

Tidal fish connectivity of reef and sea grass habitats in the Indo-Pacific

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The present study considered the influence of the tide on shallow water fish assemblages within the Wakatobi Marine National Park, Indonesia. Timed underwater visual observations were made across a gradient of intertidal to subtidal habitats from near-shore to reef crest at different tidal heights. Transient fish were found to dominate shallow water fish assemblages and the assemblage composition varied with tidal state. Fish assemblages were more diverse and abundant at higher tides in both coral and sea grass habitats, however, this was more pronounced within sea grass habitats. A tidal reduction from ≈ 2.0 m to ≈ 0.8 m (above chart datum) corresponded to a 30% reduction in fish abundance, while species richness also significantly decreased from 13.5 to 10.8 species per standardized timed observation. Fifty fish groups were reported from sea grass habitats with the most abundant being from the Engraulidae family and *Lethrinus harak*, which form important local subsistence fisheries. This research confirms the importance of tidal changes in structuring the fish fauna of Indonesian sea grass habitats and underlines the connectivity that exists between these habitats and nearby coral reefs.

INTRODUCTION

Sea grass and mangrove habitats play a fundamental role in coral reef fish life history (Nagelkerken et al., 2002; Dorenbosch et al., 2007; Unsworth et al., 2007). It is important to identify/understand the mechanisms that connect these shallow water habitats, and specifically, few studies have considered how this habitat connectivity impacts sea grass fish assemblages. In light of recent concern about the degradation of these habitats (Fortes, 1991; Orth et al., 2006) it is vital for their future management that the ecological mechanisms pertinent to their effective management are more clearly understood (Parrish, 1989; Sheaves, 2005; Larkum et al., 2006).

Tidal state is an important factor controlling fish assemblages in many shallow water environments (Sogard et al., 1989; Thompson & Mapstone, 2002), and it may have one of the greatest influences on the pattern of biological inter-habitat connectivity (Sheaves, 2005). For example, a high tidal range may be great enough to allow large predators to readily access shallow water habitats such as sea grass at high tide, altering fish assemblage structure and changing behavioural interactions (Blaber, 1986; Sheaves, 2005). Fish must develop effective strategies to maximize the resources of inter-tidal habitats in relation to tidal water movements, thereby optimizing the trade-off between predation risk and food availability (Sogard, 1992; Allouche, 2002; Sheaves, 2005).

An ebbing tide commonly results in a reduction in fish abundance and diversity (Sogard et al., 1989; Nagelkerken et al., 2000) as a consequence of environmental or predatory pressures (Young et al., 1997; Nagelkerken et al., 2000). In tropical coastal habitats tidal fish movements

to and from sea grass beds may include migration to other habitats including coral reefs (Robertson, 1980), mangroves (Nagelkerken et al., 2000) or various deeper water environments (Pessanha & Araujo, 2003), with many of these movements being for foraging (Robertson, 1980; Robblee & Zieman, 1984).

As the water level begins to fall with the ebbing of the tide the movement of fish may exist as a gradual process rather than an instantaneous mass migration when the tide turns. Previous research investigating the impact of tide on faunal assemblages has mainly documented the difference between extremes of the tide (Penn, 1975; Sogard et al., 1989; Pessanha & Araujo, 2003) or as a function of the ebbing or flooding of the tide (Bretsch & Allen, 2006). Research has not considered whether small, subtle changes in tidal level have an effect, specifically within sea grass habitats. It is not clear whether fish utilize these habitats differently at different stages of the tide or whether there is a high degree of species-specific strategies with respect to tidal height.

Despite shallow Indo-Pacific intertidal areas often being continuous sea grass, they can effectively be split into zones based on the relative amount of time they become exposed by the tide, with inshore habitats being exposed for longer periods. In many habitats changing water depth and aerial exposure causes changes in the associated floral and faunal assemblages (Chapman, 1977) and has been found to influence sea grass bed fauna in the Caribbean (Robertson, 1980; Sogard et al., 1989). Although research has commonly considered the distinct habitats of coral reef, sea grass and 'bombie/patch reef' (Kochzius, 1999; Nakamura & Sano, 2004), there has been little characterization of the fish assemblages that inhabit these inter-tidal depth and habitat gradients (Nakamura & Sano, 2004).

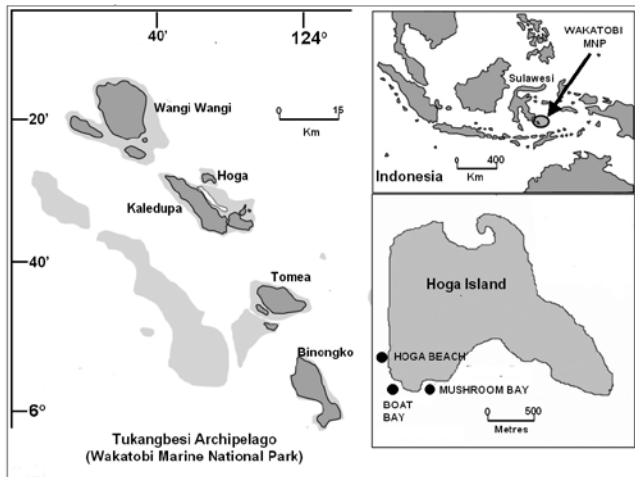


Figure 1. Location of the three study sites, Hoga Beach, Boat Bay and Mushroom Bay.

The aim of this research was to investigate sea grass fish assemblage structure with respect to tide to determine how tidal phase affects the degree of connectivity for fish assemblages between neighbouring coral reef and sea grass habitats. The following H1 hypotheses were tested: (1) shallow water sea grass and coral habitats have distinct species assemblages; (2) small changes in tidal water height effect fish assemblages inhabiting shallow water sea grass and coral habitats; and (3) small tidal changes influence the movement of fish between shallow sea grass and coral habitats.

MATERIALS AND METHODS

This study was conducted between April and May 2005 (start of the dry season) on the intertidal to subtidal sea grass beds and fringing coral reefs around Hoga Island in the Wakatobi Marine National Park (MNP) (Figure 1). The shallow water coastal habitats of this region are characterized by intertidal sea grass beds lying between fringing coral reefs and the shoreline, a representative system across large sections of the Indo-Pacific and Indian Oceans (Salita et al., 2003; Nakamura & Sano, 2004).

Study sites

Three sites, Hoga Beach, Boat Bay and Mushroom Bay were surveyed around Hoga Island (Figure 1). These sites all had similar depth profiles and tidal regimes. Local tides had a maximum amplitude of 2.3 m and are approximately semi-diurnal (Unsworth et al., 2007). At each site five habitat types were identified: inshore sea grass, mid-shore sea grass, far-shore sea grass, coral bobbies and reef flat (Figure 2). Inshore, mid-shore and far-shore sea grass habitats were defined as being ≈ 25 m, ≈ 100 m and ≈ 175 m towards the reef from the mean high water spring tide mark (MHWS) respectively. This created a water depth gradient towards the reef flat. All distances were measured horizontally and perpendicular to the beach. The coral bobbie habitat was defined as the zone comprising mostly sand and sparse sea grass ($\approx 5\%$ cover) mixed with coral boulders ($\approx 15\%$ coral cover) of < 2 m diameter (≈ 250 m from MHWS), while the

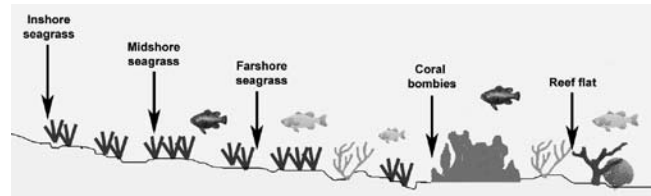


Figure 2. Schematic representation of the five habitats sampled in the present study. Fish fauna of each habitat was sampled four times at each of three tidal levels; High tide (2.3–1.9 m), Mid tide (1.6–1.3 m), and Low tide (1.0–0.7 m). This sampling was repeated at each of three sites (Hoga Beach, Boat Bay, Mushroom Bay) in the Wakatobi MNP, Indonesia.

reef flat was defined as the mid point between the coral bobbie zone and the reef crest ≈ 350 m from MHWS.

Sea grass sampling sites were selected based on a pilot study/preliminary study (estimation of % cover using 0.25 m² quadrats) that identified sea grass habitats that had $> 70\%$ cover comprising a mixed floral assemblage dominated by two species, *Thalassia hemprichii* (Ehrenberg) and *Enhalus acoroides* (L.f.) Royle. This reduced the effects of habitat complexity and structure on fish assemblages (Verweij et al., 2006).

Sampling of tidal effects on fish assemblages

Fish populations were sampled using underwater visual census, utilizing a balanced stratified sampling design (Heath, 1995) in order to reveal any effects of tidal changes. Many sea grass studies have used belt transects for fish abundance estimation (Kochzius, 1999; Nagelkerken et al., 2001) based on the methods described in English et al. (1997), and while cumulative species-distance curves showed the most appropriate belt transect length to be 70 m, the sea grass habitat variability over this spatial scale was too high in the present study for belt transects to be effective due to patchiness and changes in sea grass abundance. Thus to survey fish, a stationary point-count method by snorkelling was used (Polunin & Roberts, 1993; Watson & Quinn, 1997). This method has been commonly used to assess fish assemblages within tropical sea grass beds (Nakamura & Sano, 2004; Dorenbosch et al., 2006).

A small sample area was used in order to standardize repeat sampling and to obtain sampling areas of homogeneous habitat. The stationary point-count method used a 16 m² (4×4 m) quadrat delineated by tape measures laid out fifteen minutes prior to sampling. This quadrat size was chosen as visibility within the sampling locality is at least 5 m for 90% of the time (calculated during preliminary observations). Cumulative species-time curves ($N=5$) determined fifteen minutes to be an effective time to sample $> 90\%$ of all species. As these observations were conducted by an observer involved in wider fish monitoring programmes, numerous study training exercises had been conducted prior to sampling based on English et al. (1997). During the first 10 minutes of the 15 minute period, the observer was situated on the edge of the quadrat, while during the last 5 minutes, the observer moved slowly through the quadrat to search for fish hiding behind or under sea grass leaves.

Table 1. Mean fish abundance/100 m² (\pm SE) for the thirty most abundant seagrass fish species and families recorded at three different tidal heights (high, mid and low) within both sea grass (all distances from shore) and coral habitats (bombies and reef flat). Fish were sampled using visual observations, data are averaged across three sites (Hoga Beach, Boat Bay and Mushroom Bay).

	Coral habitats			Sea grass habitats		
	High tide	Mid tide	Low tide	High tide	Mid tide	Low tide
Engraulidae spp.	0	0	0	113.8 \pm 91.5	36.1 \pm 25.2	95.7 \pm 64.2
<i>Lethrinus harak</i> (Forsskål, 1775)	32.2 \pm 5.9	23.3 \pm 4.7	37.4 \pm 6.4	103.6 \pm 9.1	40.6 \pm 5.7	35.0 \pm 4.2
<i>Scolopsis monogramma</i> (Cuvier, 1830)	37.9 \pm 6.2	33.4 \pm 3.9	27.6 \pm 3.5	49.9 \pm 8.0	36.7 \pm 6.1	23.1 \pm 4.7
Juvenile sprat	0	0	2.7 \pm 2.7	46.9 \pm 23.7	36.1 \pm 21.6	0
<i>Cheilio inermis</i> (Forsskål, 1775)	5.1 \pm 1.5	7.0 \pm 2.5	7.0 \pm 2.3	33.0 \pm 6.4	25.1 \pm 9.7	10.9 \pm 1.9
Halichoeres spp.	9.5 \pm 4.3	1.9 \pm 1.9	1.6 \pm 1.6	38.6 \pm 10.3	18.3 \pm 5.1	7.2 \pm 3.5
Siganidae spp.	10.3 \pm 4.3	0	6.8 \pm 2.3	24.6 \pm 4.9	6.1 \pm 1.8	2.2 \pm 0.8
<i>Scolopsis lineatus</i> (Quoy & Gaimard, 1824)	20.4 \pm 4.1	20.9 \pm 5.1	13.5 \pm 2.5	11.6 \pm 3.0	9.0 \pm 2.4	11.2 \pm 9.0
<i>Scolopsis trilineatus</i> (Kner, 1868)	33.0 \pm 7.8	29.0 \pm 4.6	22.0 \pm 4.0	10.3 \pm 4.4	10.3 \pm 2.9	5.4 \pm 1.7
Labridae spp.	79.4 \pm 11.5	68.3 \pm 10.3	49.3 \pm 7.9	7.9 \pm 2.4	12.6 \pm 3.7	2.5 \pm 1.2
<i>Leptoscarus vaigiensis</i> (Quoy & Gaimard, 1824)	0	2.7 \pm 1.5	6.2 \pm 3.5	7.0 \pm 1.2	4.7 \pm 1.3	3.1 \pm 0.9
<i>Stethojulis bandanensis</i> (Bleeker, 1851)	6.8 \pm 2.5	7.9 \pm 2.7	7.4 \pm 2.3	7.6 \pm 1.6	2.9 \pm 1.0	1.1 \pm 0.5
<i>Scolopsis bilineatus</i> (Bloch, 1793)	11.6 \pm 3.5	6.5 \pm 1.8	5.4 \pm 2.2	1.6 \pm 0.8	4.2 \pm 1.8	5.3 \pm 2.8
Blennidae spp.	11.9 \pm 3.3	24.1 \pm 4.9	16.3 \pm 3.6	1.6 \pm 0.9	4.4 \pm 1.3	3.5 \pm 1.2
<i>Choerodon anchorago</i> (Bloch, 1791)	17.9 \pm 4.2	7.6 \pm 1.8	5.1 \pm 1.6	4.4 \pm 1.2	3.3 \pm 0.8	1.2 \pm 0.5
<i>Parupeneus barberinus</i> (Lacepède, 1801)	17.6 \pm 3.1	9.0 \pm 1.9	12.7 \pm 2.0	2.9 \pm 0.9	5.3 \pm 1.4	0.7 \pm 0.3
Trachinotus spp.	0	0	0	4.9 \pm 1.3	0.4 \pm 0.3	0.4 \pm 0.3
Pinguipedidae spp.	3.5 \pm 1.0	7.4 \pm 2.2	9.0 \pm 2.2	1.4 \pm 0.5	2.2 \pm 0.8	1.6 \pm 0.5
<i>Hemiramphus far</i> (Forsskål, 1775)	3.0 \pm 1.9	0	0	4.9 \pm 1.4	0	0
Monacanthidae spp.	0.3 \pm 0.3	0	0	2.3 \pm 0.9	1.6 \pm 0.5	0.7 \pm 0.3
Bothidae spp.	2.5 \pm 0.9	0.3 \pm 0.3	1.6 \pm 0.6	2.7 \pm 0.9	1.4 \pm 0.2	0.5 \pm 0.3
<i>Cheilinus chlorourus</i> (Bloch, 1791)	3.5 \pm 1.1	1.6 \pm 0.7	3.0 \pm 1.3	1.4 \pm 0.5	1.2 \pm 0.5	1.8 \pm 0.5
Gerreidae spp.	0	0	0.5 \pm 0.5	2.5 \pm 1.1	1.1 \pm 0.5	0.9 \pm 0.5
Pomacentridae sp.	266.8 \pm 28.8	222.1 \pm 29.0	236.2 \pm 31.9	2.3 \pm 1.1	1.2 \pm 1.1	0.4 \pm 0.3
Lutjanidae spp.	3.3 \pm 2.1	0	0	3.5 \pm 1.6	0.4 \pm 0.4	0
<i>Caranx melampygus</i> (Cuvier, 1833)	1.1 \pm 0.5	0.3 \pm 0.3	0	3.1 \pm 1.1	0.2 \pm 0.2	0
<i>Cheilinus undulatus</i> (Rüppell, 1835)	1.6 \pm 0.8	0.5 \pm 0.4	2.2 \pm 1.4	1.2 \pm 0.5	0.5 \pm 0.3	0.9 \pm 0.4
<i>Upeneus arge</i> (Jordan & Evermann, 1903)	0.9 \pm 0.5	1.6 \pm 0.6	2.5 \pm 1.0	1.8 \pm 0.8	0.4 \pm 0.3	0.4 \pm 0.3
<i>Caranx ignobilis</i> (Forsskål, 1775)	0	0	0	2.2 \pm 1.0	0.4 \pm 0.4	0
<i>Mulloidichthys flavolineatus</i> (Lacepède, 1801)	0	2.7 \pm 2.2	0.5 \pm 0.4	0	2.3 \pm 1.1	0

Care was taken not to count individuals or groups of fish that regularly moved in and out of the quadrat more than once (Dorenbosch et al., 2006).

Fish observations were made within three tidal height ranges: high tide (>1.9 m), mid tide (1.6–1.3 m), and low tide (0.7–1.0 m) above the low water spring tide mark; all observations were made on the flood tide between 0900 and 1600 h to reduce possible diurnal effects (Unsworth et al., 2007). The levels used represent the minimal and maximum levels of water coverage of the inter-tidal sea grass. To remove any potential for cumulative impact and error created by the presence of the observer, and consequently enabling samples to remain fully independent, no consecutive observations at the same site were conducted throughout one tidal flood. Fish were recorded to species level wherever possible; many were only classified to family or genus level; hereafter these are referred to as 'fish groups'.

The study design used four independent replicate 16 m² quadrats haphazardly placed within each of the five habitat types, these were all repeated at the three tidal heights creating twelve observations at each habitat within each site.

All observations were repeated at the three sites producing a total of one hundred and eighty samples.

Analysis

Total fish abundance and species richness data were found to be heteroscedastic and deviated from a normal distribution; transformation could not rectify this, therefore three-way PERMANOVA was used to analyse for differences in fish abundance and species richness between sites, habitats and tidal levels. PERMANOVA v.1.6 by M.J. Anderson, Department of Statistics, University of Auckland was used for this analysis. No transformation or standardization was conducted on the raw data and the analysis used Euclidean distances (999 permutations). PERMANOVA enabled a conventional univariate two-way ANOVA approach to be conducted using the concepts and assumptions of a multivariate method and included the use of pairwise comparisons.

Patterns of fish assemblage structure were analysed using multivariate non-metric multidimensional scaling

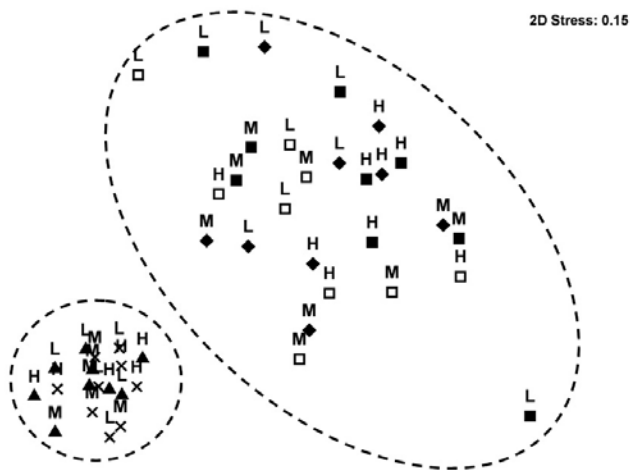


Figure 3. Two-dimensional MDS scaling configuration with superimposed Bray–Curtis similarity clusters (oval shapes) at the 40% level for comparisons between fish assemblage group abundance in the Wakatobi Marine National Park, Indonesia in five different habitats: reef flat (\blacktriangle), bobbies (\times), far-shore sea grass (\square), mid-shore sea grass (\blacklozenge) and inshore sea grass (\blacksquare) using visual observations at three tidal levels (high (H), mid (M) and low (L)). Sampling used three sites: Hoga Beach, Boat Bay and Mushroom Bay.

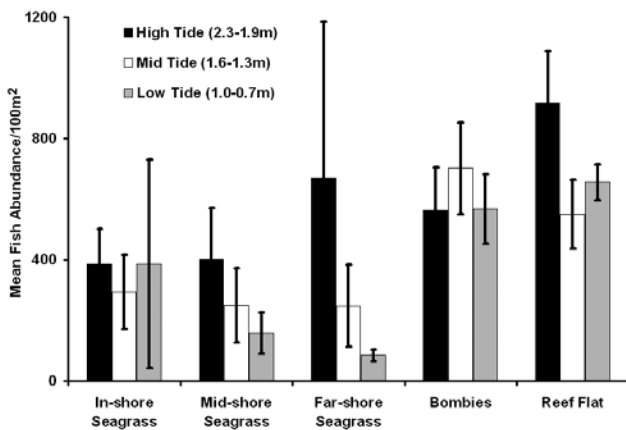


Figure 4. Mean ($\pm 95\%CI$ $N=12$) fish abundance in the Wakatobi Marine National Park, Indonesia in five different habitats: reef flat, bobbies, far-shore sea grass, mid-shore sea grass and inshore sea grass using visual observations over three tidal levels (high [dark bars], mid [grey bars] and low [white bars]) (figures were averaged over three sites: Hoga Beach, Boat Bay and Mushroom Bay).

ordination (nMDS), and Bray–Curtis cluster analysis using the PRIMER v. 6.1.5 (Clarke & Warwick, 1994). The Bray–Curtis similarity index was applied on root-root transformed data (to down weigh the influence of rare and extremely abundant species) to create a rank similarity matrix that was then converted into an ordination (Clarke, 1993). To check on the adequacy of the low-dimensional approximations seen in cluster and MDS the use of PRIMER v.6.1.5 enabled clusters from Bray–Curtis analysis to be superimposed onto the MDS ordinations. A two-way (tide and habitat) ANOSIM (in PRIMER) was used to investigate differences identified by MDS and cluster. SIMPER analysis (in PRIMER) was

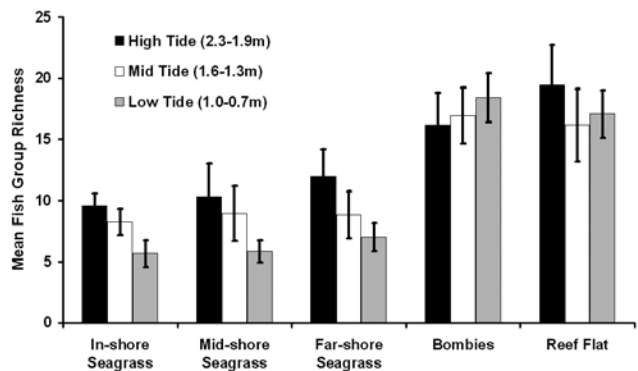


Figure 5. Mean ($\pm 95\%CI$ $N=12$) fish group richness in the Wakatobi Marine National park, Indonesia in five different habitats: reef flat, bobbies, far-shore sea grass, mid-shore sea grass and inshore sea grass using visual observations over three tidal levels: (high [dark bars], mid [grey bars] and low [white bars]) (figures were averaged over three sites: Hoga Beach, Boat Bay and Mushroom Bay).

used to ascertain the fish groups that contributed most to the dissimilarity between sites, habitats and tidal levels. All means are herein reported \pm standard errors.

RESULTS

Fifty-nine fish groups were identified from sea grass and coral habitats. The most abundant fish groups (Table 1) were Engraulidae spp. with a mean abundance of 49.1 ± 22.9 individuals per 100 m^2 and *Lethrinus harak* (48.2 ± 3.36 individuals per 100 m^2). Engraulidae spp. were infrequently observed but occurred in shoals of high numbers, which accounts for the high variability in their abundance. Contrastingly, *L. harak* was regularly observed which is highlighted by its low standard error.

Effect of habitat on fish assemblage

Coral habitats (bobbies and reef flat) had significantly higher mean fish abundance ($F_{1,179}=37.36$, $P<0.001$) and richness ($F_{1,179}=208.13$, $P<0.001$) (abundance= 568.3 ± 99.7 individuals per 100 m^2 ; fish group richness= 14.4 ± 1.0 groups per observation) than sea grass habitats (abundance= 332.3 ± 120.6 individuals per 100 m^2 ; fish group richness= 8.5 ± 0.8 groups per observation). Significant differences were also found between the assemblages of the different habitats (ANOSIM, $R>0.8$, $P<0.001$) (Figure 3).

Mean fish abundance (Figure 4) and group richness (Figure 5) declined with increasing distance from the reef crest (i.e. towards the inshore sea grass habitats) ($F_{4,179}=14.1$, $P<0.001$; $F_{4,179}=72.7$, $P<0.001$). Fish group abundance and richness were significantly affected by habitat (Table 2). High tide did not always have the highest fish abundance; likewise low tide did not always have the lowest abundance (see Figure 4). This is illustrated by a significant interaction term between habitat and tide. Fish abundance and group richness of all individual coral habitats (reef flat and bobbies) were found to differ significantly from all individual sea grass habitats (inshore, mid- and far-shore), except far-shore sea grass and both coral habitats (Table 3). Fish abundance and fish group richness did not differ significantly within any intra-

Table 2. Three-way permutational multivariate analysis of variance for fish abundance and richness between five different habitats (reef flat, bombies, far-shore sea grass, mid-shore sea grass and inshore sea grass) using visual observations at three tidal levels: (high, mid and low) over three sites (Hoga Beach, Boat Bay and Mushroom Bay).

Source	df	Fish group richness			Fish abundance		
		Mean squares	F-statistic	P-value (permutational)	Mean squares	F-statistic	P-value (permutational)
Site	2	63.5	5.36	0.009	5483.0	2.27	0.097
Habitat	4	860.1	72.7	0.001	34024.6	14.10	0.001
Tide	2	111.6	9.43	0.001	20740.6	8.60	0.002
Site×habitat	8	37.7	3.18	0.002	9038.5	3.75	0.002
Site×tide	4	11.0	0.93	0.44	1921.3	0.80	0.538
Habitat×tide	8	31.4	2.66	0.01	6450.5	2.67	0.007
Site×habitat×tide	16	12.1	1.03	0.41	6065.3	2.51	0.002
Residual	135	11.8			2412.4		
Total	179						

Table 3. P-values for pair-wise a posteriori comparisons for habitat, tide, and site following three-way permutational multivariate analysis of variance (Table 2) for fish abundance (and fish group richness shown in parentheses) over five habitats (reef flat, bombies, far-shore sea grass, mid-shore sea grass and inshore sea grass) using visual observations at three tidal levels (high, mid and low) over three sites (Hoga Beach, Boat Bay and Mushroom Bay).

	Inshore sea grass	Mid-shore sea grass	Far-shore sea grass	Coral bombies
Mid-shore sea grass	0.28 (0.52)			
Far-shore sea grass	0.88 (0.07)	0.66 (0.34)		
Coral bombies	0.001 (<0.001)	<0.001 (<0.001)	0.003 (0.53)	
Reef flat	<0.001 (<0.001)	<0.001 (<0.001)	<0.001 (0.07)	0.11 (0.73)
Tidal comparisons				
	High tide	Mid tide		
Mid tide	0.01 (0.10)			
Low tide	0.01 (0.02)	0.53 (0.34)		
Site comparisons				
	Mushroom Bay	Boat Bay		
Boat Bay	0.07			
Hoga Beach	0.61	0.16		

sea grass habitat comparisons or within coral (reef flat and bombies) habitat comparisons (Table 3).

Both coral habitats (reef flat and bombies) had a significantly different fish assemblage structure to sea grass habitats ($R=0.72$, $P<0.001$); this is illustrated by the MDS with super-imposed Bray–Curtis clusters (Figure 3). A weak difference was reported between the fish assemblages found at far-shore and inshore sea grass habitats ($R=0.09$, $P<0.01$), while all other sea grass sub-habitat comparisons were not significantly different.

Effect of tide on fish groups

The overall dissimilarity between the sea grass and coral habitats (SIMPER analysis) was mostly the result

of differences in the abundance of Pomacentridae spp. (30.8% contribution), Labridae spp. (8.2% contribution), *Lethrinus harak* (6.44% contribution) and Acanthuridae spp. (5.3% contribution). The most representative fish groups of sea grass habitats were *L. harak* (44.7% contribution), *Scolopsis monogramma* (21.7% contribution) and *Cheilio inermis* (12.55% contribution), whilst Pomacentridae spp. (46.7% contribution), Labridae spp. (11.7% contribution) *S. monogramma* (6.3 1% contribution), and *L. harak* (4.4% contribution) were the most representative of coral habitats. Large shoals of fish occurring infrequently skewed the abundance data; as a result the most representative fish groups were not always the most abundant (see Table 1). The majority of the most abundant thirty fish groups in

Table 4A and B. SIMPER analysis (PRIMER v.6.1.5) of inter-habitat dissimilarity and inter-tide dissimilarity to determine the four most dissimilar (decreasing dissimilarity top to bottom) fish species in terms of abundance for difference between (A) habitat and (B) tidal height. Fish abundance for all tables was recorded using visual observations in the Wakatobi Marine National Park, Indonesia over five different habitats, (reef flat, coral bombies, far-shore sea grass, mid-shore sea grass and inshore sea grass) at three tidal levels (high, mid and low): Hoga Beach, Boat Bay and Mushroom Bay.

(A) Inter-habitat dissimilarity				(B) Inter-tide dissimilarity			
	Inshore sea grass	Mid-shore sea grass	Far-shore sea grass	Bombic zone	High tide	Medium tide	Medium tide
Mid-shore sea grass	<i>Scolopsis monogramma</i> 9.34 <i>Chellio inermis</i> 8.13 <i>Leltrinus harak</i> 8.05 Engraulidae spp. 5.57					Medium tide <i>S. monogramma</i> 6.07 <i>Leltrinus harak</i> 5.27 <i>Chellio inermis</i> 4.96 <i>Halichoeres</i> spp. 4.90	
Far-shore sea grass	<i>S. monogramma</i> 8.77 <i>Leltrinus harak</i> 7.33 <i>Chellio inermis</i> 6.60 <i>Halichoeres</i> spp. 5.96	<i>Scolopsis monogramma</i> 9.64 <i>Chellio inermis</i> 6.70 <i>Leltrinus harak</i> 6.13 <i>Halichoeres</i> spp. 5.89			Low tide <i>S. monogramma</i> 6.64 <i>Leltrinus harak</i> 5.94 <i>Chellio inermis</i> 5.03 Siganidae spp. 4.96	<i>Leltrinus harak</i> 6.84 <i>S. monogramma</i> 6.77 <i>Chellio inermis</i> 5.52 <i>S. trilineatus</i> 5.03	
Bombic zone	Pomacentridae spp. 12.48 <i>Leltrinus harak</i> 8.18 <i>S. monogramma</i> 5.29 Labridae spp. 5.09	Pomacentridae spp. 12.44 <i>Leltrinus harak</i> 7.84 <i>Chellio inermis</i> 5.9 <i>S. monogramma</i> 5.69	Pomacentridae spp. 11.64 <i>Leltrinus harak</i> 6.85 <i>Chellio inermis</i> 5.27 Labridae spp. 4.68				
Reef flat	Pomacentridae spp. 11.7 <i>Leltrinus harak</i> 7.08 Labridae spp. 60.4 <i>S. monogramma</i> 5.7	Pomacentridae spp. 11.64 <i>Leltrinus harak</i> 6.26 <i>S. monogramma</i> 6.05 <i>Chellio inermis</i> 5.99	Pomacentridae spp. 4.72 Acanthuridae spp. 5.79 Labridae spp. 6.72 <i>Scarus</i> spp. 4.48				

Table 5. Classification of the thirty most abundant fish species groups into six categories based on habitat usage over tidal changes of seagrass in the Wakatobi Marine National park, Indonesia over five different habitats, reef flat, bombies, far-shore Seagrass, mid-shore Seagrass and inshore Seagrass using visual observations at three tidal levels (high, mid and low over three sites (Hoga Beach, Boat Bay and Mushroom Bay).

Ubiquitous to all habitats and tidal states	All sea grass habitats at all tides but infrequently in coral habitats	Exclusively within sea grass habitats	Sporadic coral and sea grass visitors	All coral and sea grass only at high tide
<i>Lethrinus harak</i>	Monacanthidae spp.	Engraulidae spp.	<i>Mulloidichthys vanicolensis</i>	<i>Hemiramphus far</i>
<i>Scolopsis monogramma</i>	<i>Gerres</i> spp.	<i>Caranx ignobilis</i>		<i>Lutjanus</i> spp.
<i>Cheilio inermis</i>	Juvenile sprat			<i>Caranx melampyngus</i>
Blenniidae spp.	<i>Leptoscarus vaigiensis</i>			
<i>Scolopsis bilineatus</i>				
<i>Halichoeres</i> spp.				
Pinguipedidae spp.				
<i>Stethojulis bandanensis</i>				
<i>Parupeneus barberinus</i>				
<i>Choerodon anchorage</i>				
Pomacentridae spp.				
Bothidae spp.				
<i>Cheilinus chlorouru</i>				
<i>Scolopsis trilineatus</i>				
<i>Scolopsis lineatus</i>				
Labridae spp.				
<i>Cheilinus undulatus</i>				
<i>Upeneus arge</i>				
<i>Trachinotus</i> spp.				
Siganidae spp.				

sea grass (90%) were ubiquitous to both sea grass and coral habitats whilst only three were exclusively found in sea grass habitats (*Trachinotus* spp., Engraulidae spp., and *Caranx ignobilis*) (Table 1). Forty-eight per cent of the ubiquitous species had >60% higher abundance in sea grass than in coral habitats (Table 1).

The high proportion of Pomacentridae sp., Labridae spp., Acanthuridae spp. and Scaridae spp. reported from the reef flat (Table 4) caused a significant difference in the fish assemblage structure ($R=0.18$, $P<0.001$) between reef flat and bommie habitats, this was despite finding no significant difference in fish abundance and richness.

Effect of tide on fish assemblage

Tide was found to have a significant effect on fish abundance ($F_{2,179}=8.6$, $P<0.001$) and richness ($F_{2,179}=9.43$, $P<0.001$) (Table 2), but did not significantly affect overall fish assemblage structure (Figure 3). Reducing water height from high tide (≈ 2.0 m) to low tide (≈ 0.8 m) caused mean fish abundance to decrease by $\approx 30\%$ (Figure 4) whilst fish group richness decreased by 32% (Figure 5). *Post-hoc* analysis found significant differences in the abundance and richness to be the result of high tide (Table 3).

Tidal differences were particularly marked within sea grass habitats but not within coral habitats resulting in a significant interaction between tide and habitat ($P<0.001$) (Figure 4). A significant difference between the fish assemblage on the intertidal sea grass habitats was found ($P<0.01$) between high and low tides. The overall dissimilarity between sea grass high and low tide was caused by *S. monogramma*

(6.6%), *L. harak* (5.9%), *Cheilio inermis* (5.0%), and Siganiidae spp. (4.9%) (Table 4B). The coral bommie habitats did not exhibit any clear change in abundance or richness related to tidal change, but the reef flat fish assemblages did show a decrease in abundance and richness from high to low tide.

Effect of tide on fish groups

A decrease in abundance was found with decreasing tidal level for 80% of the most abundant fish groups (Table 1) found in sea grass whilst only 7% increased. In coral habitats only 15 fish groups showed a decrease with decreasing tidal level, while 12 showed an increase between high and low tide (Table 1). Four fish groups *L. harak*, *Cheilio inermis*, *Gerres* spp. and groups of unidentified sprat (<2 cm length) showed decreased abundance in the sea grass as the tide fell, but showed a corresponding increase in abundance within coral habitats from high to low tide. *Hemiramphus far*, *Caranx melampyngus* and *Lutjanus* spp. were ubiquitous to both coral and sea grass habitat types; these noticeably never occurred at low tide and had much greater abundance at high than mid tide. This suggests movements to shallow sea grass habitats from deeper reef habitats only during high tide.

Table 5 describes a classification scheme for the thirty most abundant sea grass fish groups based on tidal habitat usage. The majority of fish groups (66%) were classified as 'ubiquitous to all habitats and states of tide', while 13% of groups (Monacanthidae spp., *Gerres* spp., *Leptoscarus vaigiensis* and juvenile sprat) were classified as being in 'all sea grass habitats at all tides but infrequently in coral habitats'. Two further fish groups (Engraulidae spp. and *Caranx*

ignoblis) were 'exclusively found in sea grass habitats' and *Molloidichthys vanicolensis* was the only fish group classified as 'a sporadic coral and sea grass visitor'. Ten per cent of fish groups were classified as 'only visiting coral and sea grass at high tide'.

DISCUSSION

This study found transient fish to dominate shallow water fish assemblages and the assemblage composition varied with tidal state. Fish assemblages were more diverse and abundant at higher tides in both coral and sea grass habitats, however, this was more pronounced within sea grass habitats.

Tidal effects upon fish assemblages

The present study is the first to confirm the importance of small day-time tidal changes in structuring Indo-Pacific sea grass fish assemblages over short temporal scales. This study found fish abundance, diversity and assemblage structure to change with tidal state in all sea grass and coral habitat types, indicating these fish assemblages to be in a dynamic state. Increasing fish abundance and diversity with increasing tidal level is probably the result of fish migrating from deeper water sea grass and coral habitats, into shallower habitats as a function of small changes in tidal height. This suggests an early movement of fish that is conducted prior to high tide, indicating a gradual migration with the ebbing and flooding of the tides.

These early migrations occurred at tidal heights greater than 0.7 m ensuring all habitats had at least 60 cm of water above the substratum. It may be assumed that although some species remain even at absolute low tide surviving through physiological (Taylor et al., 2005), and behavioural adaptations (e.g. the triggerfish *Rhinecanthus aculeatus* in Indo-Pacific sea grass beds remains in small water filled burrows at low tide (Unsworth, personal observation) many cannot, or choose not to utilize the conditions within the sea grass at low tide. Fish are likely to have species-specific relationships to tide, ranging from physiological factors associated with changing environmental conditions (increased temperature and UV irradiance) (Ayvazian et al., 1992), food resource use (e.g. movement of macro and meiofauna deep into the sediments to themselves survive changing conditions) (Sanchez-Jerez et al., 2002) or predation avoidance (e.g. limited water volume making avian predation a greater risk) (Hyndes et al., 1996; Young et al., 1997).

Increased food availability (small fish and invertebrates) in sea grass habitats is the most likely explanation for the increased presence of large predatory reef species (Kochzius, 1999) such as *Hemirhamphus far*, *Caranx melampygus* and *Lutjanus* spp. at high tide. Research on diel cycles within the Wakatobi MNP conducted at high tide found predators to make up a significant proportion of the fish assemblage (Unsworth et al., 2007). Research in other regions has found tidal cycles to influence the activity patterns of larger predators (fish and avian) as they forage on the tidally migrating smaller fish species, which have higher abundance at high tide (Sogard et al., 1989). Numerous great-billed herons (*Ardea sumatrana*) are commonly sited hunting for prey at low tide within the sea grass beds surrounding Hoga (Unsworth

personal observation) indicating avian predation could be an important pressure influencing day-time shallow water fish.

Coral habitats had much lower variation in fish abundance, richness and assemblage composition with tidal height compared with sea grass habitats. This is likely the result of their more environmentally stable sub-tidal location. Of particular interest were observed decreases in the density of particular fish groups in sea grass with ebbing tide (*L. harak*, *Cheilodactylus inermis* and *Gerres* spp.), with corresponding increases in their abundance within coral habitats, suggesting migration between habitats as the tide recedes. These fish groups are all crustacean feeders (e.g. amphipods, brachyurans, natantians) (Froese & Pauly, 2006). *Lethrinus harak* is also a partial consumer of polychaetes, while *C. inermis* is a consumer of gastropods (Hutomo & Peristiwady, 1996). Small crustaceans also undertake tidal and diurnal inter-habitat migrations (Penn, 1975). Such migrations may additionally have secondary effects on the foraging patterns of predatory fish.

Habitat affects on fish assemblages

Sea grass fish assemblages in the Indo-Pacific are commonly dominated by Siganidae, such as *Siganus canalisulatus* (Kuriandewa et al., 2003) or Lethrinidae, Siganidae and Scaridae (Gell & Whittington, 2002). This study found Engraulidae spp. and *Lethrinus harak* to be the dominant species. The fish assemblages reported in the present study are similar to those in Lombok (Indonesia) reported by Hutomo & Peristiwady (1996), yet contrast with those from other Indonesian and Indo-Pacific regions (Marasabessy & Hukom, 1989; Kuriandewa et al., 2003). This indicates that Indonesian sea grass beds have a highly variable fish fauna based on a combination of habitat and environmental factors mediated at local, regional and bio-regional scales. Such factors may also be altered by temporal factors associated to seasonality (wet and dry) or variability in the tidal patterns throughout the year. Temporal variation in tropical sea grass beds has received little attention and requires further study.

Due to the large influence of tide on fish assemblages within these shallow water habitats fish were classified into categories of tidal habitat use. The majority of fish groups were defined as 'Groups that are ubiquitous to all habitats and tidal states' suggesting that the majority of the fish within sea grass utilize both sea grass and coral habitats indicating a high-level of inter-habitat connectivity.

CONCLUSIONS

In conclusion this study finds fish assemblages of an Indo-Pacific sea grass and coral shallow water ecosystem to be in a dynamic state dominated by transient fish. Research confirms the importance of small tidal changes in structuring the fish fauna of Indo-Pacific sea grass habitats. These diverse fish assemblages have complex behavioural patterns that include tidal migrations to nearby habitats. This study demonstrates connectivity between fish assemblages inhabiting coral and sea grass habitats. These results should therefore have application to ecosystem level management.

The authors thank the staff at the Hoga Marine Research Centre for their logistic support and Operation Wallacea who provided financial support for travel and fieldwork. Richard Unsworth is grateful to Dr Tim Coles and Operation Wallacea for providing a doctoral studentship.

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Submitted 2 November 2006. Accepted 26 July 2007.