

# Spatial variation in the morphology of monospecific stands of the western white mangrove *Avicennia marina* var. *marina* in Shark Bay Marine Park

MICHAEL J RULE<sup>1,2\*</sup>, ALAN J KENDRICK<sup>1</sup> AND DAVID HOLLEY<sup>3</sup>

<sup>1</sup>Marine Science Program, Science and Conservation Division, Department of Parks and Wildlife, Kensington, Western Australia 6151, Australia.

<sup>2</sup>Oceans Institute, University of Western Australia, Crawley, Western Australia, Australia

<sup>3</sup>Shark Bay District, Midwest Region, Regional and Fire Services Division, Department of Parks and Wildlife, Denham, Western Australia 6537, Australia.

\* Corresponding author: michael.rule@dpaw.wa.gov.au

## ABSTRACT

Spatial variation in the morphology of mangrove stands could be expected to lead to differences in their ecological role and the ecosystem services they provide. Here we examine spatial variation in the structural morphology of stands of *Avicennia marina*, the sole mangrove inhabiting Shark Bay, Western Australia—a semi-arid environment with strong regional-scale gradients in the physical environment. Morphological variables were measured at 12 sites across a putative gradient in physical conditions from oceanic (western) to metahaline (eastern) parts of the bay and data were tested using both univariate and multivariate analyses. The multivariate analysis of the combined suite of characters found a significant difference between sites, and pairwise tests revealed significant differences for most comparisons. Changes in morphology across Shark Bay were correlated to longitude, which was used as a proxy for the salinity regime. Three distinct morphotypes associated with different salinity zones were revealed. The results suggest that the morphology of *A. marina* in Shark Bay varies across regional scales and may be influenced by background physical conditions. It is likely that the functional roles of these mangrove stands differ across the region, and thus, treating stands as uniform ‘units’ may not be appropriate for conservation management. We suggest that the conservation of *A. marina* could be enhanced by revised management zoning of Shark Bay Marine Park to include representative areas of each of the divergent morphotypes in sanctuary zones or special purpose zones configured for mangrove protection.

**Keywords:** morphology, spatial variation, structure

## INTRODUCTION

Mangroves are salt-tolerant trees that inhabit the intertidal zone of sheltered coasts and estuaries across both tropical and temperate regions (Morrisey et al. 2010). These communities can be highly productive and are ecologically and economically significant (Barbier et al. 2010; Walters et al. 2008) through providing diverse ecosystem services such as nursery habitats for fishery species, enhanced shoreline stability, food and timber (Alongi 2002; Morrisey et al. 2010). A range of physical and climatic factors, such as sediment type, tidal inundation and wave exposure, as well as temperature, rainfall and groundwater dynamics, influence whether mangrove communities can establish and how they persist in particular coastal areas (Semeniuk 1993).

Mangroves display a high level of morphological plasticity in response to environmental conditions (Feller

et al. 2010). Across small spatial scales the growth and biomass of mangroves can vary in relation to factors like rainfall and freshwater input, tidal inundation and wave action (Alongi et al. 2005). For example, within a forest, dwarf or scrub mangroves can occur at higher elevations where there is infrequent tidal inundation, greater rates of evaporation and consequently higher salinities (Naidoo 2010). In some areas, such morphological changes in mangroves may also be a result of nutrient availability, and dwarf trees have been shown to increase growth significantly when limiting nutrients have been experimentally added (Feller 1995; Lovelock et al. 2006). While many studies have sought to classify the sequential changes in forest structure and species distribution parallel to shore on the basis of local topographic features (Lugo & Snedaker 1974) or structural characteristics (Pellegrini et al. 2009), few have quantified regional-scale patterns in morphological structure (Schaeffer-Novelli et al. 1990; Ward et al. 2006), particularly in areas with strong, regional-scale environmental gradients (Agraz Hernández et al. 2011; Arreola-Lizárraga et al. 2004).

Mangroves occur prominently along coasts in the northern half of Western Australia (WA) and are listed as key ecological values in marine parks and reserves across this region. While the monsoonal and macro-tidal northern Kimberley region supports up to 19 mangrove species, they become less diverse and more fragmented further southwards in the relatively arid and micro-tidal Pilbara and Midwest regions (Duke 2006). The large, semi-enclosed embayment of Shark Bay supports the southern-most limit of extensive mangrove growth in WA, but only has a single species, *Avicennia marina* (Forsk.) Vierh. var. *marina*. Here, this mangrove occurs in numerous and often isolated stands (CALM 1996) that are typically less than 10 ha in size and rarely exceed 100

ha. Southwards from Shark Bay in WA, small and widely separated stands of this species occur at the Houtman Abrolhos Islands and Bunbury.

The semi-arid Shark Bay region has a unique marine environment where the combined influences of shallow water, high evaporation rates (Burling et al. 2003) and constrained water circulation (Nahas et al. 2005) maintain a persistent salinity gradient which ranges from oceanic (35–38 ppt) in the western and northern areas to strongly hyper-saline (60–65 ppt) in the south-eastern reaches of Hamelin Pool and L'haridon Bight (Logan & Cebulski 1970). Between these extremes, lies a distinct metahaline region and the Cape Peron and Faure salinoclines (Fig. 1). This hyper-saline environment is one of the exceptional

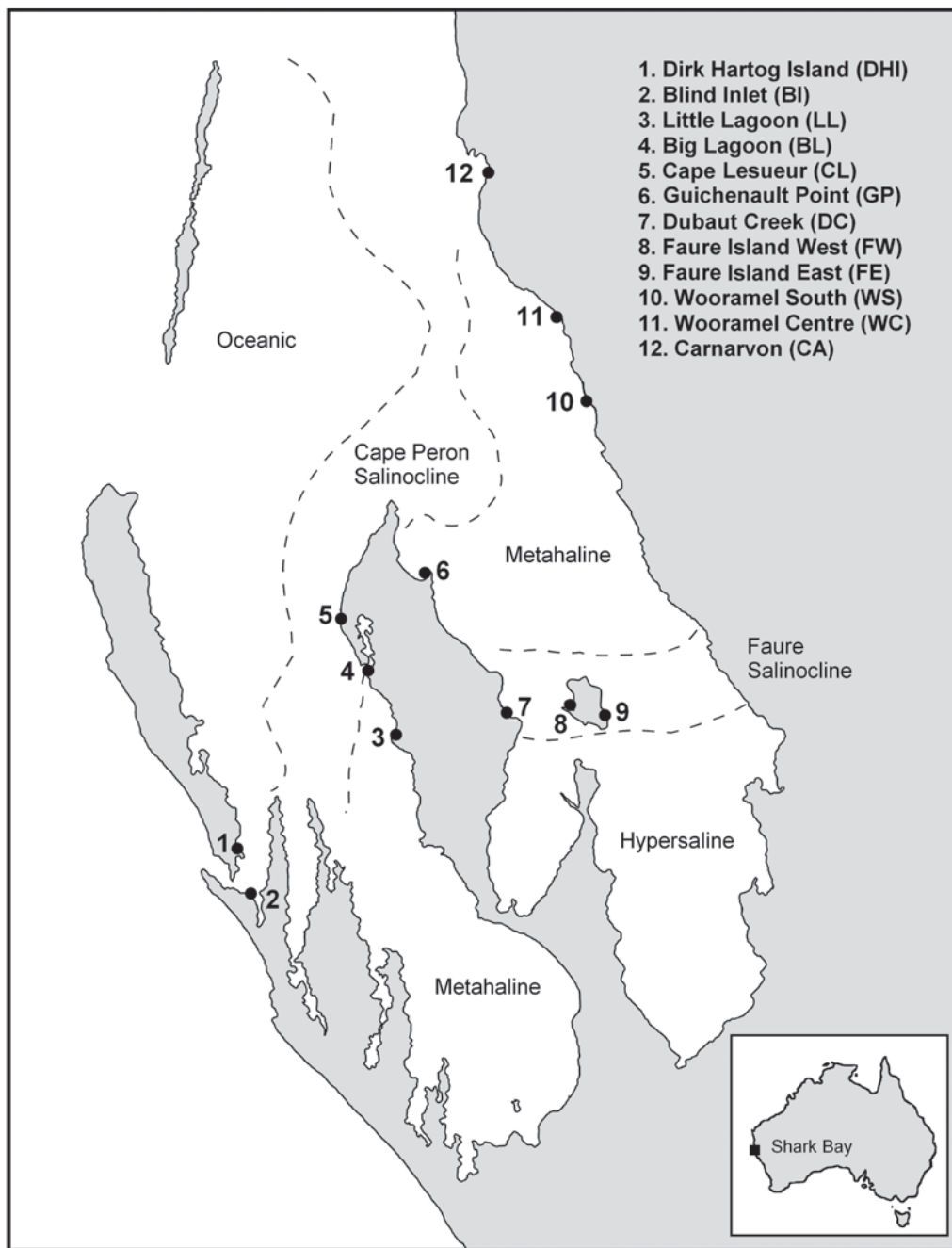


Figure 1. Mangrove sites sampled in Shark Bay. Codes used in tables are also given in parentheses.

**Table 1**

Mean ( $\pm$  SE) values for each character measured at each site. The overall mean ( $\pm$  SE) for each character is also provided. See Fig. 1 for site codes. Additional information includes: latitude and longitude of each site; aerial extent; a priori-defined salinity regime (oceanic = ocean, metahaline = meta, Cape Peron salinocline = CP sal, Faure salinocline = F sal); and conservation status (General Use = GUZ, Sanctuary = SZ, and Special Purpose = SPZ).

Character	Site												Overall mean
	DHI	BI	CL	BL	LL	GP	CA	DC	WC	FW	WS	FE	
Latitude	S26.1066	S26.1862	S25.7180	S25.7979	S25.9057	S25.6205	S24.9345	S25.8670	S25.1826	S25.8447	S25.3255	S25.8671	
Longitude	E113.2273	E113.2498	E113.4169	E113.4657	E113.5285	E113.5777	E113.6800	E113.7272	E113.8205	E113.8547	E113.8772	E113.9208	
Salinity regime	ocean	ocean	CP sal	meta	meta	meta	CP sal	F sal	meta	F sal	meta	F sal	
Conservation	GUZ	GUZ	GUZ	SPZ	GUZ	GUZ	SPZ	GUZ	SPZ	GUZ	SPZ	GUZ	
Areal extent (ha)	4.60	26.60	1.90	14.00	2.80	35.40	559.50	1.00	137.70	3.20	22.90	8.60	68.20
No. of mature trees (ha)	1120 (195.96)	960 (160.00)	9040 (1163.44)	8640 (1411.95)	2240 (530.66)	4160 (652.38)	8800 (954.99)	1520 (557.14)	6320 (598.67)	6320 (637.50)	5920 (1438.89)	7040 (1077.78)	5173 (446.75)
No. of saplings (ha)	– (521.54)	–	4000.00 (160.00)	– (160.00)	240.00 (240.00)	160.00	560.00 (97.98)	–	160.00 (632.46)	– (334.66)	2000.00 (165.72)	800.00	660.00
No. of recruits (ha)	36400 (13912.3)	6240 (3916.3)	22373.2 (18610.4)	1920 (958.3)	12720 (3430.2)	–	6720 (2964.9)	160 (160)	560 (240)	1040 (854.2)	400 (253)	1200 (357.8)	7477.77 (2291.59)
No. of pneumatophores (m)	416.00 (26.00)	363.47 (20.52)	218.13 (21.58)	340.00 (29.92)	390.40 (44.89)	256.53 (8.76)	510.93 (80.21)	59.33 (16.83)	201.33 (21.72)	518.93 (40.22)	287.73 (26.12)	259.47 (28.32)	318.52 (18.90)
Complexity	4.80 (0.58)	4.60 (0.24)	3.60 (0.40)	3.60 (0.51)	4.00 (0.55)	2.80 (0.49)	2.00 (0.63)	2.20 (0.80)	2.80 (0.49)	3.60 (0.24)	5.00 (0.45)	3.40 (0.60)	3.53 (0.18)
% cover	65.00 (2.34)	63.43 (3.72)	39.49 (4.67)	48.66 (3.63)	69.52 (3.16)	45.57 (1.82)	48.59 (4.61)	39.62 (5.29)	32.76 (7.06)	70.06 (1.87)	42.98 (3.67)	36.84 (4.21)	50.21 (1.97)
Height (cm)	370.00 (6.85)	557.50 (21.45)	118.20 (17.55)	344.00 (15.19)	414.40 (25.26)	462.40 (7.83)	311.20 (25.97)	203.71 (73.84)	118.12 (17.46)	345.60 (24.41)	188.40 (11.12)	195.20 (12.97)	302.40 (18.79)
Total diameter at 30cm (cm)	112.74 (23.46)	139.12 (25.42)	21.57 (2.72)	30.11 (4.08)	80.58 (25.71)	44.03 (3.49)	33.33 (9.32)	87.93 (28.23)	26.51 (1.53)	27.78 (1.26)	30.33 (4.17)	25.77 (3.10)	54.98 (6.37)
Total diameter at 130cm (cm)	81.05 (20.28)	114.04 (22.32)	1.52 (1.52)	20.59 (3.02)	48.77 (9.95)	31.35 (2.67)	20.63 (7.15)	31.93 (21.21)	2.44 (2.29)	18.24 (1.32)	8.51 (2.76)	7.50 (1.55)	32.21 (5.18)
No. of primary branches	2.65 (0.48)	2.75 (0.68)	2.92 (0.40)	1.56 (0.20)	3.84 (1.80)	1.28 (0.08)	1.52 (0.22)	3.28 (0.70)	1.92 (0.19)	1.20 (0.09)	2.48 (0.26)	1.56 (0.19)	2.25 (0.20)
Leaf weight (g)	1.60 (0.12)	1.72 (0.07)	1.27 (0.04)	1.37 (0.07)	1.59 (0.12)	1.70 (0.04)	1.35 (0.06)	0.94 (0.10)	1.17 (0.05)	1.34 (0.04)	1.07 (0.05)	1.27 (0.05)	1.37 (0.04)
Leaf length (cm)	12.11 (0.32)	12.32 (0.31)	9.62 (0.27)	11.56 (0.30)	10.93 (0.38)	11.88 (0.17)	10.18 (0.30)	8.63 (0.47)	10.01 (0.29)	11.16 (0.28)	8.89 (0.14)	9.20 (0.13)	10.54 (0.18)
Leaf width (cm)	3.81 (0.21)	3.66 (0.10)	3.22 (0.14)	3.49 (0.07)	3.56 (0.14)	3.78 (0.06)	3.15 (0.06)	2.82 (0.13)	2.74 (0.09)	3.54 (0.05)	3.06 (0.08)	3.32 (0.05)	3.35 (0.05)
Leaf area (cm)	27.39 (2.00)	26.79 (0.59)	20.21 (1.15)	23.92 (0.90)	25.06 (1.74)	27.00 (0.51)	19.54 (0.84)	14.60 (1.15)	16.74 (0.91)	23.86 (0.83)	16.44 (0.71)	18.83 (0.38)	21.70 (0.63)



physical and biological conservation values of Shark Bay that has led to the creation of terrestrial and marine conservation reserves in this area and its inclusion on the World Heritage List (CALM 1996; McCluskey 2008). Although the federal government has over-arching responsibility for ensuring the protection of Australia's World Heritage estate (McCluskey 2008), Shark Bay Marine Park (SBMP) was created in 1990 under the *Conservation and Land Management Act (1984)* to protect the area's important marine conservation values (CALM 1996). Management zoning is a key mechanism for ensuring the protection of ecological and social values in WA's marine parks and reserves.

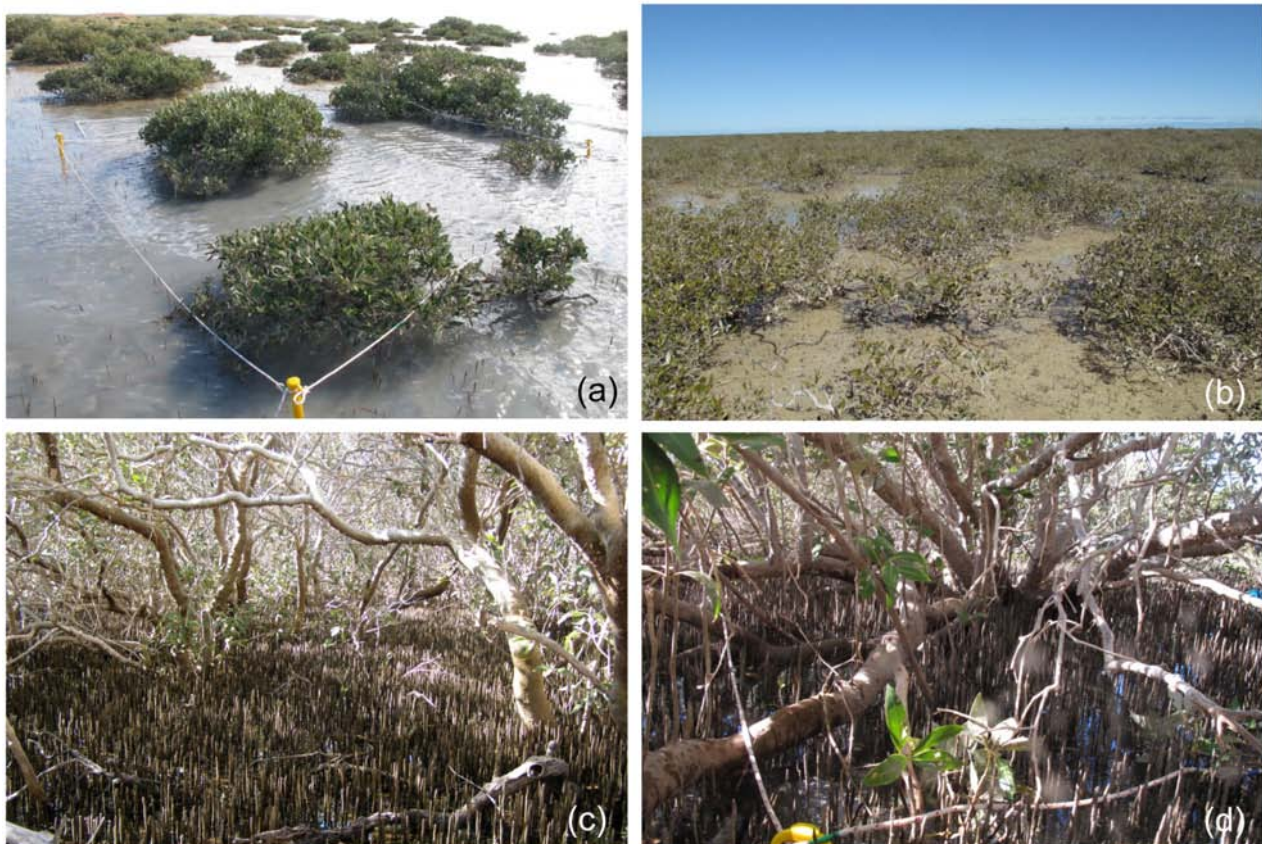
Although the ecological and conservation value of mangroves are recognised in SBMP, mangroves are poorly studied in this region (CALM 1996) and little is known, for example, about how they vary in structure in relation to Shark Bay's persistent salinity regime (Nahas et al. 2005). Managers often assume that mangroves are morphologically and ecologically uniform, such that the conservation value may be adequately preserved by the protection of 'representative' areas (Jin-Eong, 1995). However, local variations in the structure, biomass and productivity of mangroves can lead to variations in ecosystem function and habitat use across relatively small spatial scales (Lovelock et al. 2005; Twilley et al. 1986), and treating mangroves as a homogeneous unit may not be an appropriate management strategy in some areas.

Here we documented spatial variation in the morphological structure of *A. marina* stands across SBMP and investigated the potential role of the broad-scale salinity gradient in driving the observed patterns. We also assessed the adequacy of existing management zoning relating to mangroves in this distinctive marine environment.

## METHODS

### Sampling procedure

Prior to field sampling, 12 sites of relatively homogeneous mangrove cover in Shark Bay were identified from aerial imagery (Fig. 1; Table 1). Five randomly placed 5 m × 5 m plots were established at each site and the perimeter of each plot was delineated with rope suspended on stakes. A broad index of benthic structural complexity (Wilson et al. 2007) was estimated for each plot. Briefly, a semi-quantitative score (between 1 and 6) for the overall complexity of the habitat was given for each plot, based on the density and size of trees, the coverage of bare sand and the amount of woody debris present (Fig. 2). Thus, a plot composed of a small number of immature trees with little woody debris, scored low ( $c = 1$ ) while a plot composed of a range of tree-sizes (including multi-stemmed trees) with a large amount of woody debris



**Figure 2.** Examples of the variation in mangrove stand morphology across Shark Bay and the complexity scores used in this study: (a) Dubaut Creek (complexity = 1); (b) Wooramel South (complexity = 2); (c) Blind Inlet (complexity = 4); and (d) Little Lagoon (complexity = 6).

scored highly ( $c = 6$ ). While other measures of complexity have been widely used for mangroves (e.g. Arreola-Lizárraga et al. 2004), they are typically used in multi-species forests and rely on an index which is calculated from other measured variables and thus are not independent. The index used here provided an assessment of complexity which was independent of other measured characters.

Within each plot the number of mature trees (stem girth  $> 2$  cm), saplings ( $> 100$  cm in height, stem girth  $\leq 2$  cm) and recruits ( $< 100$  cm high, leaves arising directly from a single, undifferentiated stem) were counted, and the number of pneumatophores was counted within three haphazardly positioned  $1 \text{ m}^2$  quadrats. The extent of canopy cover was estimated by taking eight haphazardly selected upward-facing photographs from approximately 0.5 m above the substratum. In the few instances where the mangrove canopy was too low to use this method, downward-facing images were taken from a height of approximately 1.5 m from the substratum. The percent of foliage cover in each image was then calculated using ER Mapper software.

Within each plot, further measurements were taken on five haphazardly selected trees, or all trees if fewer than six were present. The maximum height of each tree, the trunk diameters at heights of 30 and 130 cm from the ground and the number of primary branches were counted. Where multiple primary branches were present at the heights where measurements were taken, each trunk diameter was measured and summed for the tree. Five mature leaves were collected from each tree, weighed to 0.01 g and photographed from a standard height. The maximum length, width and area of each leaf were calculated using the ImageJ software (Abramoff et al. 2004).

In order to assess the adequacy of current management zoning, the total area (ha) of mangroves within the boundary of SBMP was calculated from high-resolution (10 m pixel) ALOS (Advanced Land Observation Satellite) satellite imagery. The area of mangrove habitat was also calculated for each management zone and summed to provide a proportion of the total area of mangroves in each type of management zone.

## Statistical analyses

All data were averaged or scaled to the plot level, such that analyses were undertaken on five replicates for each variable at each site. Multivariate analyses performed using PRIMER V6 with PERMANOVA extension (Anderson et al. 2006; Clarke & Gorley 2006) were used to examine differences in the overall structure of the 12 mangrove sites. Prior to analysis, strongly correlated variables (e.g. leaf length and width) were removed from the dataset. Data were normalised as they were measured on different scales and a similarity matrix was constructed on Euclidean distances. Principal components analysis (PCA) was performed to visually assess patterns in the data and Spearman rank correlations ( $p > 0.5$ ) were used to produce eigenvectors to highlight the overall increasing

or decreasing relationships of morphological variables across the ordination. Differences in the combined suite of morphological characters between groups were examined using a one-way permutational analysis of variance (PERMANOVA; Anderson 2002) with site as a random factor. Additional, post-hoc pairwise  $t$ -tests were conducted to examine where significant differences occurred.

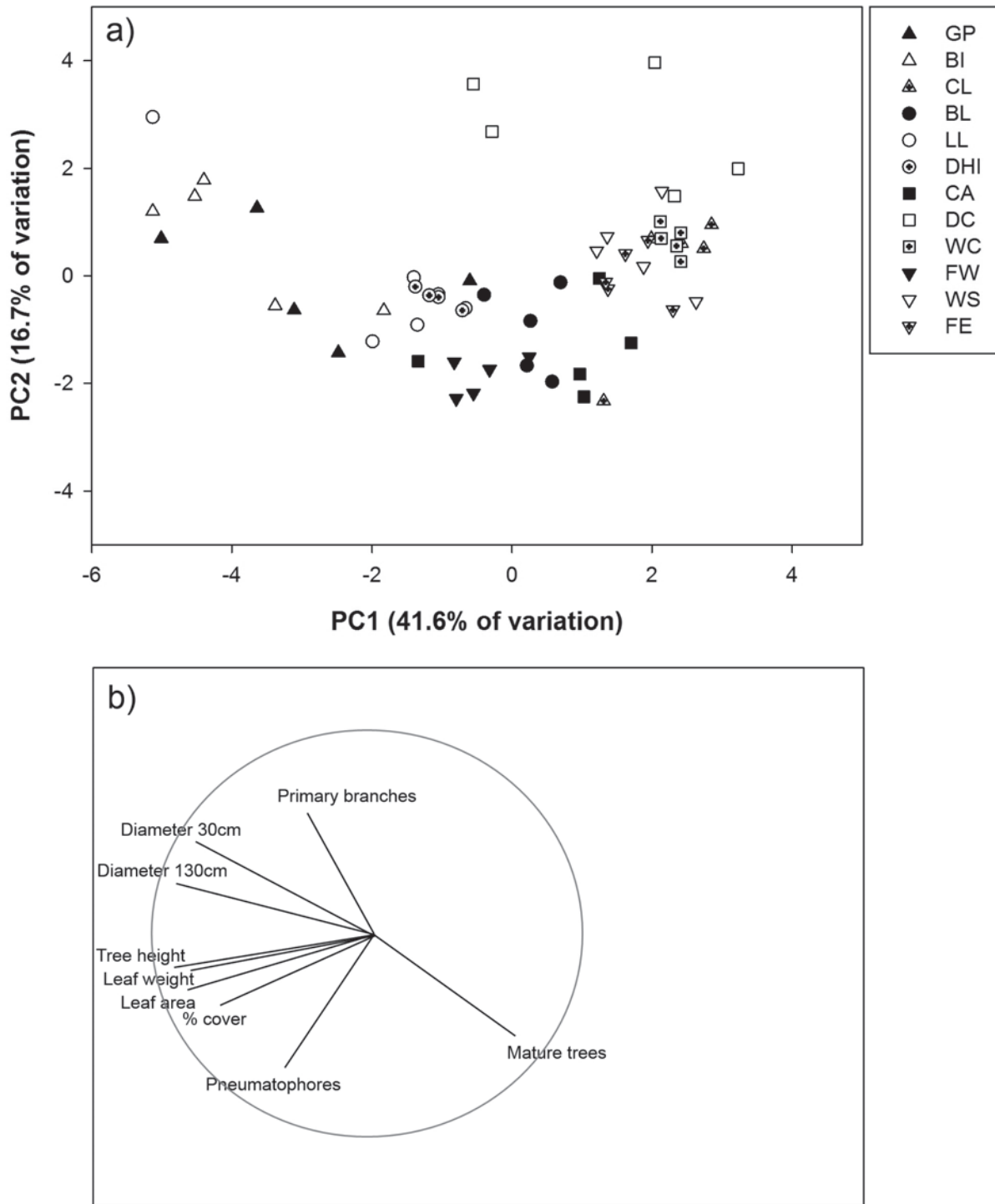
Linear regressions were performed to examine the relationships between PCA scores and the predictor variables, latitude and longitude, which provide a reasonable proxy for the strong east–west and north–south salinity gradient in Shark Bay. Prior to analysis, all variables were checked for normality and were appropriately transformed if necessary.

We tested whether the magnitude of divergence in mangrove structure between sites was related to the distance between sites. Linear distances between each site were measured and the mean dissimilarity between each pair of sites was calculated using a SIMPER analysis. The resultant dissimilarity matrix was then correlated (Pearson correlation) to the distances between sites.

A constrained canonical analysis of principal coordinates (CAP; Anderson & Willis 2003) was used to test whether mangrove structure differed between a priori-defined salinity zones (i.e. oceanic, metahaline, Cape Peron salinocline and Faure salinocline; Fig. 1; Table 1) identified in Shark Bay by Logan and Cebulski (1970). The groupings identified by the CAP analysis were formally tested using a one-way PERMANOVA using salinity zone as a fixed factor.

## RESULTS

The morphological structure of *A. marina* stands varied considerably across sites in Shark Bay (Table 1). For example, the mean density ( $\pm 1$  SE) of mature trees ranged from  $960 \pm 160.00$  trees per plot at Blind Inlet to  $9040 \pm 1163.44$  per plot at Cape Lesueur. The mean height of trees differed by  $>400$  cm between Blind Inlet ( $557.50 \pm 21.45$  cm) and Wooramel Centre ( $118.12 \pm 17.46$  cm). In the PCA based on all measured variables, PC1 and PC2 accounted for 61.0% of total variation between samples (Fig. 3a). Samples to the left of the plot (Blind Inlet and Guichenault Point, Little Lagoon) corresponded to increased tree height, diameter and larger values for leaf characteristics (Fig. 3a, b), while those to the right of the plot (Carnarvon, Wooramel South and Centre, Faure East, Dubaut Creek) corresponded with an increased number of mature trees (Fig. 3a, b). Samples from Dirk Hartog Island, Big Lagoon and Faure West formed reasonably tight site-groups in the centre of the plot. Samples from Dubaut Creek formed a disparate group at the upper right of the ordination (Fig. 3a). The vertical separation of samples in the PCA was driven by shifts in the number of primary branches, mature trees and pneumatophores (Fig. 3b). The PC1 scores were significantly correlated ( $r^2 = 0.40$ ;  $p = 0.001$ ) to longitude and also displayed a significant but weak negative ( $r^2 = -0.28$ ;  $p = 0.001$ ) correlation to



**Figure 3.** Principal components analysis (PCA) showing (a) all data and (b) a vector plot of the variables contributing to the PCA. The vector lines indicate the direction of increasing values, and the length relative to the circle indicates the strength of the correlation (Spearman). Only vectors with correlations >0.5 have been included. Site codes are given in Fig. 1.

latitude. The vertical separation of samples in the ordination (PC2 scores) was very weakly correlated ( $r^2 = 0.07$ ;  $p = 0.05$ ) to latitude.

The analysis of the combined suite of structural components by PERMANOVA returned a significant difference between sites ( $pseudo-F_{11,49} = 9.48$ ,  $p < 0.001$ ), and despite the apparent overlap in the structure of sites (Fig. 3a), pairwise comparisons revealed significant

differences for almost all comparisons (65 of 66 possible comparisons). The only comparison where morphological structure was not significantly different was for Little Lagoon and Dirk Hartog Island (Table 2).

The CAP analysis of mangrove structure in the different salinity zones (Fig. 4) separated the study sites into three distinct groups that were supported by the PERMANOVA ( $pseudo-F_{3,57} = 7.70$ ,  $p < 0.001$ ). Samples from the



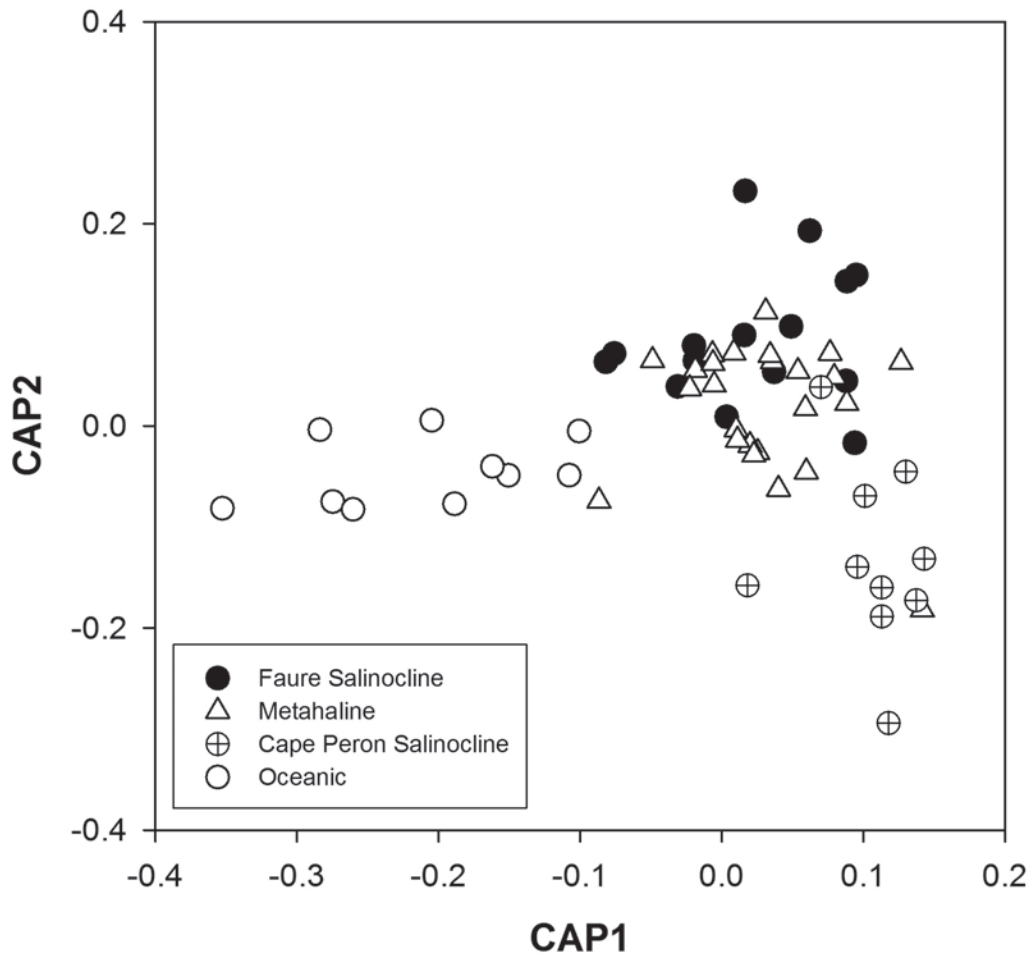


Figure 4. Results of the canonical analysis of principal coordinates (CAP) examining changes in mangrove morphology across different salinity zones.

Table 2

Summary of the pairwise comparisons (t-values) of morphological structure between sites for the single-factor PERMANOVA. Only t-values for comparisons that were significant ( $p < 0.05$ ) are shown. Tests that were not significant ( $p > 0.05$ ) are designated by 'ns'. Site codes are given in Fig. 1.

	BI	CL	BL	LL	GP	CA	DC	WN	FW	WS	FE
DHI	1.65	3.23	2.68	ns	2.40	3.09	3.55	4.22	2.56	3.81	3.70
BI		4.53	4.27	1.75	3.48	4.53	4.34	6.42	4.52	5.72	5.82
CL			2.68	2.57	3.72	2.38	2.67	2.31	3.37	1.69	1.92
BL				1.82	2.78	1.84	3.20	3.31	2.12	3.24	2.50
LL					1.80	2.11	2.70	3.02	1.60	2.66	2.55
GP						3.53	3.88	5.58	4.24	5.31	4.66
CA							2.87	2.61	2.23	2.70	2.07
DC								1.88	3.76	2.16	2.26
WN									4.88	2.29	1.79
FW										4.17	3.94
WS											1.74

oceanic salinity zone formed a discrete group to the left of the ordination, while samples from each of the other salinity classes grouped to the right. Among these samples, those from the Faure salinocline and metahaline zones formed a single group while samples from the Cape Peron salinocline zone separated clearly from this group. All

groups had a high allocation success, with 42 of 60 (70%) samples correctly classified and an overall misclassification error of 30%. Allocation success was extremely high (90%) for oceanic and Cape Peron salinocline samples while allocation was poorest among metahaline zone samples (52% correctly classified). The post-hoc pairwise tests

**Table 3**

Summary of the pairwise comparisons of morphological structure between different salinity zones derived from the one-factor PERMANOVA. Values that are significant ( $p < 0.05$ ) are shown in bold.

Test	<i>t</i>	<i>p</i> <sub>permuted</sub>
Oceanic vs Cape Peron salinocline	3.84	<b>0.001</b>
Oceanic vs metahaline	3.51	<b>0.001</b>
Oceanic vs Faure salinocline	3.71	<b>0.001</b>
Cape Peron salinocline vs metahaline	1.90	<b>0.003</b>
Cape Peron salinocline vs Faure salinocline	1.80	<b>0.009</b>
Metahaline vs Faure salinocline	1.14	0.237

revealed significant differences for all comparisons except for the comparison between metahaline samples and those from the Faure salinocline (Table 3), confirming the presence of three distinct groups; oceanic, Cape Peron salinocline, and a combined metahaline/Faure salinocline group.

## DISCUSSION

### Variation in *A. marina* structure across Shark Bay Marine Park

This study has demonstrated that the structure of *A. marina* stands varies markedly across Shark Bay, and that this variation broadly corresponds to the different salinity zones that exist in this biogeographically distinct marine environment. The suite of characters showed a negative relationship with longitude, which may be considered as a reasonable surrogate for Shark Bay's persistent salinity gradient that increases in a south-east direction into the bay. At a broad scale, the *A. marina* stands that were exposed to typically oceanic conditions were more structurally complex (Pool et al. 1977) with a lower density of tall (> 500 cm) and multi-stemmed trees, whereas stands in more saline areas were typically more dense and composed of short (< 150 cm) trees. Divergent examples of the structure of these typically discrete and isolated mangrove stands are shown in Fig. 2. Notably, mangroves are not present in the most saline parts of Shark Bay, and thus it appears that the salinity regime within Shark Bay is exerting a significant influence on the structure of mangrove stands.

The relationship between mangrove structure and salinity across Shark Bay is analogous to the variations in mangrove tree structure that occur across typically smaller spatial scales in estuaries (Lovelock et al. 2005), where physical gradients of factors like salinity and shoreline elevation can be pronounced (Agraz Hernández et al. 2011; Chen & Twilley 1999). Such environmental gradients result in the predictable zonation of estuarine mangroves, with a decline in tree height with increasing elevation from the sea (Lugo & Snedaker 1974). It is

notable that the patterns observed in this study were only moderately predictable, as illustrated by the fact that the smallest trees occurred at the Wooramel central and Cape Lesueur sites, while those at Faure Island west, which is closest to Shark Bay's persistent hypersaline zone, were of similar size to those at Big Lagoon and Dirk Hartog Island. Hence, while Shark Bay's salinity gradient is likely to influence the structure of these typically small and isolated mangrove stands, additional factors acting on mangrove growth may also contribute to the patterns observed in this study. These may include, for example, tidal inundation, elevation, differences in the recruitment and mortality of trees and the influence of sediment movement at particular sites (de Lange & de Lange 1994). In Shark Bay, such influences may occur on the eastern coast when fine sediments are episodically discharged from the Wooramel River during cyclonic floods. Subject to prevailing on-shore winds, the discharged silt is unlikely to be widely dispersed (Fraser et al. 2012) and its settlement along this shallow, low-energy coastline may significantly influence mangrove growth in this area.

We are confident that structural differences among mangrove stands observed in this study are caused by environmental conditions and do not simply reflect stands of varying ages that have recruited at different times (Fromard et al. 1998). While some sites, such as Cape Lesueur, did support a high number of apparently young trees that were relatively small with thin trunks, similarly low trees at sites like Wooramel south had comparatively thick and gnarled trunks, indicating that they were mature, but stunted, and are most likely growing in sub-optimal habitats (Naidoo 2006). For instance, mangrove growth is closely linked to nutrient availability and when trees are nutrient limited, canopy development may be retarded (Lovelock et al. 2006). Shark Bay has long been recognised as a largely P-limited system (Smith & Atkinson 1984); however, recent investigations in the area have shown that nutrient limitation is spatially variable over local scales due to differences in nutrient input and transport (Burkholder et al. 2013; Fraser et al. 2012). It is possible that spatial variability in nutrient availability interacts with the salinity regime of the area to produce the patterns in mangrove structure observed here. Additionally, while ground water availability may be particularly important to mangrove growth in areas where rainfall is limited (Susilo et al. 2005), very little information on groundwater dynamics is currently available from the region. Further research on plant and sediment nutrient content and groundwater availability would provide a more clear understanding of mangrove growth in Shark Bay.

### Implications for managing *A. marina* in Shark Bay Marine Park

Conservation management has tended to assume that mangroves along marine shorelines are structurally homogenous and ecologically similar across their spatial extent (Jin-Eong 1995). However, the wide variation in the structural complexity and density of *A. marina* across SBMP reported here suggests that these divergent



mangrove stands may function quite differently. This could include, for example, differences in primary productivity (Ewel et al. 1998) and carbon storage (Alongi 2012), their capacity to trap decomposing wrack, or the manner in which complex trunks, root structures and tree canopies provide refuge and/or feeding habitats for other organisms (Morton 1990; Storr 1990).

While the physical removal of mangroves in WA is prohibited under the *Wildlife Conservation Act (1950)* (CALM 1996), mangrove trees and their associated fauna in Shark Bay are subject to impacts from human activities such as fishing, camping and four-wheel driving. These potentially detrimental activities can be managed in SBMP by marine park zoning, as is the case in other marine reserves in WA (e.g. Mangrove Bay in Ningaloo Marine Park; CALM 2005). However, of the approximately 1500 ha of measurably dense *A. marina* identified within SBMP from satellite imagery, only about 0.54 ha (0.035%, Table 4) is currently protected in a single sanctuary zone (Big Lagoon Sanctuary Zone), which provides the highest level of conservation protection (i.e. no-take). All other mangroves in SBMP are in general use (ca. 293 ha), recreation (ca. 4.3 ha) or special purpose zones that were established for the protection of nursery areas and seagrass communities (ca. 1260 ha), which do not explicitly protect mangroves or their associated fauna from a range of potential human impacts. In addition, mangroves in many areas bridge the tenure between the SBMP boundary (which mostly extends to High Water Mark) and adjacent lands that are not all managed for conservation (CALM 1996). Thus, despite mangroves in Shark Bay being recognized for their high conservation value (CALM 1996; McCluskey 2008), the vast majority are not within management zones that confer a high level of protection.

Based on the findings of this study, we suggest that it is inappropriate to consider mangroves in Shark Bay as a single, homogeneous entity for conservation management. We identified three structurally distinct mangrove types: oceanic mangroves which comprised tall, low density mangroves with a high canopy cover (i.e. Blind Inlet and Dirk Hartog Island); mangroves associated with the Cape Peron salinocline which had high densities of both mature trees and saplings with thinner trunks (Cape Leseuer, Carnarvon); and a combined metahaline/Faure salinocline type which comprised smaller trees with reduced leaf

characteristics (Faure Island, Wooramel coast). We recommend that future conservation planning targets representative mangrove stands of each of these structural forms. This would acknowledge the fact that, for example, a relatively small area (ca. 31 ha) of tall, low density mangroves occur in association with oceanic salinities in the western parts of Shark Bay. In this context, threatening processes that may be impacting on a relatively small proportion the total mangrove area may, in fact, be impacting on a large proportion of mangroves of a particular structural form. Threatening processes that currently impact on mangroves and their associated fauna include fishing (e.g. for mud crabs, *Scylla* spp.) and damage to trees and pneumatophores caused by campers or four-wheel drive vehicles. Notably, the significance of these threatening processes will vary depending upon the structure of the mangroves and the location and size of different stands. Smaller and stunted trees are, for example, much more susceptible to damage from vehicles, while fished species like mud crabs are more likely to be significantly depleted from relatively small and isolated mangrove stands.

We suggest that future management planning for SBMP should ensure that zoning provides adequate conservation protection for a significantly greater area of mangroves than is currently the case. This could be achieved by their inclusion in sanctuary zones or appropriately configured special purpose zones aimed at mangrove protection. As a matter of priority, further research should be undertaken to increase knowledge of how Shark Bay's marine environment drives the observed differences in mangrove structure and how differently structured mangrove stands contribute to the maintenance of biodiversity and ecological processes across Shark Bay.

## ACKNOWLEDGEMENTS

The authors would like to acknowledge Parks and Wildlife staff Kathy Murray and Bart Huntley for GIS support and image analysis, and Wayne Moroney for field support. Thanks also to Shaun Wilson and Tom Holmes (Parks and Wildlife), Ray Froend (Edith Cowan University) and Margie Mohring (University of Western Australia) for their comments on the draft. Rainfall data were provided by the Australian Bureau of Meteorology. The manuscript was improved by the comments of two anonymous reviewers.

## REFERENCES

- Abramoff MD, Magalhaes PJ, Ram SJ (2004) Image processing with ImageJ. *Biophotonics International* **11**, 36–42.
- Agraz Hernández CM, García Zaragoza C, Iriarte-Vivar S, Flores-Verdugo FJ, Moreno Casasola P (2011) Forest structure, productivity and species phenology of mangroves in the La Mancha lagoon in the Atlantic

**Table 4**

Summary of the area (ha) of and the relative proportion of mangroves in different conservation zones in the SBMP.

Conservation zone	Mangrove area	% of total mangroves in SBMP
Special Purpose Zone	1262.43	80.87
General Use Zone	293.72	18.82
Recreation Zone	4.31	0.28
Sanctuary Zone	0.54	0.04
Total	1561.00	100.00

- coast of Mexico. *Wetlands Ecology and Management* **19**, 273–293.
- Alongi DM (2002) Present state and future of the world's mangrove forests. *Environmental Conservation* **29**, 331–349.
- Alongi DM (2012) Carbon sequestration in mangrove forests. *Carbon Management* **3**, 313–322.
- Alongi DM, Clough BF, Robertson AI (2005) Nutrient-use efficiency in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*. *Aquatic Botany* **82**, 121–131.
- Anderson MJ (2002) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**, 32–46.
- Anderson MJ, Gorley RN, Clarke KR (2006) *PERMANOVA + for PRIMER: Guide to software and statistical methods*. PRIMER-E, Plymouth.
- Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* **84**, 511–525.
- Arreola-Lizárraga JA, Flores-Verdugo FJ, Ortega-Rubio A (2004) Structure and litterfall of an arid mangrove stand on the Gulf of California, Mexico. *Aquatic Botany* **79**, 137–143.
- Barbier E, Hacker SD, Kennedy C, Koch EW, Stie AC, Silliman BR (2010) The value of estuarine and coastal ecosystem services. *Ecological Monographs* **81**, 169–193.
- Burkholder D, Fourqurean J, Heithaus M (2013) Spatial pattern in seagrass stoichiometry indicates both N-limited and P-limited regions of an iconic P-limited subtropical bay. *Marine Ecology Progress Series* **472**, 101–115.
- Burling MC, Pattiaratchi CB, Ivey GN (2003) The tidal regime of Shark Bay, Western Australia. *Estuarine Coastal and Shelf Science* **57**, 725–735.
- CALM (1996) *Shark Bay Marine Reserves Management Plan 1996–2006*. Department of Conservation and Land Management, Perth.
- CALM (2005) *Management Plan for the Ningaloo Marine Park and Murion Islands Marine Management Area 2005–2015*. Department of Conservation and Land Management, Perth.
- Chen R, Twilley RR (1999) Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. *Estuaries* **22**, 955–970.
- Clarke KR, Gorley RN (2006) *PRIMER v6: User Manual*. PRIMER-E, Plymouth.
- De Lange WP, de Lange PJ (1994) An appraisal of factors controlling the latitudinal distribution of mangrove (*Avicennia marina* var. *resinifera*) in New Zealand. *Journal of Coastal Research* **10**, 539–548.
- Duke NC (2006) *Australia's Mangroves*. University of Queensland Press, Brisbane.
- Ewel KC, Twilley RR, Jin-Eong O (1998) Different kinds of mangrove forests provide different goods and services. *Global Ecology and Biogeography Letters* **7**, 83–94.
- Feller IC (1995) Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). *Ecological Monographs* **65**, 477–505.
- Feller IC, Lovelock CE, Berger U, McKee KL, Joye SB, Ball MC (2010) Biocomplexity in mangrove ecosystems. *Annual Review of Marine Science* **2**, 395–417.
- Fraser MW, Kendrick GA, Grierson PF, Fourqurean JW, Vanderklift MA, Walker DI (2012) Nutrient status of seagrasses cannot be inferred from system-scale distribution of phosphorus in Shark Bay, Western Australia. *Marine and Freshwater Research* **63**, 1015–1026.
- Fromard F, Puig H, Mougin E, Marty G, Betoulle JL, Cadamuro L (1998) Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. *Oecologia* **115**, 39–53.
- Jin-Eong O (1995) The ecology of mangrove conservation and management. *Hydrobiologia* **295**, 341–353.
- Logan BW, Cebulski DE (1970) Sedimentary environments of Shark Bay, Western Australia. *AAPG Memoir* **13**, 1–37.
- Lovelock CE, Ball MC, Choat B, Engelbrecht BMJ, Holbrook NM, Feller IC (2006) Linking physiological processes with mangrove forest structure: phosphorus deficiency limits canopy development, hydraulic conductivity and photosynthetic carbon gain in dwarf *Rhizophora mangle*. *Plant, Cell & Environment* **29**, 793–802.
- Lovelock CE, Feller IC, McKee KL, Thompson R (2005) Variation in mangrove forest structure and sediment characteristics in Bocas del Toro, Panama. *Caribbean Journal of Science* **41**, 456–464.
- Lugo AE, Snedaker SC (1974) The ecology of mangroves. *Annual Review of Ecology and Systematics* **5**, 39–64.
- McCluskey P (2008) *Shark Bay World Heritage Property Strategic Plan 2008–2020*. Prepared for the Department of Environment and Conservation, Perth and for the Department of Environment, Water, Heritage and Arts, Canberra.
- Morrisey DJ, Swales A, Dittman S, Morrison MA, Lovelock CE, Beard CM (2010) The ecology and management of temperate mangroves. *Oceanography and Marine Biology: An Annual Review* **48**, 43–160.
- Morton R (1990) Community structure, density and standing crop of fishes in a subtropical Australian mangrove area. *Marine Biology* **105**, 385–394.
- Nahas EL, Pattiaratchi CB, Ivey GN (2005) Processes controlling the position of frontal systems in Shark Bay, Western Australia. *Estuarine, Coastal and Shelf Science* **65**, 463–474.

- Naidoo G (2006) Factors contributing to dwarfing in the mangrove *Avicennia marina*. *Annals of Botany* **97**, 1095–1101.
- Naidoo G (2010) Ecophysiological differences between fringe and dwarf *Avicennia marina* mangroves. *Trees* **24**, 667–673.
- Pellegrini JAC, Soares MLG, Chaves FO, Estrada GCD, Cavalcanti VF (2009) A method for the classification of mangrove forests and sensitivity/vulnerability analysis. *Journal of Coastal Research* **SI56**, 443–447.
- Pool DJ, Snedaker SC, Lugo AE (1977) Structure of mangrove forests in Florida, Puerto Rico, Mexico, and Costa Rica. *Biotropica* **9**, 195–212.
- Schaeffer-Novelli Y, Cintrón-Molero G, Adaime RR, de Camargo TM (1990) Variability of mangrove ecosystems along the Brazilian coast. *Estuaries and Coasts* **13**, 204–218.
- Semeniuk V (1993) The mangrove systems of Western Australia: 1993 Presidential Address. *Journal of the Royal Society of Western Australia* **76**, 99–122.
- Smith SV, Atkinson MJ (1984) Phosphorus limitation of net production in a confined aquatic ecosystem. *Nature* **307**, 626–627.
- Storr GM (1990) Birds of the Shark Bay area, Western Australia. In *Research in Shark Bay: Report of the France–Australie Bicentenary Expedition Committee* (eds PF Berry, SD Bradshaw, BR Wilson). Western Australian Museum, Perth.
- Susilo A, Ridd PV, Thomas S (2005) Comparison between tidally driven groundwater flow and flushing of animal burrows in tropical mangrove swamps. *Wetlands Ecology and Management* **13**, 377–388.
- Twilley RW, Lugo AE, Patterson-Zucca C (1986) Litter production and turnover in basin mangrove forests in southwest Florida. *Ecology* **67**, 670–683.
- Walters BB, Ronnback P, Kovacs JM, Crona B, Hussain SA, Badola R, Primavera JH, Barbier E, Dahdouh-Guebas F (2008) Ethnobiology, socio-economics and management of mangrove forests: A review. *Aquatic Botany* **89**, 220–236.
- Ward GA, Smith TJ, Whelan KRT, Doyle TW (2006) Regional processes in mangrove ecosystems: spatial scaling relationships, biomass, and turnover rates following catastrophic disturbance. *Hydrobiologia* **569**, 517–527.
- Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology* **151**, 1069–1076.