

## Faunal relationships with seagrass habitat structure: a case study using shrimp from the Indo-Pacific

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**Abstract.** Caridean shrimp were used as a model group to investigate the effects of seagrass floral habitat complexity on Indo-Pacific fauna. Relationships between shrimp and seagrass habitat characteristics were explored using both multivariate and multiple linear regression modelling approaches. Epifaunal shrimp assemblages were sampled in the Wakatobi Marine National Park, Indonesia. Seagrass habitat complexity had a significant positive impact on shrimp abundance ( $F_{3,59} = 17.51$ ,  $P < 0.001$ ) and species richness ( $F_{3,59} = 10.88$ ,  $P < 0.001$ ), while significantly altering shrimp assemblage structure (ANOSIM global  $R = 0.397$ ,  $P < 0.001$ ). In contrast to studies from other bioregions and faunal groups, species diversity and evenness were inversely related to habitat complexity. Changes in shrimp abundance, diversity and assemblage structure with habitat complexity are considered to reflect changes in individual species habitat specialisation. High complexity habitats were dominated by habitat specialists, whereas low complexity seagrass had higher numbers of habitat generalists. Generalist species may be more adapted to the reduced food availability and increased predatory pressures associated with reduced habitat complexity. Although similar patterns were observed at all sites, inter-site differences in shrimp abundance were observed. This indicates that although the present study demonstrates the importance of small-scale changes in seagrass habitat complexity to faunal assemblages, other factors related to larger spatial-scales are also important.

**Additional keywords:** caridean shrimp, habitat complexity, habitat structure, Indonesia, seagrass.

### Introduction

Understanding the link between habitat and its associated fauna is an important concept within ecological research, one that is vital for the conservation of increasingly degraded and fragmented habitats (Bentley *et al.* 2000; Hauser *et al.* 2006). This link can be important even at small spatial scales where habitat variability can be important in controlling faunal abundance and diversity (Bell and Westoby 1986a; Hauser *et al.* 2006).

In many degraded ecosystems, a major conservation concern is the potential survivorship of diverse assemblages as habitat is lost. With a reduction in the structural complexity of a habitat the fauna of many ecosystems has been found to alter in its habitat usage and exhibit behavioural plasticity (Bentley *et al.* 2000; Attum *et al.* 2006). Decreasing complexity may alter the habitat potential for newly settling fauna by decreasing the availability of space, reducing niche diversity (Orth *et al.* 1984), providing less shelter from predation and physical stress (Verweij *et al.* 2006), and reducing the available food resources through less sediment trapping (Hicks 1985).

As the structural complexity of a habitat reduces, assemblage shifts have been reported from comprising mostly habitat specialists, to assemblages dominated by habitat generalists that are able to deal with the altered habitat (Bentley *et al.* 2000). Where habitats are characterised as containing generalist species the potential for survival with reducing vegetation is higher than with habitat specialists that are much more sensitive to change and disturbance.

The investigation of habitat structural complexity and fauna requires the consideration of the multiple components that build the habitat structure. Most studies that consider marine habitat relations have lacked multiple components. With the exception of recent work in the temperate north-east Atlantic (Attrill *et al.* 2000; Hauser *et al.* 2006, Jackson *et al.* 2006), there has been little consideration of whether habitat complexity in a natural 'in field' setting can enhance faunal assemblages as most studies have used artificial substrata to examine complexity (Hill and Wassenberg 1993; Verweij *et al.* 2006).

In marine environments, habitat complexity is widely considered to positively affect faunal assemblages across a range of different habitats (Bell and Westoby 1986a; Hauser *et al.* 2006). Yet most of this research, particularly in the context of seagrass beds, has been geographically limited to Australia, Europe and the Americas, with little consideration of the diverse Indo-Pacific.

Seagrass ecosystems create a highly complex habitat that has been found to increase faunal abundance and diversity relative to unvegetated habitats (Connolly 1994; Jenkins *et al.* 1997). There is growing global concern that seagrass ecosystems are now experiencing an unprecedented level of damage, deterioration and overexploitation mostly attributed to human activities (Orth *et al.* 2006). Effective management of seagrass ecosystems requires a greater understanding of their structuring processes (Parrish 1989).

The central Indo-Pacific is where marine faunal diversity is maximal and consequently trophic interactions become more complex. Currently, there is limited information regarding the macro-invertebrates residing within seagrass beds of the central Indo-Pacific region; this represents a cause for concern owing to their high biomass and important trophic linkages with other marine fauna (Greening and Livingston 1982; Barba *et al.* 2005; Garcia Raso *et al.* 2006; Hindell 2006; Unsworth *et al.* 2007). Caridean and dendrobranchiate shrimps commonly dominate tropical seagrass beds and comprise mixed trophic assemblages that contain both predatory and herbivorous species (Bauer 1985a, 1985b). In view of their dominance and diverse trophic roles, seagrass-dwelling shrimps constitute an important link between primary production and higher trophic levels (De Grave *et al.* 2006), yet research on seagrass shrimp assemblages in the central Indo-Pacific has not yet progressed beyond the species inventory work of Ledoyer (1969, 1984).

The present study used shrimp as a model group to investigate the effects of floral habitat complexity on Indo-Pacific seagrass fauna. Relationships between epifaunal shrimp and seagrass habitat complexity were explored using a multiple linear regression modelling approach. It was hypothesised that habitats of increasing complexity would support a greater abundance and diversity of caridean shrimp and alter their assemblage structure. Such a change in assemblage structure would be from a highly complex habitat dominated by habitat specialists, to less complex habitats containing mostly habitat generalists.

## Materials and methods

### Study sites

The present study was conducted between March and April 2005 on the inter-tidal seagrass beds around Hoga Island, within the Wakatobi Marine National Park (Unsworth *et al.* 2007). The seagrass beds lie between fringing reefs and the shoreline, and are representative of habitats found across large sections of the Indo-Pacific and Indian Oceans (Unsworth *et al.* 2007). Over an area comprising three adjacent bays (100 m apart) around the SW tip of Hoga Island (Hoga Beach, Boat Bay and Mushroom Bay), seagrass beds (Fig. 1) were sampled for shrimp and their habitat and environmental characteristics (Table 1).

At each of the three sites, four areas of different habitat complexity were identified; these encompassed the full range of

seagrass within that individual site and were based on increasing concentrations of seagrass cover, height and biomass. The six individual levels were determined using a range of levels of seagrass percentage cover (1 = 0–13; 2 = 14–25; 3 = 26–45; 4 = 46–55; 5 = 56–65; 6 = 66–90) that corresponded to an appropriate range of values of seagrass biomass and height (see Table 2). Cover of algae was relatively consistent throughout all samples, so was not considered as a component to determine complexity categories (Table 2).

Seagrass beds were found to have no significant difference in seagrass species assemblage structure ( $R = 0.3$ ,  $P = 0.1$ ) but varied in total seagrass cover ( $F_{2,54} = 41.53$ ,  $P < 0.001$ ) between sites. Differences were the result of a greater range of cover in Boat Bay. Following the classification of these seagrass concentrations into six habitat levels (1 = lowest; 6 = highest) of increasing complexity no differences were found within complexity levels. Significant differences in total seagrass cover were evident between levels of increasing complexity, reflecting the choice of these categories (Tables 3 and 4).

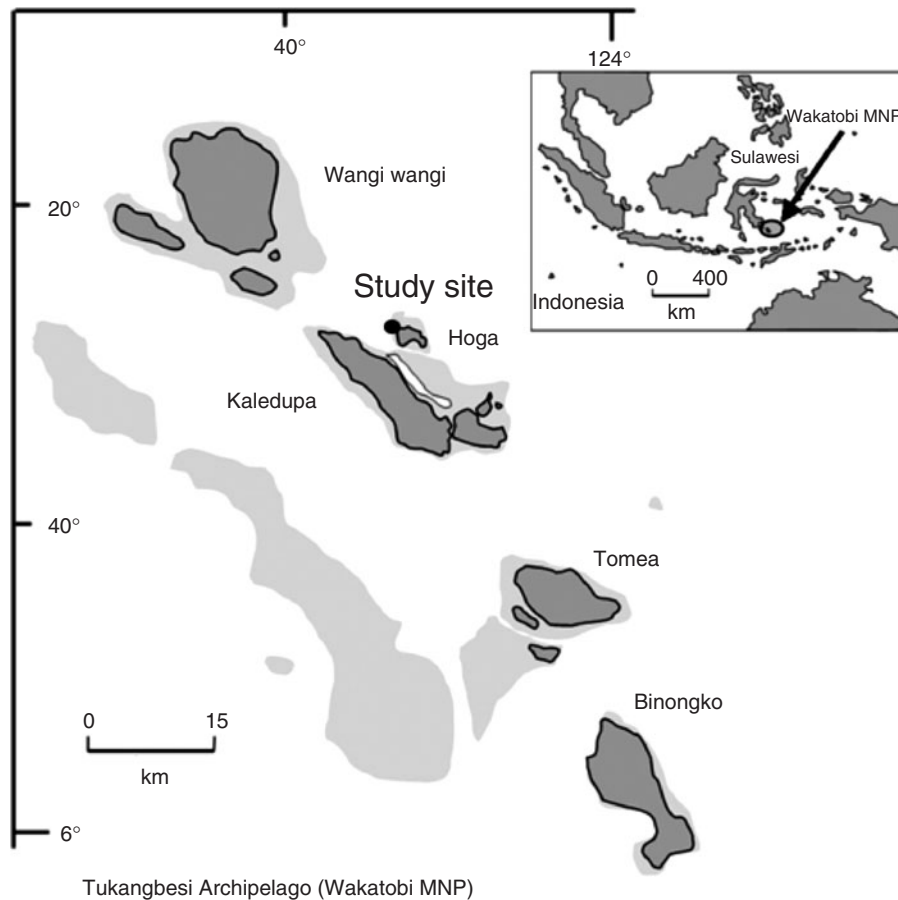
In order to control for the impacts of habitat connectivity, all sampling sites were located equidistant from the reef. Environmental characteristics were standardised as all sites had similar depth, topography and currents; additionally all sites had similar levels of human exploitation.

### Seagrass habitat and environmental data

Seagrass leaf abundance and percentage cover were estimated by conducting visual leaf counts for all species within five 0.25 m<sup>2</sup> quadrats placed haphazardly at each of the four areas at the three sites. These estimates were carried out while snorkelling. The percentage live cover of all other groups (e.g. coral and macroalgae) was also estimated in each quadrat. Dry weight biomass (gDW) of seagrass was estimated by calculating mean biomass per leaf ( $n = 20$ ) and multiplying this by the number of leaves within each quadrat. To calculate mean biomass per leaf, twenty leaves of each species within each quadrat were haphazardly collected, and scraped of all epiphytic matter and dried in the sun for 12 h (or until they had reached constant weight by regular weighing) and weighed. Mean seagrass height was quantified within each quadrat by measuring the length (to the nearest cm) of 20 seagrass leaves. Each area was then marked using a floating buoy for later sampling of epifaunal shrimp.

The quantification of habitat complexity has been attempted with different methodologies but remains a very difficult and often subjective concept to measure (Gee and Warwick 1994; Hauser *et al.* 2006). The present study quantified seagrass cover, biomass, leaf density and height as measures of habitat complexity as these have successfully been used in other studies (Heck and Wetstone 1977; Attrill *et al.* 2000). This also allows for the interpretation of results to be placed into the wider context of established global monitoring programs such as SeagrassWatch and SeagrassNET.

To monitor water temperature and light intensity, a HOBO light and temperature logger (Onset Computer Corporation) was placed on the seabed at each sampling site for six daylight hours (1000 to 1600 hours). Water clarity was measured using a horizontal Secchi disk and a measuring tape while snorkelling. Salinity was measured at each site using an analogue refractometer.



**Fig. 1.** Location of the study sites on Hoga Island in the Wakatobi Marine National Park, south-east Sulawesi, Indonesia.

**Table 1.** Location, sampling regime, and mean ( $\pm$ s.e.) environmental variables and habitat characteristics of the three seagrass areas used to sample in the Wakatobi Marine National Park, Indonesia

Variable	Mushroom Bay 05°28'32.8"N, 123°45'51.3"E	Boat Bay 05°28'36.3"N, 123°45'47.7"E	Hoga Beach 05°28'35.3"N, 123°45'40.0"E
No. of areas sampled	4	4	3
Total samples	20	20	15
Seagrass (% cover)	48 $\pm$ 5.4	46 $\pm$ 6.4	43 $\pm$ 5.8
Water clarity (m)	5.5 $\pm$ 0.2	5.8 $\pm$ 0.3	5.8 $\pm$ 0.4
Temp ( $^{\circ}$ C)	31.5 $\pm$ 0.1	29.5 $\pm$ 0.2	30.5 $\pm$ 0.1
Light intensity (Lux)	45 697 $\pm$ 4658	51 230 $\pm$ 8932	54 423 $\pm$ 8402
Salinity (‰)	35 $\pm$ 3	35 $\pm$ 3	35 $\pm$ 3

### *Shrimp fauna*

Five independent samples of epifaunal seagrass-dwelling shrimp were collected within each of the four areas of variable habitat complexity (at least 50 m apart from each other). Samples were considered independent as they were a minimum of 5 m from each other. This sampling was repeated at each of the three spatially separate sites. Five samples were missing from the Hoga Beach site as a result of disruption of sampling by local fishermen, resulting in a total of 55 samples rather than 60. Each separate sample (regarded as semiquantitative) was taken using

a standardised push net technique; this is a standardised means of sampling epifaunal shrimp (Bauer 1985b; De Grave *et al.* 2006). The net had a mouth of 0.1 m<sup>2</sup> and 1-mm mesh size. The net was pushed over the seafloor for 10 m, sampling a total volume of 1 m<sup>3</sup> of water. All samples were preserved in 70% alcohol and identified in the laboratory. Shrimp are known to have diel peaks in abundance; therefore all sampling was undertaken between 1900 and 2300 hours (De Grave *et al.* 2006). Potential lunar effects (S. De Grave, unpubl. data) were standardised by sampling within 3 days of the full moon. All shrimp

**Table 2. Mean ( $\pm$ s.e.) habitat characteristics of six levels of habitat complexity (1 = lowest, 4 = greatest) sampled in the Wakatobi Marine National Park, Indonesia**

Habitat complexity level	<i>Thalassia hemprichii</i>	<i>Enhalus acoroides</i>	<i>Cymodocea rotundata</i>	<i>Halophila ovalis</i>	Mean seagrass % cover	Mean seagrass biomass (g per 50 m <sup>2</sup> )	Mean seagrass height (cm)
1	5.94 $\pm$ 2.87	0.97 $\pm$ 0.45	3.1 $\pm$ 1.29	1.57 $\pm$ 0.60	10.7 $\pm$ 2.29	1.04 $\pm$ 0.92	11.1 $\pm$ 2.2
2	1.94 $\pm$ 0.76	1.47 $\pm$ 0.60	9.87 $\pm$ 2.84	1.93 $\pm$ 0.62	15.2 $\pm$ 2.66	2.37 $\pm$ 0.28	20.2 $\pm$ 5.2
3	27.9 $\pm$ 6.19	0.97 $\pm$ 0.37		0.47 $\pm$ 0.29	29.3 $\pm$ 6.32	5.83 $\pm$ 0.88	45.3 $\pm$ 4.5
4	39.4 $\pm$ 2.53	3.25 $\pm$ 0.95	9.6 $\pm$ 1.99	0.05 $\pm$ 0.05	51.5 $\pm$ 1.36	12.6 $\pm$ 1.54	53.7 $\pm$ 7.9
5	46.2 $\pm$ 4.68	11.5 $\pm$ 1.06	5.79 $\pm$ 1.68	0.07 $\pm$ 0.05	63.3 $\pm$ 4.21	29.5 $\pm$ 3.83	71.0 $\pm$ 7.9
6	49.0 $\pm$ 6.49	32.7 $\pm$ 4.08			81.7 $\pm$ 6.67	110.0 $\pm$ 20.5	80.2 $\pm$ 10.1
All	32.2 $\pm$ 2.73	7.06 $\pm$ 1.25	5.99 $\pm$ 0.95	0.5 $\pm$ 0.14	45.5 $\pm$ 3.19	21.5 $\pm$ 4.15	39.1 $\pm$ 12.0

**Table 3. Two-way general linear models (GLM) ANOVA for seagrass cover, shrimp abundance, and shrimp species richness (and ANOSIM for shrimp assemblage structure) between six levels of habitat complexity (1 = lowest, 6 = greatest) in the Wakatobi Marine National Park, Indonesia**

F: F-ratio; MS: mean squares; R: global R

Source of variation	d.f.	% Total seagrass cover			Shrimp abundance			Shrimp species richness			Assemblage structure	
		MS	F	P	MS	F	P	MS	F	P	R	P
Complexity	5	5872.2	47.2	<0.0001	22425	10.6	<0.0001	16.7	10.6	<0.0001	0.5	<0.0001
Error	49	124.5			2110			1.570				
Total	54											

**Table 4. Significant pairwise comparisons of total seagrass cover (T), shrimp abundance (A), shrimp species richness (R) and shrimp assemblage structure (S) between six levels of habitat complexity (1 = lowest, 6 = greatest) following two-way general linear models (GLM) ANOVA (Tukeys) and ANOSIM (pairwise tests) in the Wakatobi Marine National Park, Indonesia**

Habitat complexity level		Habitat complexity level				
		2	3	4	5	6
1	T			<0.0001	<0.0001	<0.0001
	A				<0.001	<0.001
	R	<0.01			<0.05	
	S			<0.001	<0.001	<0.001
2	T			<0.0001	<0.0001	<0.0001
	A			<0.05	<0.001	<0.0001
	R			<0.001	<0.0001	<0.01
	S	<0.001		<0.001	<0.001	<0.001
3	T			<0.01	<0.0001	<0.0001
	A				<0.01	<0.001
	R			<0.05	<0.001	
	S			<0.001	<0.001	<0.001
4	T				<0.05	<0.0001
	A			<0.001		<0.05
	S				<0.001	
5	T					<0.05

species were classified as either habitat specialists or as habitat generalists based on the work of Ledoyer (1969, 1984). Species were also classified as invertebrate commensals, sandy habitat residents or habitat generalists (Ledoyer 1969, 1984).

*Data analysis*

Summary statistics were calculated and all mean values are displayed together with their standard errors. Total shrimp abundance and species richness were analysed using two-way general linear models (GLM) ANOVA and Tukey’s pairwise comparisons using Minitab (ver. 13). Analysis of differences in shrimp assemblage structure was conducted using multi-variate non-metric multidimensional scaling ordination (nMDS) and Bray–Curtis cluster analysis using the computer package PRIMER (ver. 6.1.5) (Clarke and Warwick 1994). A two-way ANOSIM was used to investigate differences identified from MDS and CLUSTER (Clarke and Warwick 1994).

Data of shrimp abundance from all sites represented 55 independent samples for which seagrass habitat environmental characteristics had been collected. A multiple regression model using SPSS (version 13) was developed to relate the key attributes of the habitat to individual species and diversity indices used to represent the assemblage. As ecological and structural habitat variables (e.g. seagrass % cover and seagrass biomass) are often inter-linked to each other as a result of colinearity, the dataset was subjected to a varimax rotated principal component analysis (PCA) (Barnes and De Grave 2002). The main reason for transforming a set of variables into principal components is that PCA substitutes orthogonal linear combinations of variables for the original variables, essentially removing colinearity, while maintaining the original multivariate data structure (Barnes and De Grave 2002). Within the multiple regression model each original habitat variable was replaced by the PCA axis with which that variable was highly correlated. Because of the varimax rotation, only one original variable was strongly correlated with any given PCA axis. In the multiple regression model all seagrass and

habitat variables were simultaneously entered, and their partial correlation co-efficients extracted, as well as overall goodness-of-fit measures of the model. Partial correlation co-efficients take account of the variability induced by the other variables and effectively remove it. Therefore, a comparison between partial correlation coefficients allows a direct comparison of the effect of any variable in the model with any other, without having to allow for additional variability (Barnes and De Grave 2002).

## Results

Seventeen species of shrimp were recorded within seagrass surrounding Hoga Island, with a mean density of  $83 \pm 8.6$  shrimp  $m^{-3}$  (Table 3). The shrimp assemblage was numerically dominated by *Chlorocurtis jactans*. This was also the most frequently sampled species, occurring in 98% of samples (Table 3). At the family level, the fauna was dominated by the nocturnally active Processidae, contrastingly, the Hippolytidae were not numerically abundant (Table 3). Several commensal taxa occurring on sea anemones and sponges were considered to have been accidentally caught in the net when it was dragged along the bottom. Other taxa that were only caught in very low numbers (and the commensal taxa) were not considered further in any analysis, leaving 13 species within the analysis.

The four defined levels of increasing seagrass habitat complexity related to increases in seagrass cover, biomass, leaf density and height (Table 2). We consider these categories to be representative of a range of habitat complexity.

Variable seagrass complexities contained different proportions of individual floral species. *Thalassia hemprichii* and *Enhalus acoroides* were present at all sites, whereas *Halophila ovalis* was only abundant in areas of reduced habitat complexity. *Cymodocea rotundata* was most abundant at intermediate levels of habitat complexity (Table 2).

### Effect of seagrass habitat complexity on shrimp assemblages

Seagrass habitat complexity had a significant positive effect on shrimp abundance and richness, and significantly altered species assemblage structure (Table 3). A positive relationship was found between abundance and habitat complexity, with a 340% increase in shrimp abundance from complexity levels 1 through to 6 (Fig. 2). These differences were significant between all pairwise levels of complexity (Tukeys pairwise comparisons), except between levels 1 and 2, and 1 and 3 (Table 4). Species richness was greatest at the highest habitat complexity (Fig. 2), although significant differences were only observed between the highest and lowest complexities (level 6 to both levels 1 and 2).

Differences between the shrimp assemblage structure were observed with increasing habitat complexity, which was apparent from the nMDS (Fig. 3), and this indicates a degree of separation between different levels of complexity. These differences were all significant, except between the lowest levels of complexity (5 and 6) (Tables 3 and 4). The greater spread of samples within the nMDS at lower habitat complexities indicated that these assemblages are more variable than those that are highly clumped at higher complexities, the dominance of a few species at high complexity may also have masked any variability (Table 5). This may reflect the higher diversity present at lower complexities.

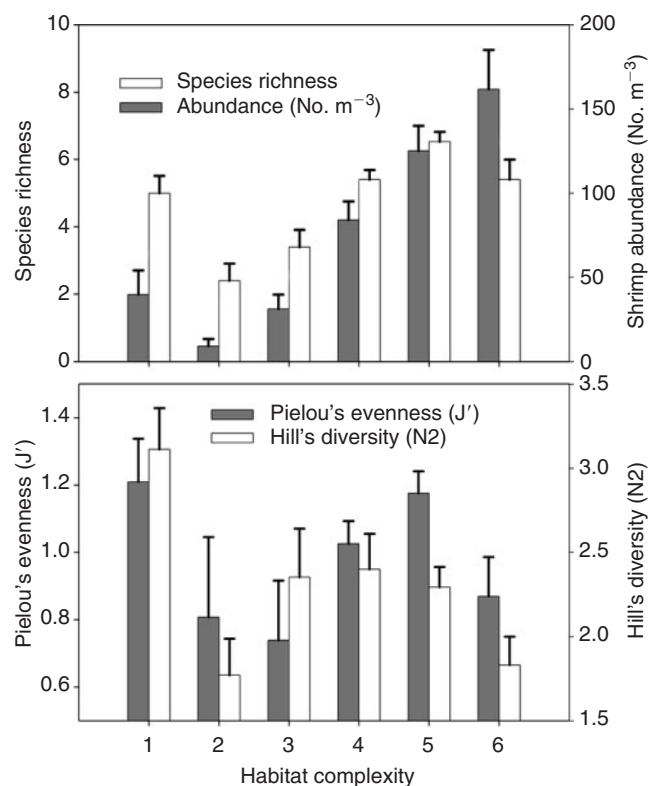


Fig. 2. Mean (+s.e.) shrimp assemblage characteristics following push netting at six levels of habitat complexity (1 = lowest, 6 = greatest) in the Wakatobi Marine National Park, Indonesia.

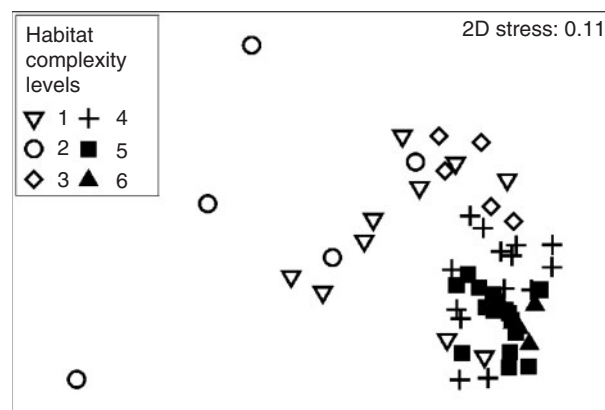


Fig. 3. Two-dimensional nMDS scaling configuration conducted using PRIMER for sample comparison of shrimp assemblage in the Wakatobi Marine National Park, Indonesia at six levels of seagrass habitat complexity (1 = lowest, 6 = greatest).

### Effect of seagrass habitat complexity on shrimp species

There was considerable variation in the abundance of different species, which is apparent from the spread of the species in the MDS configuration (Fig. 3). The difference in the association of these species with habitats of differing complexity helps to explain these patterns (Table 5). Those seven species observed within the central cluster were ubiquitous at all levels

**Table 5. Mean ( $\pm$ s.e.) shrimp species characteristics from push netting at six levels of habitat complexity (1 = lowest, 6 = greatest) in the Wakatobi Marine National Park, Indonesia**  
 Categories of habitat usage are displayed for all species (S: seagrass specialist; G: habitat generalist; C: invertebrate commensal; n: sandy habitats). Total abundance and richness of seagrass specialists and habitat generalists at each level of habitat complexity are also included

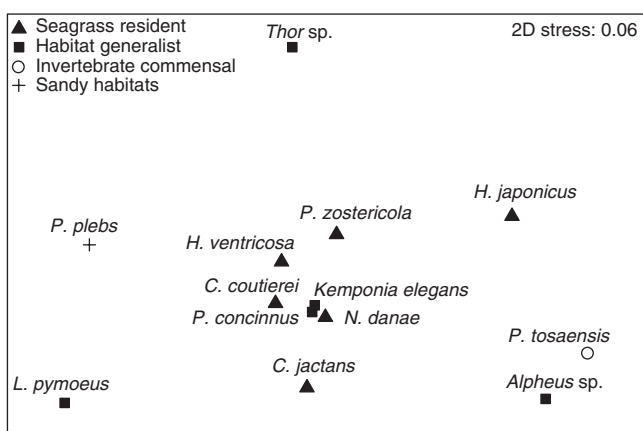
Species	Family	Habitat usage	Habitat complexity						Total	Frequency in samples
			1	2	3	4	5	6		
<i>Alpheus</i> sp.	Alpheidae	G	0.1 ( $\pm$ 0.1)			0.3 ( $\pm$ 0.2)			0.1 ( $\pm$ 0.1)	3
<i>Athanas</i> sp.	Alpheidae	G	0.1 ( $\pm$ 0.1)							1
<i>Chlorocurtis jactans</i> (Nobili, 1904)	Pandalidae	S	26 ( $\pm$ 10)	7 ( $\pm$ 3.5)	$\pm$ 21 ( $\pm$ 7.1)	64 ( $\pm$ 9.4)	100 ( $\pm$ 12)	140 ( $\pm$ 21)	65 ( $\pm$ 7.3)	54
<i>Chytomanninus coutierei</i> (Nobili, 1904)	Processidae	S	3.9 ( $\pm$ 1.7)	1 ( $\pm$ 0.5)		4.3 ( $\pm$ 2.6)	3.3 ( $\pm$ 0.7)	3.4 ( $\pm$ 1.3)	3.2 ( $\pm$ 0.8)	34
<i>Hayashidonus japonicus</i> (de Haan 1844)	Processidae	S				0.1 ( $\pm$ 0.1)	0.3 ( $\pm$ 0.2)		0.1	5
<i>Hippolyte ventricosa</i> (H. Milne Edwards, 1837)	Hippolytidae	S	3.7 ( $\pm$ 1.6)	0.2 ( $\pm$ 0.2)	$\pm$ 0.2 ( $\pm$ 0.2)	1.3 ( $\pm$ 0.5)	4.1 ( $\pm$ 1.4)		2.2 ( $\pm$ 0.5)	26
<i>Latreutes pymoeus</i> (Nobili, 1904)	Hippolytidae	S					0.2 ( $\pm$ 0.1)		0.1 ( $\pm$ 0)	2
<i>Lysmata</i> sp.	Hippolytidae	G	0.1 ( $\pm$ 0.1)							1
<i>Nikoides danae</i> (Paulson, 1875)	Processidae	S	2 ( $\pm$ 0.8)	0.4 ( $\pm$ 0.4)	$\pm$ 8.2 ( $\pm$ 2.1)	4.9 ( $\pm$ 1)	4.3 ( $\pm$ 1.4)	4.2 ( $\pm$ 0.6)	4 ( $\pm$ 0.6)	44
<i>Palaemon concinnus</i> (Dana, 1852)	Palaemonidae	G	1 ( $\pm$ 0.6)			6.1 ( $\pm$ 1.3)	7.4 ( $\pm$ 1.1)	9.2 ( $\pm$ 1.4)	4.7 ( $\pm$ 0.7)	38
<i>Palaemonella rotumana</i> (Borradaile, 1898)	Palaemonidae	G	0.2 ( $\pm$ 0.1)	0.2 ( $\pm$ 0.2)	$\pm$ 0.2 ( $\pm$ 0.2)	$\pm$ 0.2 ( $\pm$ 0.2)	0.1 ( $\pm$ 0.1)		0.1 ( $\pm$ 0)	5
<i>Kemponia elegans</i> (Paulson, 1875)	Palaemonidae	G	1.1 ( $\pm$ 0.6)	0.2 ( $\pm$ 0.2)	$\pm$ 1.6 ( $\pm$ 0.5)	2.5 ( $\pm$ 0.8)	3.5 ( $\pm$ 0.6)	3.8 (1)	2.3 ( $\pm$ 0.3)	39
<i>Periclimenes tosaensis</i> (Kubo, 1951)	Palaemonidae	C				0.1 ( $\pm$ 0.1)			0.1 ( $\pm$ 0)	3
<i>Periclimenaeus</i> sp.	Palaemonidae	C			$\pm$ 0.2 ( $\pm$ 0.2)					1
<i>Philocheras plebs</i> (Kemp, 1916)	Crangonidae	N	1.4 ( $\pm$ 0.7)	0.2 ( $\pm$ 0.2)		0.3 ( $\pm$ 0.2)	0.3 ( $\pm$ 0.2)		0.4 ( $\pm$ 0.2)	7
<i>Processa zostericola</i> (Hayashi, 1975)	Processidae	S	0.3 ( $\pm$ 0.2)			0.3 ( $\pm$ 0.2)	2 ( $\pm$ 0.5)	1.6 ( $\pm$ 0.5)	0.8 ( $\pm$ 0.2)	19
<i>Thor</i> sp.	Hippolytidae	G	0.2 ( $\pm$ 0.1)			0.1 ( $\pm$ 0.1)			0.1 ( $\pm$ 0)	3
Seagrass generalist abundance			2.8 ( $\pm$ 1)	0.2 ( $\pm$ 0.2)	1.8 ( $\pm$ 0.6)	8.9 ( $\pm$ 2)	11 ( $\pm$ 1.2)	13 ( $\pm$ 1.9)	7.3 ( $\pm$ 0.9)	
Seagrass specialist abundance			37 ( $\pm$ 14)	9 ( $\pm$ 4.3)	29 ( $\pm$ 8.3)	75 ( $\pm$ 11)	114 ( $\pm$ 14)	149 ( $\pm$ 23)	75 ( $\pm$ 8.1)	
Seagrass specialist richness			5	4	4	5	6	6	7	
Seagrass generalist richness			6	5	4	4	4	4	10	

of habitat complexity. Of these ubiquitous species *C. jactans*, *Hippolyte ventricosa*, *Palaemon concinnus* and *Processa zostericola* all showed increasing abundance with increasing habitat complexity.

Those species that had a more isolated distribution within the nMDS reflect species that only occurred at particular levels of complexity (e.g. *Hayashidonus japonicus*, *Latreutes pymoeus*, *Philocheras plebs*) (Table 5). Most species in the central cluster of the nMDS were known seagrass residents (specialists) (based on Ledoyer 1969, 1984). The categories 'sandy habitat residents' and 'habitat generalists' comprised most of the outliers within the species nMDS configuration (Fig. 4).

#### Effect of seagrass cover on shrimp assemblages

Seagrass cover ranged from 4 to 99%. As a result of the logarithmic relationship observed between seagrass % cover and seagrass biomass ( $R^2 = 0.8649$ ,  $P < 0.001$ ), values for biomass could not be plotted against shrimp abundance. This log relationship meant that the spread of biomass values was



**Fig. 4.** Two-dimensional MDS scaling configuration for inter-species comparison of shrimp samples taken at six levels of seagrass habitat complexity (1 = lowest, 6 = greatest) in the Wakatobi Marine National Park, Indonesia. Each species is characterised based on its habitat usage.

low and they were mostly clumped towards the lower end of the range, preventing the description of any true relationships between shrimp and seagrass biomass.

No clear relationships were observed between overall seagrass cover (%) and overall shrimp abundance, richness or any individual measure of diversity, these variables were therefore removed from the multiple regression model and only individual seagrass species were found to have relationships with shrimp. Those relationships that were found to exist are displayed in Table 6. Shrimp abundance was well described by our multiple regression model (high  $F$ -value), with 48% ( $R^2$ ) of the variance being explained by the model. This indicates that the significant positive relationships between shrimp abundance and % cover for both *Enhalus acoroides* and *Thalassia hemprichii* are likely to be strong relationships (Table 6). Shrimp diversity (Simpson's and Hill's  $N_2$ ) and evenness also displayed significant inverse relationships with % cover of *E. acoroides* and *T. hemprichii* (Table 6). We found shrimp abundance to increase with cover of both *E. acoroides* and *T. hemprichii*, whereas species richness only increased with *T. hemprichii*. Species diversity and evenness declined with % cover of both *E. acoroides* and *T. hemprichii* (Fig. 4).

Consideration of the abundance and diversity of habitat specialists (seagrass residents) relative to the habitat generalists indicates that both of these groups increased in abundance from low to high habitat complexity (Table 5). However, species richness of habitat generalists increased as complexity reduced (Table 5).

#### Effect of seagrass cover on individual shrimp species

The most significant individual species relationship was between the most abundant species (*C. jactans*), and both % cover of *E. acoroides* and *T. hemprichii* (Table 6); the most dominant relationship being with *E. acoroides*, which explained 53% of the variance (Fig. 5). A strong positive relationship was also found between *P. concinnus* and *T. hemprichii* (Fig. 5) and to a lesser extent *E. acoroides* and algal cover (Table 6). Weaker relationships were observed between *Kemponia elegans* and both *E. acoroides* and *T. hemprichii*; and *P. zostericola* with both *E. acoroides* and *T. hemprichii* (Table 6).

**Table 6.** Multiple regression model parameters, partial correlation coefficients and their significance

The model was used to describe the relationship between seagrass-dwelling shrimp and descriptors of habitat in the Wakatobi Marine National Park, Indonesia. Only coefficients that show significance are given. The global results of each model are shown as ANOVA  $F$  ratios, and variance explained (adjusted  $R^2$  value) (\*\* $P < 0.01$ , \* $P < 0.05$ )

	Adjusted $R^2$	$F$ -Ratios	<i>Halophila ovalis</i> (% cover)	<i>Cymodocea rotundata</i> (% cover)	Algae (% cover)	<i>Enhalus acoroides</i> (% cover)	<i>Thalassia hemprichii</i> (% cover)
<i>Chlorocurtis jactans</i>	0.53	9.78**	—	—	—	0.683**	0.543**
<i>Hayashidonus japonicus</i>	0.07	1.57	—	0.395*	—	—	—
<i>Hippolyte ventricosa</i>	0.03	1.21	—	0.284*	—	—	—
<i>Palaemon concinnus</i>	0.48	7.92**	—	—	0.305*	0.521**	0.608**
<i>Kemponia elegans</i>	0.12	2.10*	-0.289*	—	—	0.296*	0.264*
<i>Processa zostericola</i>	0.14	2.24*	—	—	—	0.303*	0.390*
Number of shrimp species	0.15	2.36*	—	—	—	—	0.427*
Shrimp abundance	0.48	8.09**	—	—	—	0.631*	0.529*
Pielou's evenness ( $J'$ )	0.41	6.29**	0.342*	—	—	-0.507**	-0.554**
Simpson's ( $1 - \lambda'$ )	0.17	2.56*	—	—	—	-0.366**	-0.334**
Hills diversity ( $N_2$ )	0.12	2.15*	—	—	—	-0.337*	-0.297*

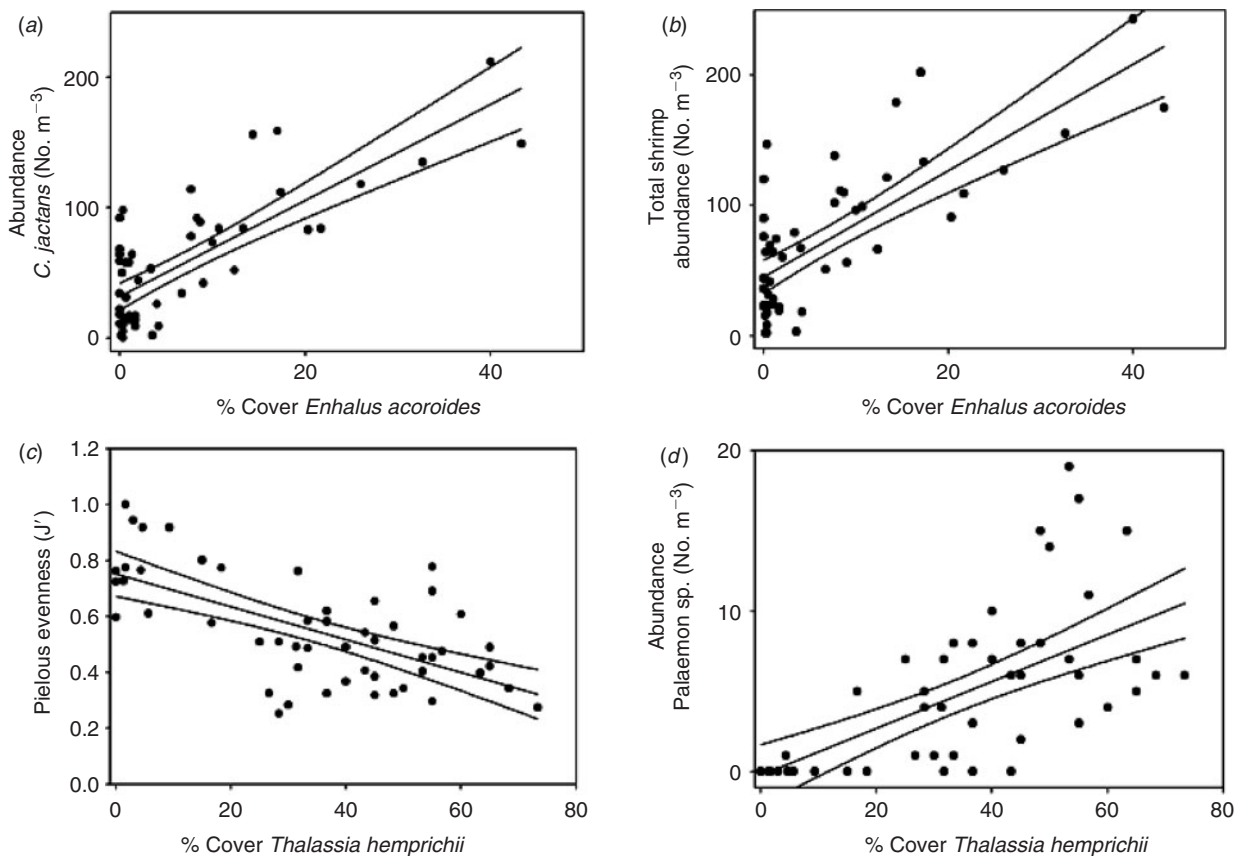
## Discussion

The present study is the first to consider small-scale attributes of seagrass habitat complexity in relation to a group of invertebrate fauna within the Indo-Pacific. Seagrass beds with higher floral biomass, cover and structural complexity were found to support over three times the concentrations of caridean shrimp than low complexity seagrass. As the overall abundance of shrimp was related to seagrass complexity, we would expect that shrimp diversity and species richness would also increase as shelter increases and a wider range of niches became available (Heck and Wetstone 1977). However, the present study found no clear relationship between caridean shrimp richness and either habitat categories or any individual descriptor of complexity.

We found strong positive relationships between both seagrass cover and complexity, and several of the individual dominant shrimp species, but not all species increased in abundance and this did not translate into diversity increases. Both species diversity (Simpson's and Hill's  $N_2$ ) and evenness (Pielou's) were strongly and inversely related to increasing seagrass cover and complexity. This demonstrates that although broad-scale relationships between flora and fauna do exist in many biogeographic regions, they are also multifaceted and may not represent all ecological situations. A species response to the characteristics and availability of a habitat as well as the ability of the species to compete for resources may explain the observed patterns.

Species adapt to their environment through a combination of morphological, behavioural, or physiological adaptations to the various selection pressures of the habitat (Futuyma and Moreno 1988). The changes in shrimp assemblage abundance, diversity and structure with habitat complexity reflect changes in their habitat adaptations and specialisations. The present study found both habitat specialists and generalists to increase in abundance with increased complexity, but habitat specialists dominated in higher complexity habitats (those species adapted to a seagrass environment). But as habitat complexity reduced, the richness of habitat generalists increased. This suggests that different adaptations may be necessary for using lower complexity seagrass where predatory pressures and food resources may be different, adaptations that may have greater prevalence to species that move between different habitats. At high complexities mechanisms of competitive exclusion may be influential as individual species become dominant (Gause 1934).

As seagrass biomass and cover increased, *Enhalus acoroides* and *Thalassia hemprichii* became dominant, occupying a much greater proportion of the entire floral assemblage. This created a larger three-dimensional structure. This was a result of the size (length and size of blades) of these species in relation to the other two locally abundant floral species (*Halophila ovalis* and *Cymodocea rotundata*). Species of *Cymodocea* and *Halophila* are regarded as early colonizers, particularly species



**Fig. 5.** Faunal relationships between shrimp and seagrass species % cover following push netting within the Wakatobi Marine National Park, Indonesia. (a) *Chlorocurtis jactans* v. % cover *Enhalus acoroides*; (b) total shrimp abundance v. % cover *E. acoroides*; (c) Pielou evenness ( $J'$ ) v. % cover *Thalassia hemprichii* and (d) *Palaemon* sp. v. % cover *T. hemprichii*.

of *Halophila*, which quickly become out-competed (competition for light) by larger species owing to their small size (Duarte *et al.* 2000).

Colonising flora (*Halophila* sp. and *Cymodocea* sp.) was at greater abundance in areas of low cover. This may have created large variation in the broader type of available niches, but these would have been at much lower abundance (e.g. round leaves, thin leaves and strap-like leaves rather than a flora dominated by large algal covered strap-like leaves). This may provide habitat for a more diverse, but less abundant fauna dominated by habitat generalists, which has a more evenly spread shrimp assemblage structure. With reducing complexity there also becomes greater variability in habitat type as sand and rubble create alternative niches that can be used by different specialists and also for habitat generalists.

With increasing seagrass biomass and habitat complexity, high niche availability along with increased leaf surface area probably account for the increased abundance of shrimp. Although niche diversity within high complexity seagrass may be less variable on a broad scale, the larger mature leaves of the dominant species (*E. acoroides* and *T. hemprichii*) are known to support a greater abundance and diversity of mature epiphytic assemblages (Hemminga and Duarte 2000). These may be an important food resource, sustaining a greater abundance and species number of seagrass habitat specialists. Higher abundance of macrofauna in seagrass beds with higher cover and biomass can be explained by decreased predation efficiency at higher habitat complexity (Stoner and Graham-Lewis 1985; Nelson and Bonsdorff 1990). Equally, this may be the result of preferential choice of dense seagrass habitats by prey as a short-term escape mechanism from predation (Bell and Westoby 1986b), which may be particularly true in central Indo-Pacific seagrass beds, as they are dominated by crustacean-feeding fish (Unsworth *et al.* 2007). Any adaptations and niche separation at high complexities may also be additionally influenced by competition and competitive exclusion.

The present study could be interpreted with respect to the paradigm that shrimp abundance increases are a function of a standard species area curve owing to increased leaf area (Gee and Warwick 1994). However, a species area curve assumes homogeneous vegetation. Indo-Pacific seagrass vegetation is not homogeneous, particularly in mixed *T. hemprichii* and *E. acoroides* beds. Mature seagrass is continually degrading, with older leaves replaced by younger fresh ones. Older leaves often split and fragment at the tip and then curl-up near the base of the shoot. Older leaves also have greater levels of epiphytic cover and load (Hemminga and Duarte 2000). Mature seagrass beds of high biomass and cover therefore create an intricately complex habitat that is more than just additional surface area.

*Chlorocurtis jactans*, and to a much lesser extent *Palaemon concinnus* and *Nikoides danae*, dominated the diverse caridean shrimp assemblage in the current study. *C. jactans* and *P. concinnus* were both significantly associated with the distribution and abundance of the largest seagrass species; *T. hemprichii* and *E. acoroides*. Interestingly, the dominant *C. jactans* belongs to the Pandalidae, whereas seagrass beds elsewhere are usually dominated by Hippolytidae (Greening and Livingston 1982), or sometimes numerically dominated by Processidae, a nocturnally active family (De Grave *et al.* 2006). This may reflect a

biogeographical pattern at the regional scale, which is beyond the spatial scale of the present study.

Many species of caridean shrimp were found to be present at only the highest or lowest levels of complexity. *Hayashidonus japonicus* and *Latreutes pymoeus* were only present at high habitat complexities, which indicates that their ecological niche may only be present under such conditions. In contrast, *Philocheiras plebs* was only present at lower complexities; its presence is presumably linked to the species in this genus being primarily sand dwellers as bare patches of sand are more abundant at low habitat complexity.

Inter-site differences in shrimp abundance were observed; however, these did not reflect changes to the observed relationships between shrimp and seagrass cover, biomass or complexity. This indicates that although the present study demonstrates the importance of small-scale changes in seagrass habitat complexity to macro-faunal assemblages, other factors related to larger spatial-scales are also important. Spatial variations in seagrass faunal assemblages are common and have been attributed to the impact of nearby habitats (Skilleter *et al.* 2005), organic matter (Alongi and Chrisoffersen 1992), accumulation of drifting algae, and flow velocity (Bostrom and Bonsdorff 1997). The continuity of vegetation, often referred to as 'landscape-effects', may also be impacting these shrimp assemblages (Hovel and Fonseca 2005). The impacts of such landscape-effects are clearly important and require further consideration in understanding important Indo-Pacific faunal assemblages. As the current study did not cover a large spatial scale, the effects observed may be partially obscured by more localised influential variables. We can only postulate that larger scale impacts, such as landscape-effects and variability in macroalgal abundance, may have influenced shrimp abundance between sites in the present study.

The present findings, although important in their own right, suggest the requirement for the investigation of the influence of seagrass habitat on further faunal groups using seagrass habitats. Other abundant invertebrate groups in seagrass, such as molluscs and echinoderms, are highly important as human food sources, these commonly use the three dimensional structure of seagrass, often grazing widely on epiphytic algae. As a consequence, their assemblages may also be affected by seagrass structural complexity.

The importance of invertebrate macrofauna, particularly caridean shrimp, in supporting economically important fisheries should not be underestimated as they are known to be a major food resource for fish inhabiting Indo-Pacific seagrass beds (Hutomo and Peristiwady 1996; Unsworth *et al.* 2007). Developing a greater understanding of the factors influencing this fauna is important for the long-term protection of seagrass habitats, as globally they are under increasing anthropogenic pressure (Orth *et al.* 2006). The present study highlights how high floral spatial variability within Indo-Pacific seagrass beds, can, at least on local-scales have a large influence over a faunal group such as caridean shrimp. It is important that future seagrass management considers the conservation of habitat structure and complexity in addition to the fauna it supports.

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