4	P > D: 364%	P > D: 327%	P > D: 352%	P > D: 74%
	Sparse	4	P > D: 359%	P > D: 527%	P > D: 100%	P > D: 608%
<i>Metapenaeus bennettiae</i>	Dense	3	-	P > D: 1604%	P > D: 7107%	P > D: 351%
	Sparse	3	-	P > D	P > D: 654%	P > D: 723%
<i>Metapenaeus ensis</i>	Dense	2	-	-	P > D: 384%	P > D: 22%
	Sparse	2	-	-	D > P: 41%	D > P: 117%
<i>Penaeus esculentus</i>	Dense	2	-	-	D > P: 417%	D > P: 128%
	Sparse	2	-	-	D > P: 380%	D > P: 1072%

Continued on next page

Table 7 (continued)

Summary		Frequency ^b				
All comparisons between proximal and distal beds	D > P	19 from 28	23 from 30	18 from 46	19 from 44	78 from 148
	P > D	9 from 28	7 from 30	28 from 46	25 from 44	69 from 148
Comparisons between proximal and distal beds for dense seagrass	P > D	9 from 14	13 from 15	11 from 24	13 from 22	46 from 74
	D > P	5 from 14	2 from 15	13 from 23	9 from 22	29 from 74
Comparisons between proximal and distal beds for sparse seagrass	P > D	10 from 14	10 from 15	7 from 22	6 from 22	33 from 73
	D > P	4 from 14	5 from 15	15 from 22	16 from 22	40 from 73

^aWhere a species was only present in either the proximal or distal beds, it was not possible to estimate percent effect size, so only the direction of the difference is shown; where that species was not present in either bed type, this is shown as not present

^bTotal frequency included results where the effect size is less than 10%, but binomial probabilities could not be calculated here because comparisons of the abundance of species are not independent of each other

tated sediments. This intervening sediment matrix, fine muds in western Moreton Bay and coarser sand in the eastern region, provides few structural refuges for nekton moving to and from the mangroves during high tide. Although the seagrass beds closer to the mangroves were higher on the shore than those further away, it is unlikely that differences in tidal inundation time among treatments could account for the observed patterns. The intertidal gradient in Moreton Bay is relatively small, with only a 10 to 15 min interval between the time that sites low on the shore were inundated and when the water reached the sites closer to the mangroves.

The connectivity of seagrass and mangroves clearly influenced the composition and densities of the small epibenthic fish and invertebrates and is likely to have also affected the trophic flows within the seagrass. Relatively large rates of organic matter production via litterfall within mangroves forests is converted to detritus (Hogarth 1999), which is then exported to adjacent habitats (Gong et al. 1984, Robertson et al. 1991). Seagrass beds closer to adjacent mangrove forests are likely to receive greater amounts of this exported detritus than beds further away, in turn providing enhanced food supplies for detritivores. The distribution of juveniles prawns, especially *Penaeus* (= *Melicertus*) *plebejus* and *Metapenaeus bennettiae*, was consistent with this model, with greater numbers in proximal than distal beds (Skilleter et al. 2005). The stable isotope signature of prawns caught in mangrove creeks indicates they could be assimilating some carbon from mangrove sources, whereas those further away assimilate little carbon from mangroves (Loneragan et al. 1997). Detritus and small detritivores are an important component of the diet of juvenile prawns (Ruello 1973, Wassenberg & Hill 1987), so prawns may have obtained some dietary benefit from their

use of seagrass beds close to mangroves. Other detritivorous/iliophagous species including flat-tailed mullet *Liza argentea*, sea mullet *Mugil cephalus* and silver mullet *Valamugil georgii* were abundant in nearby mangroves but were rarely caught in the seagrass beds (Skilleter & Loneragan 2007). These species may use mangroves preferentially during high tide, perhaps because of the increased availability of *in situ* detritus, and then move as schools back to subtidal refuges as the tide recedes, without utilising the nearby seagrass for extended periods of time. If this is the case, they would not be expected to gain a benefit from using seagrass close to the mangroves.

During high tide, when mangroves are inundated, nekton may take advantage of the additional shelter provided by the shallow water (McIvor & Odum 1988, Vance et al. 1996, 2002, Paterson & Whitfield 2000) and/or the increased structural complexity found within mangroves (Laegdsgaard & Johnson 1995, Manson et al. 2005, Meager et al. 2005). Mangroves also often support increased densities of macroinvertebrate prey compared with other nearby habitats (Laegdsgaard & Johnson 1995, Sheridan 1997, Manson et al. 2005), providing enhanced opportunities for foraging when the forest is flooded. Large numbers of small fish also shelter among the roots and pneumatophores within the forest, providing an enhanced food supply for piscivores specialising on small individuals (Sheaves 2005). Movement by nekton between the mangroves and seagrass beds, whether for increased shelter or food resources, would be enhanced when the 2 types of habitat are closer together than when they are more distant to each other because of the reduction in time needed to cross the intervening mudflats, where there is little protection from predators. The expectation would be that mangrove-associated

species would have greater densities in the patches of seagrass close to mangroves than those further away, a pattern previously described for temperate systems (Jelbart et al. 2007). Many of our results also support this model. We would also predict that those species more abundant in proximal seagrass beds would be assimilating a greater proportion of carbon and nitrogen from a mangrove source than those in seagrass further from the mangroves. This could be tested through appropriate analysis of stable isotopic signatures.

Macrobenthic predators, such as *Acanthopagrus australis*, *Tetractenos hamiltoni*, *Gerres subfasciatus* and *Centropogon australis* (Bell et al. 1978, Linke et al. 2001, Miller & Skilleter 2006), were consistently more abundant in the proximal seagrass than in beds further away. Another predator, the weeping toad *Torquigener pleurogramma* (Potter et al. 1988), showed a similar pattern, although numbers were too small to analyse. These species were also abundant in the nearshore mangroves, suggesting they move among different interconnected estuarine habitats to forage (Skilleter & Loneragan 2003, Nagelkerken et al. 2015).

The mangrove goby *Mugilogobius stigmaticus* and half-bridled goby *Arenigobius frenatus* were more abundant in proximal than distal seagrass beds, consistent with results from a temperate estuary in Australia (Jelbart et al. 2007). Both species are closely associated with mangroves (Laegdsgaard & Johnson 1995, Skilleter & Loneragan 2007) and seagrass (York et al. 2006), and *M. stigmaticus* also moves further upshore into the saltmarsh and clay pans (Thomas & Connolly 2001). No published information is available on the diet of these gobies in seagrass or mangroves, but related species consume primarily meiofauna and small macrofauna, foraging within seagrass but also over bare mud (e.g. Robertson 1980, Coull et al. 1995). *M. stigmaticus* consumes copepods and crab larvae when foraging in nearby saltmarsh (R. Connolly pers. comm.).

The six-lined trumpeter *Pelates sexlineatus* was also more abundant in proximal seagrass beds, but it is unlikely that this species was taking advantage of enhanced food or refuges in the mangroves. The diet of *P. sexlineatus* comprises mainly macrocrustaceans (amphipods, tanaids, ostracods and copepods) (Sanchez-Jerez et al. 2002), all common and abundant in seagrass beds. *P. sexlineatus* has a strong association with seagrass (Edgar & Shaw 1995, Sanchez-Jerez et al. 2002) and was only rarely caught in the mangroves in this study (Skilleter & Loneragan 2007), although it uses mangroves elsewhere (Bell et

al. 1984). Jelbart et al. (2007) also found that *P. sexlineatus* was more abundant in seagrass close to mangroves than in beds further away in a temperate estuary in New South Wales. It is possible that the abundance of prey items was greater in proximal than distal beds in response to elevated amounts of detritus exported from the mangroves supporting greater abundances of seagrass-associated benthic prey for the trumpeter. More specific dietary studies in relation to availability of food in different mosaics are required.

Some species, such as the hairy pipefish *Urocampus carinirostris* and the carid shrimps *Latreutes porcinus* and *L. pygmaeus*, occurred in greater numbers in dense than in sparse seagrass but showed no consistent response to the connectivity between seagrass and the nearby mangroves. Hairy pipefish are seagrass specialists that have a sit-and-wait feeding strategy, targeting small crustaceans, such as amphipods, mysids and copepods (Howard & Koehn 1985). The effectiveness of this strategy is often enhanced in habitats with increased structural complexity (e.g. Heck & Orth 1980, Coen et al. 1981), so these species would benefit from being in dense compared with sparse seagrass. The pipefish and the carid shrimps are also small and relatively slow-moving and may be susceptible to predation when moving between different habitats, so they are unlikely to move into nearby mangroves across unprotected mudflats. These species were rare or did not occur in samples collected from the adjacent mangrove forests. In contrast, the southern pygmy squid *Idiosepius notoides*, also a sit-and-wait ambush predator consuming small crustaceans (Kasugai 2001), was consistently more abundant in dense seagrass beds further away from the mangroves than those close to the forest. This species may avoid areas used extensively by larger predators transiting between the mangroves and adjacent habitats.

The presence or absence of mangroves in the intertidal zone may be critical for maintaining patterns of increased biodiversity and biomass of fish assemblages in other nearshore habitats, and this influence of the connectivity may operate over a range of spatial scales. Our results and those of Jelbart et al. (2007) indicate that connectivity is important within specific estuarine systems over scales of hundreds of metres to kilometres. At larger scales (10s to 100s of km), Nagelkerken et al. (2001) found that species richness and the abundance of fish assemblages were greater in seagrass beds with adjacent mangroves than in areas without mangroves, and Mumby et al. (2004) found that the biomass and community

composition of fish utilising nearby coral reefs were greater when mangroves were present than absent. These critical linkages between mangroves and other components of estuarine and coastal systems suggest that the loss or degradation of mangroves is likely to have serious implications for the overall function and value of nearby habitats.

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