

Habitat structure, disturbance and the composition of sand-dwelling goby assemblages in a coral reef lagoon

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ABSTRACT: Coral reef lagoons and back reef areas are composed more of sand than hard reef habitat. They support a diverse mix of fishes, including species restricted to sandy habitats and those dependent on both hard and soft substrata. However the resident assemblages associated with sand and the factors affecting their distribution and abundance are poorly understood. Here we examine spatial co-variation in the abundance of burrowing goby assemblages and habitat characteristics in the lagoon at Lizard Island (Great Barrier Reef). The aim was to identify which key habitat-variables should be incorporated into models to predict the structure of sand-dwelling fish communities. We focused on 10 common sand goby species from 7 genera: *Amblyeleotris*, *Cryptocentrus*, *Ctenogobius* and *Vanderhorstia* (associated with burrows constructed by alpheid shrimps), and *Amblygobius*, *Oplopomus* and *Valenciennea* (free-living, burrowing species). Spatial patterns were examined by stratifying the lagoon into 6 recognizable habitat zones, and conducting visual transects in replicate sites within each zone. The abundance of all goby species encountered and habitat variables (depth, distance from reef, topography, disturbance of different types, sediment composition) were recorded in each transect. Habitat characteristics and fish abundance, diversity and species composition differed markedly among habitat types and sites within habitats. There was a strong association between sites grouped according to habitat characteristics and goby assemblage. These changes reflected species-specific responses to different combinations of habitat variables and their interactions. All habitat variables measured were at least partially correlated, either positively or negatively, with the abundance of some of the species. Depth, distance from consolidated reef, sediment composition and the level of disturbance were particularly important. Our study indicates that sandy habitats, although superficially uniform, support highly structured fish communities influenced by a wide range of factors.

KEY WORDS: Gobiidae · Soft-sediment · Disturbance · Tropical fish · Habitat association · Lagoon

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INTRODUCTION

Soft sediment habitats occupy a large area, and are potentially important components of coral reef ecosystems, particularly in lagoons and sheltered reef areas (Thomassin 1978, Dubinsky 1990, Birkeland 1997). They support a diverse suite of infaunal and epibenthic invertebrates and fishes that are specialized for life on sand (Jones 1984, St John et al. 1989, Jones et al. 1990, Adams & Ebersole 2002). In addition, many reef-

dwelling fishes initially recruit into sandy habitats before migrating onto reefs (Shulman 1984, 1985, Adams & Ebersole 2002) or actively forage over sand as adults (Jones et al. 1991, 1992). This suggests that there are important ecological linkages between reef and sand habitats on coral reefs. In contrast to reefs, sandy habitats offer little structural heterogeneity and remain relatively uniform over large areas. Nevertheless, constituent communities are often diverse and exhibit distinct spatial patterns in species composition

(Jones 1984, Jones et al. 1990, 1991). These patterns are not well understood and the processes structuring soft sediment assemblages associated with coral reefs have received relatively little attention.

Despite their superficial uniformity, sandy habitats are not homogenous either in space or time. Numerous studies in temperate waters indicate that subtle gradients in the composition of sediments, and levels of physical and biological disturbance, are likely to be key factors influencing the structure of soft-sediment communities (Woodin 1978, Brenchley 1981, Lake 1990). In coral reef lagoons, sediment grain-size varies as a result of assortment by physical processes, such as wind-driven wave and tidal action. This often leads to a predominance of coarse sediments in shallow water or exposed areas. Biological agents of disturbance, such as sand prawns *Callinassa* spp., holothurians, large teleost fishes and rays may also generate large-scale patchiness in habitat structure (Suchanek et al. 1986, Jones et al. 1988, Berkenbusch et al. 2000). While it could be predicted that changes in sediment composition and disturbance regimes will exert a strong influence on the distribution and abundance of sand-dwelling fishes, few studies have addressed these hypotheses.

Coral reef lagoons support a wide array of small fishes that are exclusively associated with sandy habitats near reefs (Randall et al. 1990, Lieske & Myers 1994). This includes species from many families including toadfishes (Batrachoididae), gobies (Gobiidae), wrasses (Labridae), sand tilefishes (Malacanthidae), dartfishes (Microdesmidae), sand perches (Pinguipedidae), coral breams (Nemipteridae), and lizardfishes (Synodontidae). Of these, gobies are the most notable for their high diversity and abundance on mobile substrata in lagoons and back reef environments. Some species are associated with rubble or live in burrows that they construct themselves (e.g. species of the genera *Amblygobius*, *Oplopomus*, *Signigobius*, *Valenciennea*) (Hudson 1977, St John et al. 1989, Randall et al. 1990, Clark et al. 2000). Others form commensal relationships with burrowing alpheid shrimps, acting as 'look outs' for predators (e.g. species of the genera *Amblyeleotris*, *Cryptocentrus*, *Ctenogobius*, *Vanderhorstia*) (Karplak et al. 1972, Polunin & Lubbock 1977, Preston 1978, Randall et al. 1990). Despite their ubiquitous presence in sandy reef environments, few studies have addressed the factors influencing the distribution and abundance of sand-dwelling gobies.

In this study, we examine the role that physical habitat structure and disturbance processes play in structuring a lagoon assemblage of sedentary, soft-sediment dwelling gobies at Lizard Island (Great Barrier Reef). The aim was to detect key habitat variables that could be used to predict the structure of

these fish communities. We predicted that species might exert different habitat preferences based on a range of factors including depth, distance from reef, sediment grain size or exposure to physical or biological regimes of disturbance, all of which may, to some degree, co-vary in space. To detect potential relationships, we stratified the lagoon into recognizable zones according to depth and position. At replicate sites within each zone, we measured both goby abundances and a variety of continuous physical and biological variables. We then used variance partitioning and partial correlation approaches to identify contributions of and interactions between different sets of continuous variables to goby assemblages.

MATERIALS AND METHODS

Study area and habitats. This study was carried out in the lagoon at Lizard Island (14° 40' S, 145° 27' E), on the northern Great Barrier Reef, during March/April 1994. Six soft-sediment habitat types or 'zones', classified by depth, proximity and orientation to reef, were identified in the lagoon (Fig. 1). The 'reef flat' habitat occurred at an average depth of 1.5 m and was located



Fig. 1. Sample locations within the lagoon at Lizard Island (14° 40' 8" S, 145° 27' 34" E), northern Great Barrier Reef. Arrows indicate direction of prevailing south-east wind. ▽ Reef flat, ◇ Sheltered back reef, △ Front reef slope, ○ Back reef slope, □ Central lagoon, ○ Lagoon entrance

30 m from of the reef perimeter of the lagoon. This distance from shelter, in combination with shallow depth, meant that these sites were subject to wave disturbance. The 'sheltered back-reef' habitat lay in approximately 2 m water depth and was located ~13 m to the leeward side of the reef perimeter, hence was protected from the prevailing south-easterly trade-wind generated waves. 'Front reef slope' sites ranged from 2 to 6 m and were approximately 30 m to the windward side of the consolidated reef perimeter. The 'back reef slope' habitat encompassed the same depth range as the front reef slope, but was on the leeward side of the reef. Both front and back reef slopes differed from other habitats in their aspect, with slopes of up to 20° not uncommon. The 'central lagoon' habitat averaged 9 m in depth, and was approximately 200 m from the nearest contiguous reef. The 'lagoon entrance' habitat lay in the main channel of the lagoon at 13 m depth and was sampled at least 10 m from the large bommies (isolated coral reefs) in the center of the channel.

Study species. Gobies were the commonest family of resident fishes in soft-sediment habitats on Lizard Island. We chose to focus on the 10 most common burrowing species. Six species, *Amblyeleotris steinitzi*, *Cryptocentrus cinctus*, *Ctenogobiops feroculus*, *C. pomastictus*, *Vanderhorstia ambanoro* and *V. ornatisima* occur with, and use, the burrows of alpheid shrimps. The other 4 species, *Amblygobius phalaena*, *A. sphinx*, *Oplopomus oplopomus*, and *Valenciennesa longipinnis* usually excavate their own burrows and were only occasionally found with alpheid shrimps. The 2 *Ctenogobiops* species were difficult to reliably distinguish in the field and, hence, pooled for analysis.

Sampling design. Three sites were identified within each habitat zone classification, and eight 10 × 2 m transects were randomly deployed and visually sampled within each site. As sites were entirely contained within a single habitat, they were treated as nested within habitat zone. Fish were counted as the tape was laid to minimize underestimation caused by fish disappearing into their burrows.

Benthic cover under each transect was estimated from 50 regular point-intercepts, each separated by 20 cm. We recognized 9 habitat categories: (1) undisturbed sand, (2) rippled sand (wind-generated disturbance), (3) invertebrate-disturbed sand (primarily by sand prawns *Callinassa* spp.), (4) fish-disturbed sand (ray feeding pits), (5) rubble (coral/shell fragments between 1 and 12 cm), (6) dead coral (loose fragments > 12 cm), (7) coralline rock (anchored dead coral > 12 cm), (8) soft coral, and (9) hard coral. We also recorded the maximum height difference between the lowest and highest points within each 1 × 2 m section of each transect as a measure of topography and a qualitative measure of aspect (flat or sloped).

Two sediment samples were collected from random positions along each transect to measure sediment grain characteristics. Each sample was a 10 cm deep core, which was extracted with a 125 ml specimen jar, sterilized in 10% Sodium Hypochlorite (NaOCl), then washed and dried. Grain size was analyzed to 7 fractions by dry sieving.

Analysis of habitat structure. All continuous variables were inspected graphically for univariate normality. Transformation was required for some variables, so we calculated the optimal transform from the slope of power plots of log(variance) versus log(mean). Distance to nearest reef was re-expressed as log₁₀, and depth re-expressed as $x^{0.25}$. Sediment grain sizes were unimodally distributed, but sometimes weakly skewed, within each site, so we used the median value per transect as our summary measure of grain size. Grain size, topography, and amount of undisturbed sand did not require transformation.

The variables representing type of disturbance (invertebrate vs wave ripples) presented an analytical problem, as the different disturbances were effectively mutually exclusive and hence non-linear. A principal components analysis (PCA) on the correlation matrix of these 2 disturbance variables identified 2 axes, which corresponded with disturbance type and intensity, respectively. Scores on the first axis were approximately normal, and represented either wave ripple (positive values) or invertebrate disturbance (negative values). Consequently, we replaced the 2 disturbance variables, wave ripples and invertebrate disturbance, with the first principal component score (henceforth called 'disturbance type') for each transect.

We tested whether the habitat zone classifications had different suites of physical conditions using multivariate analysis of variance (MANOVA). Sites were nested within habitat zone, so the linear model was (excluding intercept and error term) continuous variables = habitat zone + site(habitat zone). Habitat zone was tested over site(habitat zone), and site(habitat zone) tested over the residual. Differences between habitat zones were then displayed using canonical discriminant analysis (CDA). These analyses were carried out using the SAS procedures GLM and CANDISC, respectively.

Analysis of fish abundance. We carried out an analysis of the univariate descriptors of total goby abundance and species richness using the distributional checks and linear model described above. Differences between the means of the main effect of habitat zone were assessed using Tukey's HSD test. Variance components and their confidence intervals were calculated for the random factor site(habitat zone) and expressed as a percentage of the random variation in the model.

Prior to multivariate analysis of the fish data, boxplots suggested transformation of all species was required. We transformed all species by $x^{0.25}$, this transform was derived from the log(variance) versus log(mean) power plots. Habitat zone differences in fish assemblage structure were tested and displayed with MANOVA/CDA as outlined above.

Analysis of fish-habitat associations. As a prerequisite to measuring correlations between fish assemblage composition and continuous habitat variables, it was necessary to identify how much information the habitat-zone classification, and the suite of variables that characterized these habitats, shared. This consideration is central to removing confounding between classification and continuous variables (Jones & Syms 1998). We ran a linear discriminant function analysis (DFA) and used habitat zone misclassification rates as a measure of redundancy of the different habitat measures.

The DFA of habitat variables suggested that independent effects of continuous habitat variables were

Table 1. Multivariate analysis of variance of continuous habitat variables. Habitat zone was tested over site(habitat zone), and site(habitat zone) tested over error

Source	Pillai's Trace	F-value	Numerator df	Denominator df	p
Habitat zone	4.522	17.36	30	55	<0.0001
Site(habitat zone)	2.183	6.01	72	756	<0.0001

unlikely to be separated out from the categorical effect of 'zone'. Consequently, the large amount of shared information in the habitat zone classification and continuous habitat variables precluded a simple analysis of correlations between fish and habitat parameters. However, the nature of this redundancy was explored by measuring the interactions between different sets of habitat variables—higher order interactions would indicate that association of fish with habitat parameters are conditional on many other factors, whereas lower order interactions would indicate conditionality on a more restricted set of factors. Main effects, in contrast, would imply their effects were not conditional on any other factors. Following collinearity diagnostics, we used the variance partitioning approach of Whitaker (1984) to identify main effect contributions and interactions between different sets of continuous variables: physical structure (distance from reef, depth, topography); sediment type (median grain size); and disturbance regime (amount of disturbed sand and the disturbance type variable derived from PCA outlined above). This approach has been widely used to examine relationships between 2 sets of multivariate data (see Borcard et al. 1992, Belgrano et al. 1995a,b, Syms 1998). Partial correlations between fish abundance and these variables were calculated to display direction and strength of these associations.

RESULTS

Habitat structure

Both habitat zones and sites within habitats differed significantly in their physical characteristics, sediment grain size, and disturbance regime (Table 1). The first 2 canonical discriminant axes explained 88.03% of this between-group variation, and corresponded with orthogonal patterns in depth (CD1) and distance from contiguous reef (CD2) (Fig. 2). 'Reef flat' and 'shallow back reef' habitats were characteristically shallow, wave-disturbed habitats with coarse sediment, found reasonably close to reefs. 'Central lagoon' sites lay at the other extreme of this continuum of physical descriptors. They were generally further from contiguous reef, deeper, had fine sed-

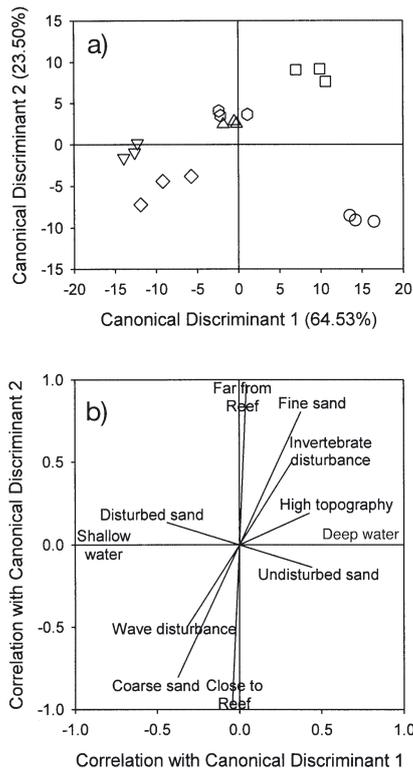


Fig. 2. Canonical discriminant analysis of benthic characteristics. (a) Projection of sites in ordination space. ∇ Reef flat, \diamond Sheltered back reef, \triangle Front reef slope, \circ Back reef slope, \square Central lagoon, \circ Lagoon entrance. (b) Structure coefficients (correlation coefficients) of benthic variables with ordination axes

Table 2. (a) Analysis of variance of total goby abundance (square-root transformed). Variance component (confidence interval) of site(habitat zone) = 43.98% (12.74, 87.99) of total random variation in the model. (b) Tukey's HSD test of differences between number of individuals in each habitat zone. Dark lines join habitats that do not differ from each other. Numerical values are the back-transformed mean number (square root) of individuals per 20 m² transect

(a)					
Source	df	MS	F	p	
Habitat zone	5	51.643	8.47	0.0012	
Site(habitat zone)	12	6.098	7.28	<0.0001	
Error	126	0.838			
(b)					
Lagoon entrance	Central lagoon	Shallow back reef	Reef flat	Front reef slope	Back reef slope
23.893 (4.888)	10.875 (2.760)	7.618 (2.698)	5.171 (2.274)	3.272 (1.809)	0.157 (0.396)

iments and were subject to a high degree of invertebrate disturbance (Fig. 2). 'Front reef' and 'back reef' slopes were intermediate in depth, and were characterized by reduced levels of either invertebrate or wave-disturbed sand. However, both slope habitats lay at approximately 20° from horizontal, and we commonly observed miniature 'land-slides' of sand during sampling. Hence, they were subject to a type of disturbance that was not quantified. The 'lagoon entrance' habitat was anomalous and characterized by deep water, close proximity to reef, coarse sediments, and absence of any sign of disturbance (Fig. 2).

Fish abundance and species richness

Total abundance of gobies differed markedly between habitats and among sites (Table 2). Maximum abundance was found in the 'lagoon entrance' habitat (average of ~24 individuals per transect), and the lowest number in the 'reef flat' and the 2 reef slope habitats (0.157 to 5.171 individuals per transect). The 'central lagoon' and 'sheltered back reef' habitats tended to be intermediate (7.618 to 10.875 individuals per transect), but a Tukey's test did not clearly separate these from the other habitats. In addition to these differences among zones, there was a sizeable variance compo-

nent attributable to the random factor of site, nested within habitat (~44%).

The mean number of species per transect also differed significantly among habitats and sites (Table 3), but the pattern did not closely match that for total abundance. 'Central lagoon' and 'reef flat' habitats were most speciose (2.25 to 2.8 species per transect). The 'lagoon entrance' and 'sheltered back reef' habitats were intermediate in richness (~2 species per transect), while the 2 slope habitats were the least speciose (~1 species or less per transect). As with abundance, there was a considerable amount of variation among sites within habitats (~34%).

Goby assemblage and species distributions

The species composition of goby assemblages also differed markedly among habitat zones and sites within zones (Table 4), and most species were uncom-

Table 3. (a) Analysis of variance of goby species richness. Variance component (confidence interval) of site(habitat zone) = 34.03% (8.88, 71.35) of total random variation in the model. (b) Tukey's HSD test of differences between number of species in each habitat zone. Lines join habitats that do not differ from each other. Numerical values are the mean number of species per 20 m² transect

(a)					
Source	df	MS	F	p	
Habitat zone	5	19.680	7.342	0.0023	
Site(habitat zone)	12	2.681	5.127	0.0001	
Error	126	0.523			
(b)					
Central lagoon	Reef flat	Lagoon entrance	Shallow back reef	Front reef slope	Back reef slope
2.792	2.250	2.083	1.875	1.125	0.250

Table 4. Multivariate analysis of variance of goby community structure. Habitat zone was tested over site(habitat zone), and site(habitat zone) tested over the error

Source	Pillai's Trace	F-value	Numerator df	Denominator df	p
Habitat zone	4.482	7.70	45	40	<0.0001
Site(habitat zone)	2.421	3.86	108	1134	<0.0001

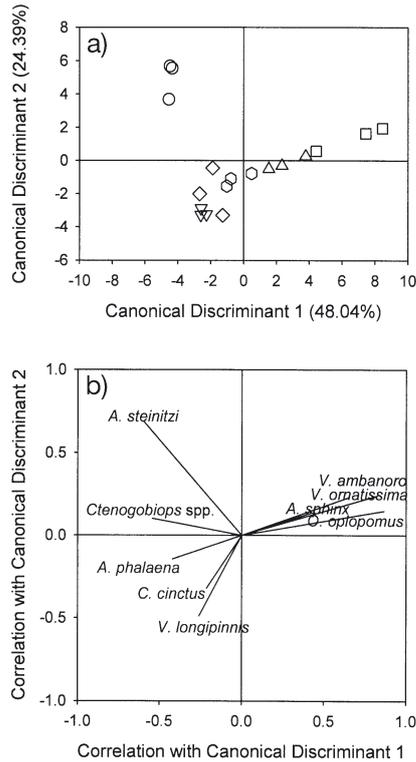


Fig. 3. Canonical discriminant analysis of goby assemblage. (a) Projection of sites in ordination space. ▽ Reef flat, ◇ Sheltered back reef, △ Front reef slope, ○ Back reef slope, □ Central lagoon, ○ Lagoon entrance. (b) Structure coefficients (correlation coefficients) of fish species with ordination axes

mon at most sites. Canonical discriminant analysis showed that in terms of goby assemblages, sites were grouped according to their habitat classification (Fig. 3). There were 2 identifiable trends in the spatial variation in assemblage structure, which explained ~72% of the between-group variation (Fig. 3). These trends and site groupings closely matched those identified for habitat variables, indicating a predictable relationship between fish assemblage and habitat structure (see

Fig. 2). There was a trend in goby community structure from shallow to deep sites, with the exception of the lagoon entrance. Both 'reef flat' and 'sheltered back reef' habitats contained *Ctenogobius* spp., however these habitats differed in their representation of other species. *Valencienna longipinnis* and *Amblygobius phalaena* were common in 'reef flats' but not 'sheltered back reefs', while *Cryptocentrus cinctus* and *Amblyeleotris steinitzi* exhibited the opposite pattern (Fig. 4). The 'front slope', 'back reef slope' and 'central lagoon' habitats were characterized by *Oplopomus oplopomus*, with *Vanderhorstia ornatissima*, *V. ambanoro*, and *Amblygobius sphinx* appearing only in 'central lagoon' habitats. The goby assemblage in the deeper water of the 'lagoon entrance' habitat shared species in common with the shallow water assemblages, but with a great abundance of and numerical dominance by *A. steinitzi*, and with fewer *Ctenogobius* spp. and *A. phalaena* (Fig. 4).

Fish-habitat relationships

The association between gobies and the habitat parameters that characterized each zone was complex and species-specific (Table 5). For most species, variation in abundance was explained by 3 or more continuous variables and/or their interactions. The proportion of total variance explained ranged from ~89% for *Amblyeleotris steinitzi*, one of the most abundant species, and ~13% for *Amblygobius sphinx*, one of the rarest (Table 5). Physical factors (a combination of depth, distance from reef and topographic complexity) and the interaction between physical factors and sediment grain size were consistently important. However, the abundance of each species exhibited a unique relationship with a different combination of habitat variables.

Partial correlation analysis showed that the abundance of *Amblygobius phalaena* was largely explained

Table 5. Variance partitions among different sets of continuous habitat variables. Figures are percent of total variance explained by main effect and interactions between physical, disturbance, and grain size parameters. Blank values signify <5% variation explained

	<i>Amblygobius phalaena</i>	<i>Amblygobius sphinx</i>	<i>Ctenogobius</i> spp.	<i>Vanderhorstia ornatissima</i>	<i>Vanderhorstia ambanoro</i>	<i>Amblyeleotris steinitzi</i>	<i>Cryptocentrus cinctus</i>	<i>Valencienna longipinnis</i>	<i>Oplopomus oplopomus</i>
Physical (P)	6.68			9.65	11.46	30.04	20.23	30.22	
Disturbance (D)	6.81		13.54	11.12	7.01	9.47	7.24	8.07	
Grain size (G)	5.00							8.81	17.16
P × D					7.48	24.08			
P × G	5.49	12.97	17.83	44.74	33.86	24.99			35.73
D × G									
P × D × G							5.86	6.70	15.59

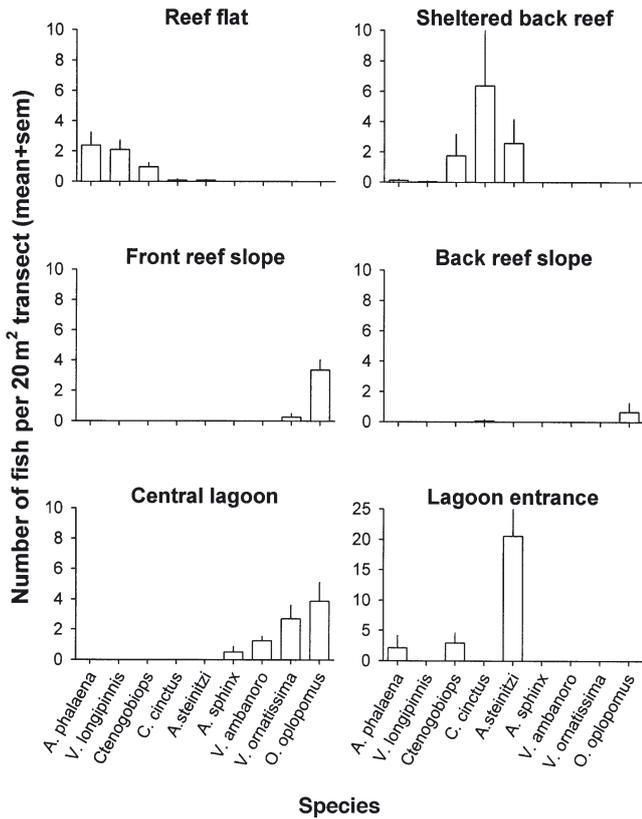


Fig. 4. Species-frequency histograms of the goby assemblage in different habitats

by depth, topography, the amount of disturbance and sediment grain size (Table 6). It was largely restricted to shallow water, high topography areas, where there was coarse sand and little disturbance of any kind (Table 6). Thus, its abundance was positively correlated with topography and grain size, and negatively correlated with depth and disturbance. Its congeneric *Amblygobius sphinx* was more abundant with increasing distance from contiguous reef, although the rela-

tionship was relatively weak (Table 6). Its abundance was also to some degree conditional on small sediment grain size (Table 5).

The combined *Ctenogobiops* species were strongly associated with coarse, undisturbed sediments, their abundance positively correlated with median grain size and negatively correlated with disturbance of any kind (Table 6). The abundances of the congeneric species *Vanderhorstia ornatissima* and *V. ambanoro* were both positively correlated with depth and distance from contiguous reef, and were negatively correlated with disturbance and sediment grain size (Table 6). The negative partial correlation with type of disturbance indicated an association with invertebrate disturbance. The only factor that appeared to separate them was that *V. ambanoro* appeared to be associated with lower topography.

Amblyeleotris steinitzi was associated with unique combinations of physical factors, disturbance and sediment grain size (Table 6). It was found in greater abundance on coarse sediments, close to contiguous reef. This species was found both in shallow and deep water, but the common physical factor was the presence of coarse sediments (hence its correlation with both deep water and wind ripple disturbance, which did not actually occur together at a single site).

Cryptocentrus cinctus and *Valenciennesa longipinnis* were associated primarily with the physical parameters of the habitat, to some degree conditional on grain size and disturbance regime (Table 5). However, the form of this relationship differed for the 2 species. *C. cinctus* was found close to contiguous reef in shallow, undisturbed, flat sediments (Table 6). In contrast, *V. longipinnis* was found in coarse, undisturbed sediments, further from reef in shallow water, but in areas of sloping topography (Table 6). *Oplopomus oplopomus* was unique in that it was associated with fine, topographically complex sediments, far from contiguous reef.

Table 6. Partial correlations between goby species and continuous habitat variables. Positive correlation with disturbance type signifies association with wind ripples, negative correlation signifies association with invertebrate disturbance. Blank values represent non-significant correlations

	Distance from reef	Depth	Topography	Amount of disturbance	Type of disturbance	Grain size
<i>Amblygobius phalaena</i>		-0.18	0.24	-0.25		0.24
<i>Amblygobius sphinx</i>	0.17					
<i>Ctenogobiops</i> spp.				-0.42		0.27
<i>Vanderhorstia ornatissima</i>	0.48	0.33		-0.32	-0.43	-0.33
<i>Vanderhorstia ambanoro</i>	0.34	0.38	-0.21	-0.21	-0.32	-0.30
<i>Amblyeleotris steinitzi</i>	-0.61	0.64	-0.25	-0.63	0.17	0.30
<i>Cryptocentrus cinctus</i>	-0.27	-0.38	-0.33	-0.33		
<i>Valenciennesa longipinnis</i>	0.31	-0.46	0.26	-0.29		0.37
<i>Oplopomus oplopomus</i>			0.23			-0.61

DISCUSSION

The assemblages of fish resident in the soft-sediment habitats associated with coral reefs have received little attention. The vast majority of the research on reef fishes has focused on species using hard substrata (see Sale 1991, 2002). Many large coral reef fishes appear to use sandy habitats in the lagoon and back reef areas, either as recruitment sites as juveniles or as foraging sites as adults (Shulman 1984, 1985, Jones et al. 1991, Adams & Ebersole 2002). However, these habitats are numerically dominated by smaller species that spend their whole lives in open sandy environments. While there is a fragmented literature on their habitat use (Hudson 1977, Hoffman & Robertson 1983, Sano 1990, Nemtsov 1994, Buettner 1996, Clark et al. 2000), and symbiotic associations between gobies and alpheid shrimps (Karplak et al. 1972, Polunin & Lubbock 1977, Preston 1978), there has been no systematic study on sand-dwelling assemblages as a whole.

Soft sediment habitats superficially appear to provide little structure or heterogeneity for constituent animal communities. Despite this, some fish species appear to exercise preferences for certain types of sand habitat, particularly in relation to sediment characteristics (e.g. St John et al. 1989, Sano 1990). In this study, we quantified the structure and heterogeneity of soft sediment habitats in a tropical lagoon using a broad range of measures. We then examined the association between these goby assemblages and the habitat structure, and found an unexpectedly strong association between the two.

The soft sediment habitat in Lizard Island lagoon was far from homogenous. Shallow depth, coarse sediments, and high levels of wave-disturbance characterized the shallow reef flat and sheltered back reef habitats. In contrast, the central lagoon habitat was deeper, with fine sediments and high levels of invertebrate disturbance generated by *Callinassa* sand prawns. This pattern was also correlated with the distance from consolidated hard reef. The shallow, coarse sediment habitats were close to the reef, whereas the fine-sediment central lagoon habitats were far from the reef. Slope habitats lay between these extremes, in terms of both distance from reef and sediment grain size. In addition, slope habitats were not subject to either invertebrate or wave disturbance. The lagoon entrance site was similar to the shallow sites in sediment grain size and distance to reef, but was in deep water and not subject to either wave or invertebrate disturbance. Covariation in habitat characteristics generated recognizable habitat types in different parts of the lagoon.

Different goby assemblages were found in the different habitat types. There was a strong correspondence between sites grouped according to habitat character-

istics and fish assemblages. Two distinct types of assemblage could be identified. The first type of assemblage was a suite of species found exclusively in fine-sediment habitats. This assemblage appeared in a gradient from the reef slope habitats to central lagoon. *Oplopomus oplopomus* occurred on reef slope and central lagoon habitats, whereas *Vanderhorstia ambanoro*, *V. ornaticissima*, and *Amblygobius sphinx*, were common only in central sites.

The second type of assemblage was only found in coarse-sediment habitats, but the composition varied between the coarse-sediment habitats. The reef flat habitat was dominated equally by *Amblygobius phalaena*, *Valenciennesia longipinnis*, and *Ctenogobius* spp., with occasional *Cryptocentrus cinctus* and *Amblyeleotris steinitzi*. It is noteworthy that the distribution of *V. longipinnis* at Lizard Island was similar to the distribution of that species at One Tree Island, in the southern Great Barrier Reef (St John et al. 1989). In contrast with the reef flat, the sheltered back reef habitat assemblage was composed of more individuals, and dominated by *C. cinctus*, *A. steinitzi*, and *Ctenogobius* species. *A. phalaena* and *V. longipinnis* were only occasionally recorded. The deeper lagoon entrance site represented an amalgam of the other coarse sediment assemblages, and was strongly dominated by *A. steinitzi* in addition to lower numbers of *Ctenogobius* spp. and *A. phalaena*.

In general, gobies were not simply correlated with any single habitat characteristic. There were identifiable species-specific relationships with a range of habitat factors, and more often than not, the effect of one factor was conditional upon the effect of another. Physical characteristics, corresponding with depth, the distance from reef, and topography, were important for most species, either as 'main' effects, or in combination with other factors. The 'interaction' between physical characteristics and sediment grain size was important for many species. However, physical characteristics also interacted with disturbance regime, and with both disturbance and grain size for some species. Within these combinations of factors, however, main effects of physical structure, sediment grain size, and disturbance regime were also important correlates.

The complexity of these correlations between gobies and habitat indicated 3 important features. First, simple provision of one or more habitat characteristics is unlikely to result in any particular species occupying that habitat. The predicted response of a goby assemblage to a novel habitat is likely to be conditional on a range of other conditions. Second, very few species shared common responses to sets of habitat conditions. The exception was *Vanderhorstia ambanoro* and *Amblyeleotris steinitzi*, whose distributions were correlated with physical structure, disturbance regime,

their interaction, and a physical structure and disturbance interaction. This does not imply they were found in the same habitat, however. *V. ambanoro* was found far from the reef, in fine-grained invertebrate disturbed habitats, whereas *A. steinitzi* was found close to the reef in coarse-grained wave-disturbed habitats. Finally, even species such as *Vanderhorstia ornatisima*, *Oplopomus oplopomus*, *V. ambanoro* and *Amblygobius sphinx* that were strongly correlated at the site level did not share the same correlations with finer-scale continuous habitat variables.

It is likely that the structure and stability of sediments are important for the species that occupy these habitats. Small fishes may be subject to higher predation risk (Munday & Jones 1998) and gobies may rely on burrows for shelter and protection. There was no clear relationship between goby distribution across habitats, and whether the species built burrows or shared with alpheid shrimps. In deeper habitats, both *Vanderhorstia* shrimp-associates and the non-associated *Amblygobius sphinx* and *Oplopomus oplopomus* equally characterized the habitat. Similarly in shallower and coarse sediment habitats, both shrimp-associates and burrowing species co-occurred. It appeared that, with the exception of sloping habitats, wave and invertebrate disturbance intensity was not strongly correlated with the ability to make or occupy burrows. In sloping habitats, however, the instability of the sediments might have been responsible for the low abundance of gobies. An additional factor that has been implicated in driving goby distributions is the abundance of prey. Gobies have been reported to be more abundant in habitats with higher prey abundance (St John et al. 1989), and different prey species may in turn be more abundant in different sediment types (Jones 1984, Jones et al. 1990). The role of sediment stability, distribution of shrimps and prey, and their interactions with disturbance regime is worthy of more examination.

Soft-sediment habitats and fish communities are clearly more heterogeneous than they appear. The role of habitat characteristics in structuring these fish communities rivals their hard-reef counterparts. Sand-dwelling species appear to respond to a wide range of factors, with responses to any single factor contingent upon the levels of the others. Ultimately, the key processes determining the distribution and abundance of individual species need to be teased out by experiment, or careful structural modeling where experimentation is not possible. We hypothesize that the interaction between the physiographic structure of the reef, its associated sediments, and biological and physical disturbance regimes will be of primary importance in understanding the processes that generate distribution patterns in this little-studied component of the coral

reef seascape. Consequently, any natural or anthropogenic modification of sediment deposition or natural disturbance regimes is likely to be just as problematic for the community as any habitat change or degradation in other marine environments.

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