High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats

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ABSTRACT: Marine ecosystems throughout the Indo-Pacific region are highly threatened by anthropogenic stressors, yet the faunal interaction between different component habitats remains poorly understood. This information is vital as stress on one inter-connected habitat may have cascade effects on other habitats. The present study focused on the impact of inter-habitat connectivity on seagrass fish assemblages, specifically between seagrass, mangrove and reef habitats. Fish were sampled using a seine net within 3 seagrass habitats (seagrass near to reef, seagrass near to reef and mangrove, and seagrass near to mangrove) within eastern Indonesia. Visual surveys were also conducted within mangrove habitats. Fish abundance and species richness in seagrass beds in close proximity to mangroves was at least twice that found in seagrass beds that were distant from mangrove habitat. The trophic structures of seagrass fish assemblages change from being dominated by predators and omnivores close to the reef, to assemblages high in planktivores and herbivores close to mangroves. We found that mangroves enhance the fish assemblages of nearby seagrass beds probably by increasing the availability of shelter and food provision. This study indicates that Indo-Pacific seagrass beds play an important fish nursery role, which is influenced by the availability of nearby reef and mangrove habitats. Our research supports the need for ecosystem-level management of shallow water tropical habitats, but also suggests that successful management requires local-level knowledge of habitat interactions to successfully enhance or conserve fish assemblages.

KEY WORDS: Mangrove · Seagrass · Coral reef · Connectivity · Fish · Trophic · Indo-Pacific · Indonesia

INTRODUCTION

Seagrass beds have enormous biological, economic and social value (Costanza et al. 1997, de la Torre-Castro & Rönnbäck 2004), yet they are currently facing an unprecedented level of anthropogenic stress and degradation (Orth et al. 2006). At present, our knowledge of these systems remains poor for the majority of bioregions (Kenworthy 2000, Sheaves 2005, Orth et al. 2006). This is particularly evident within the Indo-

Pacific region, and more specifically for the southeast Asian region (Sheaves 2005, Unsworth et al. 2007).

Connectivity between tropical shallow water habitats influences many fish and crustacean assemblages (Nagelkerken et al. 2000, Mumby et al. 2003). In this study we define inter-habitat connectivity as the migration of fauna between habitats, both at different stages of their life cycle (Cocheret de la Morinière et al. 2003, Nakamura & Sano 2004) and on a daily basis following diel and tidal cycles (Sogard et al. 1989, Unsworth et al.

2007). Most previous tropical marine habitat connectivity studies have focused on coral reefs (Nagelkerken et al. 2001, Nakamura & Sano 2004, Mumby 2006), with the impact of habitat connectivity on seagrass fish assemblages remaining poorly understood (Dorenbosch et al. 2006). Such information is important for ecosystem-level management and is vital for conserving habitats that are heavily exploited and widely threatened (Sheaves 2005, Orth et al. 2006). The few available studies from the Indo-Pacific region have focused on the influence of the spatial configuration of adjoining habitats to seagrass beds and their impact on fish assemblages and have indicated varying degrees of connectedness, yet no ecological basis has been provided to explain the observed patterns (Kochzius 1999, Dorenbosch et al. 2006); therefore, understanding of seagrass fish assemblage connectivity is poor, particularly within the diverse Indo-Pacific region (Kochzius 1999, Nakamura et al. 2004, Unsworth et al. 2007).

Limited knowledge of seagrass fish assemblages is also exacerbated by studies using protocols that exclude diel sampling. Although it is well recognised that shallow water habitats experience diel faunal migrations (Nagelkerken et al. 2000, Unsworth et al. 2007), the majority of research on seagrass fish assemblages has not included diel sampling (e.g. Nagelkerken et al. 2000, Mumby et al. 2003, Dorenbosch et al. 2006, Verweij et al. 2006). Exclusive day-time sampling has the potential to under-sample an assemblage by over 45% (Unsworth et al. 2007). Research is required that provides sound ecological evidence to explain the observed variability in seagrass fish assemblages of the Indo-Pacific, a region containing the world's most diverse marine fauna.

Habitat connectivity may also result from export of organic carbon and nutrients; for example, mangroves are net exporters of organic material (Boto & Bunt 1981, Nedwell et al. 1994). The organic material may be locally exported from mangroves to nearby tidal flats (Lee 1995, Meziane & Tsuchiya 2000) and has the potential to stimulate the food web resulting in increased faunal abundance (Alongi 1990). We propose that a stimulated food web may enhance local fish assemblages.

When inundated by tide, mangroves provide fish from seagrass beds and reefs with rich and productive areas where they may forage for food; additionally they provide structure and shade that may serve as protection from predation (Laegdsgaard & Johnson 2001, Nagelkerken & van der Velde 2002, Verweij et al. 2006). For fish migrating between habitats, the journey between a seagrass bed and a proximate mangrove will incur a lower risk of predation and reduced energetic cost compared with a distant mangrove (Sheaves 2005). We hypothesise that the proximity of feeding grounds and areas of shelter, such as man-

groves or reefs, to seagrass beds may, therefore, enhance fish abundance or richness by providing individuals with favourable spatial characteristics associated with those nearby habitats compared with those lacking such nearby habitats. Reefs may also affect seagrass fauna by providing clear oceanic water from deeper water that has the potential to increase the flushing rate of seagrass beds and potentially act as a source of additional zooplankton and fish larvae. We theorize that nearby reefs may increase the abundance of predatory reef fish undergoing diel and tidal feeding migrations (Kochzius 1999).

Although mangroves are generally considered important habitat for juvenile reef fish (Nagelkerken & van der Velde 2002, Mumby et al. 2003), this is not the case within the Indo-Pacific, where in some cases mangroves play a very limited nursery role for coral reef fish species (Laroche et al. 1997, Dorenbosch et al. 2006). It may be that mangroves have indirect or secondary impacts on the juvenile fish in adjacent habitats. This is particularly important in light of recent findings that juvenile fish settlement is selective, indicating that habitat characteristics are an important determinant of the structure of juvenile fish assemblages (Pollux et al. 2007). Juvenile fish in the presence of 2 nursery habitats (e.g. mangrove and seagrass) may undertake ontogenetic migrations between habitats to allow for longer periods of development within areas of relative shelter, rather than facing potentially higher reef predation rates; this also allows for the consumption of particular food items that enhance juvenile growth (Cocheret de la Morinière et al. 2003, Nakamura et al. 2003). Research in the Caribbean has recently documented that the value of seagrass and mangrove habitats as a juvenile habitat should not be generalised *a priori*, since habitat configuration may interact with the degree of connectivity between seagrasses, mangroves and coral reefs (Dorenbosch et al. 2007). By providing areas of temporary shelter or foraging it might be expected that where seagrass, mangrove and reef habitats are closely connected, a more beneficial ecosystem is created compared with one missing these separate components. As a result we postulate that seagrass beds adjacent to mangroves and reefs will have higher juvenile fish abundance than those seagrass beds far away.

The present study used the example of the Wakatobi Marine National Park (MNP), Indonesia (Fig. 1) to provide a detailed analysis of the impact of adjacent habitats on the fish assemblages of seagrass beds. We aimed to examine how the presence or absence of adjacent mangrove and reef habitats influences seagrass fish assemblages. To do this we compared the abundance, species richness, assemblage structure, and trophic composition of fish using seagrass habitats in close proximity to mangroves and coral reefs.
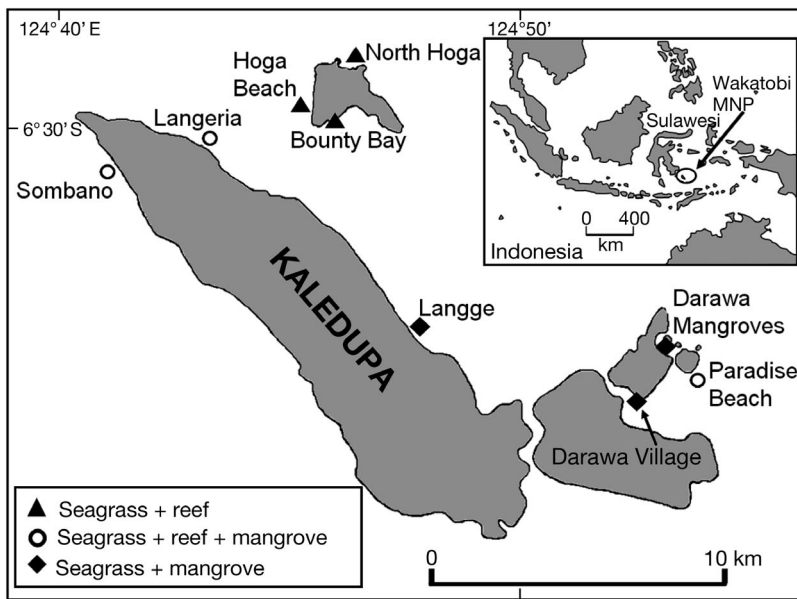
Fig. 1. Location and habitat type of the 9 study sites within the Kaledupa subregion of the Wakatobi Marine National Park (MNP), Indonesia

MATERIALS AND METHODS

Study area. Investigations of habitat influences on seagrass fish assemblages were conducted between July and August 2006 on intertidal seagrass beds throughout the Kaledupa subregion of the Wakatobi MNP (Fig. 1). Three broad categories of seagrass were identified: (1) seagrass beds between fringing reefs and the shoreline (Sg Cor); (2) seagrass beds between fringing reefs and mangroves (Sg Cor-mg); and (3) seagrass beds surrounding mangroves, but far from reefs (Sg Mg). Three independent sites of each habitat type were used throughout the area (Fig. 1). Sites near to reefs were between 0.5 and 1.0 km from the reef, while those that were far from the reef were between 1.5 and 3.0 km away. Sites far from mangroves were between 3.5 and 6.0 km away. These distances were considered to be sufficient to reduce any mangrove nutrient or organic matter out-welling to negligible levels (Lee 1995).

Of the 9 sites where observations were made (Fig. 1), Langge, Langeria, Bounty Bay, Sombano, Darawa Village and Darawa mangroves were all located in bays sheltered from the prevailing weather and currents, with reduced water turbulence and movement. Paradise Beach, north Hoga and Hoga Beach were all exposed locations, offering little shelter. Although fishing is conducted within all areas of the MNP there is no evidence to suggest that fishing pressure varies between sites used in this study.

Seagrass and intertidal mangroves are abundant within the Kaledupa subregion of the Wakatobi MNP, dominating large areas of the shoreline and covering large coastal areas (>50 km^2). Seagrass beds in this region are dominated by 2 species, *Thalassia hemprichii* (Ehrenberg) and *Enhalus acoroides* (L.f.) Royle (Unsworth et al. 2007). Low shore intertidal mangroves of the region are dominated by *Rhizophora* spp. mixed with lower densities of *Avennicia* spp. and *Brugiera* spp. higher up the shore. Seagrass is abundant in both the outer edges of the mangrove and the internal channels. The Wakatobi MNP experiences semidiurnal tides with maximum amplitudes of 2.3 m. The low tides always empty the mangroves of water and also expose large areas of seagrass to the air on the larger spring tides.

Habitat and environmental data. Percentage cover of seagrass and other live substrate was estimated at all sites (20 replicate 0.25 m^2 quadrats placed arbitrarily). 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 6 daylight hours (10:00 to 16:00 h). Water clarity was measured using a horizontal Secchi disk and a measuring tape whilst snorkelling. Salinity was measured at each site using an analogue refractometer. Six sediment mini-cores were collected (30 mm diameter) and transported to the laboratory for analysis of total organic content (TOC) and particle size. Percentage TOC of the sediment was calculated by incinerating samples in a muffle furnace set at 550°C. Sediment particle size was determined using a Malvern longbed Mastersizer X and the parameter phi (Φ, an inverse descriptor of sediment porosity) was calculated (Folk 1966).

Beach seining. Beach seine netting is an effective method for sampling diurnal near-shore seagrass fish assemblages (Cocheret de la Morinière et al. 2003, Unsworth et al. 2007). However, there are concerns that seine nets under-sample fast swimming and pelagic fish species, such as jacks and trevallies, and also small fishes such as gobies and blennies (Gell & Whittington 2002). Additionally, during daylight hours large fish may be better at net avoidance thereby biasing the sampled community structure. Many of these drawbacks of beach seine netting have been discussed by English et al. (1997) and Nagelkerken et al. (2001). Despite these known problems, this approach remains

one of the only non-destructive methods for quantitatively sampling night-time fish populations. Guest et al. (2003) found that seine nets are more appropriate than trawling or trapping to determine the relative proportion of species in a seagrass habitat and estimating the density of most species.

Seine netting was conducted at ~1.2 ± 0.2 m above chart datum during the day (09:00 to 16:00 h) and at night (19:00 to 01:00 h). This was the most appropriate water height for the seine net to work effectively. Ten replicate seine net samples (16 × 1.4 m, 2 × 1 m cod end, 23 mm stretched mesh) were hauled both day and night for 50 m through the seagrass into the shore. This method created a 12 m 'arc' that sampled an area of seagrass of approximately 600 m^2. All fish caught were identified to species where possible and then returned to the sea at least 100 m away from the sampling point. Sample independence was maintained as all seine hauls were at least 5 m apart and conducted over 2 or 3 sampling trips. No adjacent hauls were conducted consecutively, which allowed sufficient time for the site to recover from sampling disturbance.

Underwater visual census (UVC) within mangroves. UVC was used to determine a minimum estimate of the use of mangrove habitats by juvenile and adult fish observed within seagrass habitats. This was a minimum estimate as no night-time sampling was possible with this technique. Sampling fish assemblages within dense mangroves is logistically difficult. Nets can only catch fish as they move in or out of the habitat and do not create quantifiable density estimates, and traps have high selectivity, whilst the use of poisons (e.g. rotenone) are not appropriate within areas of high conservation value. Day-time UVC was chosen as this method provides fish richness, size and density estimates. Difficulties associated with the use of UVC within mangroves, such as observer bias and fish behaviour, are extensively discussed by Nagelkerken et al. (2002). Before the study began, a training exercise was conducted to reduce observer bias (see English et al. 1997). At all of the sites in close proximity to mangroves (Fig. 1) 6 independent 50 × 2 m transects were conducted within dense mangrove forest. These were conducted at high tide (>2 m) to ensure complete flooding of the habitat. Transects were measured with a tape. It was not always possible to complete the entire 50 m transect due to the high density of the mangrove; therefore, transects were often discontinued and restarted at the next available location.

Data analysis. For the data analysis a distinction had to be made between juvenile and adult fish densities. Fish were classified using maturity data from FishBase (when available) or using the commonly applied 'rule of thumb' that individuals smaller than one-third of the maximum species' length were juvenile (Nagelkerken & van der Velde 2002, Lugendo et al. 2005, Dorenbosch et al. 2006). For species with a maximum length >90 cm, individuals were recorded as juveniles when <30 cm long. All maximum length data were obtained from FishBase (Froese & Pauly 2006). To analyse trophic status patterns of the fish assemblages between different habitat types all species were assigned to feeding categories based on information from a number of sources providing data for both adults and juveniles (Hutomo & Peristiwady 1996, Khalaf & Kochzius 2002, Nakamura et al. 2003, Froese & Pauly 2006). After analysis, the 40 most abundant fish species were categorised into 1 of 3 groups of habitat association (species associated to seagrass near mangrove, species associated to seagrass near mangrove and reef, no habitat associations). This simple categorisation was only based on the species having a proportionally (~50%) higher mean day and night abundance within that specific habitat over other habitats.

All mean summary statistics were calculated with their standard error. A 2-way nested General Linear Model (GLM) ANOVA on $\log_{10} (x + 1)$-transformed data was used to analyse any differences in fish abundance, species richness and individual trophic categories between different habitats and sites. Analysis of differences in fish assemblage structure between habitat type and time of day was conducted using multivariate non-metric multidimensional scaling ordination (MDS) and Bray-Curtis cluster analysis using the computer package PRIMER (Clarke & Warwick 1994). The Bray-Curtis similarity index was applied on square-root transformed data (to down-weigh the influence of rare and extremely abundant species) to generate a rank similarity matrix, which was then converted into an MDS ordination. 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 to be superimposed upon the MDS ordination (Clarke & Gorley 2006). A 2-way analysis of similarities (ANOSIM) was used to investigate differences identified from MDS and CLUSTER (Clarke & Warwick 1994). ANOSIM was also used to determine overall significant differences in trophic structure of fish assemblages.

RESULTS

Habitat and environmental variables

Variability existed in both the seagrass habitat structure and the environmental conditions among the 9 sites (Table 1). Seagrass cover was mostly around 70 ± 10% and was highest at the North Hoga site (Sg Cor)

Table 1. Environmental and habitat variables (mean ± SE) of 9 seagrass beds used in the present study located within the Kaledupa subregion of Wakatobi Marine National Park (MNP), Indonesia. Sg Cor = seagrass + reef, Sg Cor-mg = seagrass + reef + mangrove, Sg Mg = seagrass + mangrove, TOC = total organic content

Site	Habitat type	Sediment size (Φ)	Sediment TOC (%)	Seagrass cover (%)	Water clarity (m)	Temperature (°C)	Light intensity (lux)	Salinity (‰)
Bounty Bay	Sg Cor	2.5 ± 0.3	5.1 ± 0.3	73.2 ± 5.0	5.5 ± 0.2	31.5 ± 0.1	45697 ± 4658	35 ± 3
Hoga Beach	Sg Cor	1.8 ± 0.1	3.7 ± 0.1	70 ± 3.2	5.8 ± 0.4	30.5 ± 0.1	54423 ± 8402	35 ± 3
North Hoga	Sg Cor	0.3 ± 0.3	4.0 ± 0.4	79.5 ± 3.0	5.6 ± 0.1	29.5 ± 0.1	52132 ± 4631	34 ± 2
Langeira Beach	Sg Cor-mg	2.4 ± 0.4	5.3 ± 0.3	79 ± 3.8	5.3 ± 0.2	28.4 ± 0.0	44950 ± 4422	34 ± 2
Paradise Beach	Sg Cor-mg	1.3 ± 0.1	4.3 ± 0.2	68.7 ± 4.2	10.7 ± 0.4	27.7 ± 0.1	55234 ± 7654	–
Sombano Beach	Sg Cor-mg	2.0 ± 0.3	6.2 ± 0.2	78 ± 2.8	4.7 ± 1.0	30.4 ± 0.0	43779 ± 6031	–
Darawa Mangroves	Sg Mg	3.9 ± 0.1	4.9 ± 0.2	56.7 ± 1.6	4.5 ± 0.1	28.3 ± 0.0	46024 ± 3908	–
Derawa Village	Sg Mg	1.5 ± 0.2	4.4 ± 0.4	70.3 ± 2.8	6 ± 0.1	28.3 ± 0.0	38888 ± 3177	33 ± 2
Langge	Sg Mg	2.7 ± 0.1	4.3 ± 0.2	48.8 ± 6.2	2.9 ± 0.2	32.2 ± 0.1	17376 ± 9298	–

and lowest in Langge (Sg Mg) where water clarity and light intensity were also lowest. Water clarity (Secchi depth) was generally 5 ± 1 m except in Paradise Beach (Sg Cor-mg) where water was very clear (10.7 ± 0.4 m) and at Langge (Sg Mg) where water was highly turbid (2.9 ± 0.2 m). Temperature and salinity did not show large inter-site variability (Table 1). The sediment content changed between the different sites indicating differences in their physical condition. Low values of Φ (an inverse descriptor of sediment porosity) at North Hoga (Sg Cor) and Paradise Beach (Sg Cor-mg) indicated they are high energy sites whereas the fine sediment at the Darawa mangroves, Bounty Bay (Sg Cor), Langeira (Sg Cor-mg) and Langge (Sg Mg) suggested that these sites may have had low water movement. Organic content of the sediment was also highly variable among sites, with the highest values recorded at Sombano (Sg Cor-mg), Langeira (Sg Cor-mg) and Bounty Bay (Sg Cor).

Fish assemblages

Total fish assemblage. Fish abundance and species richness in seagrass beds were at least 2 times greater in those habitats in close proximity to a mangrove relative to those far from mangroves (Table 2). These differences were highly significant during both day and night (Table 3). Significant site and habitat interactions

Table 2. Summary statistics (mean ± SE) for fish assemblages sampled within seagrass beds during the day and at night at 9 sites of 3 habitat types (Sg Cor = seagrass + reef, Sg Cor-mg = seagrass + reef + mangrove, Sg Mg = seagrass + mangrove) located within the Kaledupa subregion of Wakatobi MNP, Indonesia. Group means for all 3 sites for each habitat type are shown in **bold**

Habitat type Site	Fish abundance (no. per 600 m^2)		Fish species richness (no. species per 600 m^2)	
	Night	Day	Night	Day
Sg Cor				
Bounty Bay	15.6 ± 2.8	21.8 ± 25.0	5.6 ± 0.7	4.0 ± 1.5
Hoga Beach	19.2 ± 7.0	37.3 ± 11.3	5.5 ± 1.0	4.4 ± 0.6
North Hoga	4.6 ± 1.2	1.5 ± 0.2	2.1 ± 0.6	1.5 ± 0.2
Mean	**8.7 ± 2.4**	**7.3 ± 2.2**	**3.6 ± 0.5**	**2.8 ± 0.3**
Sg Cor-mg				
Langeria	27.8 ± 5.7	23.8 ± 8.7	8.6 ± 1.1	7.2 ± 0.9
Paradise Beach	9.7 ± 1.2	5.2 ± 1.2	4.1 ± 0.7	2.9 ± 0.4
Sombano	92.8 ± 11.4	44.3 ± 11.3	10.9 ± 0.6	6.4 ± 0.6
Mean	**36.2 ± 7.5**	**18.9 ± 3.3**	**6.9 ± 0.7**	**5.2 ± 0.5**
Sg Mg				
Darawa Village	41.5 ± 6.2	31.8 ± 15.6	11.7 ± 0.9	5.7 ± 0.7
Darawa Mangrove	101.6 ± 18.1	63.8 ± 17.9	11.0 ± 0.8	6.5 ± 0.5
Langge	25.3 ± 4.0	10.5 ± 3.6	8.0 ± 0.7	3.5 ± 0.8
Mean	**39.0 ± 5.1**	**12.4 ± 1.6**	**9.4 ± 0.5**	**4.7 ± 0.4**

Table 3. Two-way GLM ANOVA and ANOSIM between 3 seagrass habitat types (seagrass + reef, seagrass + reef + mangrove, seagrass + mangrove) for differences in fish abundance, fish species richness and fish assemblage structure during the day and at night in the Kaledupa subregion of the Wakatobi MNP, Indonesia. Fish were sampled both day and night using a beach seine net. All Tukey's pairwise inter-habitat comparisons were significantly different (p < 0.001)

Source	df	Fish abundance			Fish species richness			Fish assemblage	
		MS	F	p	MS	F	p	Global r	p
Day									
Habitat	2	1776.4	11.31	<0.001	91.039	23.99	<0.001	23%	<0.01
Site	1	19.4	0.12	0.73	4.466	1.18	0.28		
Interaction	2	567.3	3.61	<0.05	29.422	7.75	<0.001		
Night									
Habitat	2	203.19	28.79	<0.001	6514.8	8.06	<0.001	29%	<0.001
Site	1	9.07	1.28	0.26	166.3	0.21	0.65		
Interaction	2	71.26	10.10	<0.001	1527.5	1.89	0.16		
Total	89								

illustrated that not all sites conformed to this pattern indicating a site effect (Tables 2 & 3). Low fish abundance at 2 of the 6 sites in close proximity to mangroves (Langge and Paradise Beach) was masked by high abundance at the other 4 sites. Species richness displayed less intra-habitat variability; only 1 site (Paradise Beach) did not conform to the overall trend of increasing richness with the presence of mangroves (Table 2). The fish assemblage also changed significantly among the 3 different habitat types for both day and night (Table 3). Fish assemblage structure differed significantly between day and night, and between seagrass beds close to mangroves and those far from mangroves (p < 0.001), but no differences in fish assemblage was observed between seagrass beds with mangroves and reefs (Sg Cor-mg) compared with those associated with just mangroves (Sg Mg).

Adult and juvenile assemblages. Seagrass beds in close proximity to both mangrove and reef habitats (Sg Cor-mg) had at least twice the number of juvenile fish than those with only 1 adjacent habitat (Fig. 2). This increase was fish family dependent (Fig. 3) as higher densities of Acanthuridae, Apogonidae and Plotosidae were observed when all 3 habitats were in close proximity (Sg Cor-mg), but Lethrinidae and Mullidae had greater abundance in the absence of reef proximity (Sg Mg). Some families, such as Muglidae and Carangidae, had greater abundance in the absence of mangroves (Sg Cor). As a proportion of the total fish assemblage, juvenile fish comprised ~14% except in seagrass adjacent to both mangroves and coral reefs (Sg Cor-mg) where 43% of the assemblage were juveniles.

A total of 114 species of fish were identified. *Atherinomorus lacunosus*, *Naso vlamingii*, *Apogon melas* and *Apogon ceramensis* were the most abundant and were all associated with seagrass that had mangroves in close proximity (Table 4). Of the 40 most abundant

fish species, 17 were associated with seagrass beds in close proximity to mangroves, yet far from reefs (Sg Mg), while 11 species were associated with seagrass close to both mangroves and reefs (Sg Cor-mg) and 5 species associated with seagrass close to reefs (Sg Cor) (Table 4).

Sixty-three species of fish, at a density of 160 ± 62 fish per 600 m², were recorded within mangrove habitats and were characterised by high variability due to very large shoals of *Atherinomorus lacunosus* and *Apogon ceramensis* (2 species that were highly abundant within seagrass). Of these species 38 were also recorded within seagrass habitats (Table 4) indicating that a minimum (daytime estimates only) of 30% of all species using seagrass also use mangrove habitat.
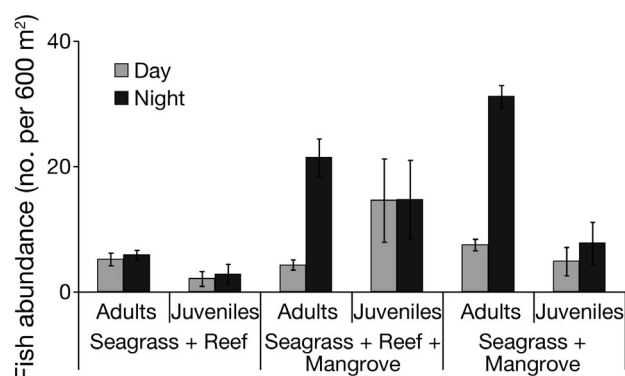

Fig. 2. Mean (±SE, n = 30) abundance of all juvenile fish shown as a comparison with total adult fish abundance within the 3 seagrass habitat types in the Kaledupa subregion of the Wakatobi MNP, Indonesia. All results are averaged over 3 sites and 10 repeat samples using a beach seine net for each habitat for both day and night. Fish were classified as juvenile using maturation data when available (Froese & Pauly 2006) or when necessary on the basis of being less than one-third of the maximum adult length (Nagelkerken & van der Velde 2002)
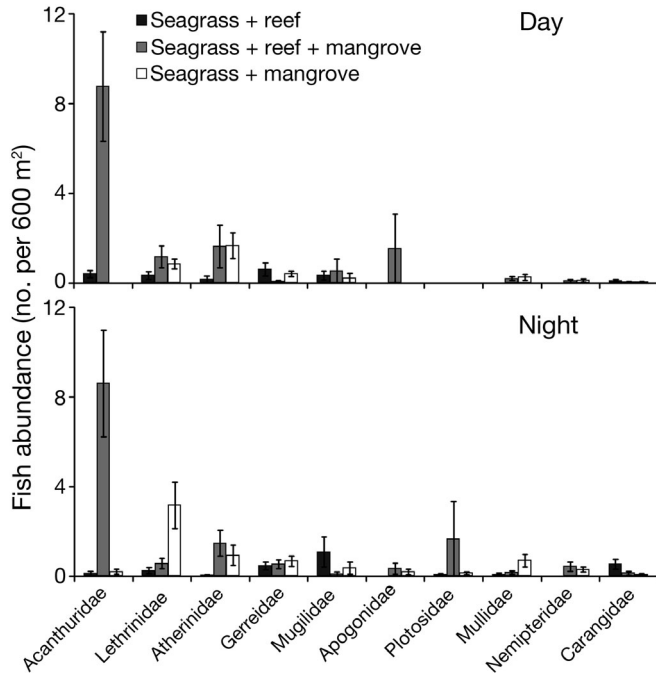
Fig. 3. Mean (±SE, n = 30) abundance of the 10 most abundant families of juvenile fish during both day and night within 3 seagrass habitat types in the Kaledupa subregion of the Wakatobi MNP, Indonesia. All results are averaged over 3 sites and 10 repeat samples using a beach seine net for each habitat for both day and night. Fish were classified as juvenile using maturation data when available (Froese & Pauly 2006) or when necessary on the basis of being less than one-third of the maximum adult length (Nagelkerken & van der Velde 2002)

Trophic structure. Seagrass beds in close proximity to mangroves (Sg Cor-mg and Sg Mg) differed significantly in their trophic structure from those without mangroves nearby (Sg Cor) (Global r = 0.17, p < 0.01). The time of day also significantly altered the trophic structure in all habitat types (Global r = 0.19, p < 0.01). Predatory fish were a dominant component of the fish assemblage in all types of seagrass bed during both day and night; these fed on both fish and invertebrates or exclusively on invertebrates (Fig. 4). Planktivorous fish were also highly abundant and mostly (>90%) consisted of 1 highly abundant seagrass/ shoreline dwelling species, *Atherinomorus lacunosus*. Seagrass beds in close proximity to both reefs and mangroves were the only habitat that contained large numbers of herbivores; this large increase in herbivorous fish was dominated (>90%) by juveniles of the commercially important reef fish, *Naso vlamingii*. Night-time resulted in a significant increase in predatory fish (Table 5) feeding on both fish and invertebrates or exclusively on invertebrates; this was particularly evident within seagrass habitats that were adjacent to mangroves, but far from reefs (Sg Mg) (Fig. 4).

A significant positive correlation was observed between total fish abundance and sediment TOC content (Pearson's coefficient = 60%, p < 0.05, df = 8) (Fig. 5). Significant correlations were also observed between the abundance of predatory fish and sediment porosity Φ, exclusive invertebrate feeders (Pearson's coefficient = 63%, p < 0.01, df = 8), and invertebrate and fish feeders (Pearson's coefficient = 40%, p < 0.05, df = 8). Microhabitat variability (flora), salinity, water clarity and temperature showed no correlation with the observed fish abundance or richness.

DISCUSSION

This study found that seagrass fish fauna increased in abundance and richness, and had different trophic and assemblage structures when in the proximity of mangrove (Tables 2 & 3). Seagrass habitats were also found to be important for juvenile fishes, particularly when in close proximity to reefs and mangroves (Table 4, Figs. 2 & 3). The present study also suggests that local environmental conditions may have additional impacts on the connectivity of seagrass beds with nearby habitats (Fig. 5).
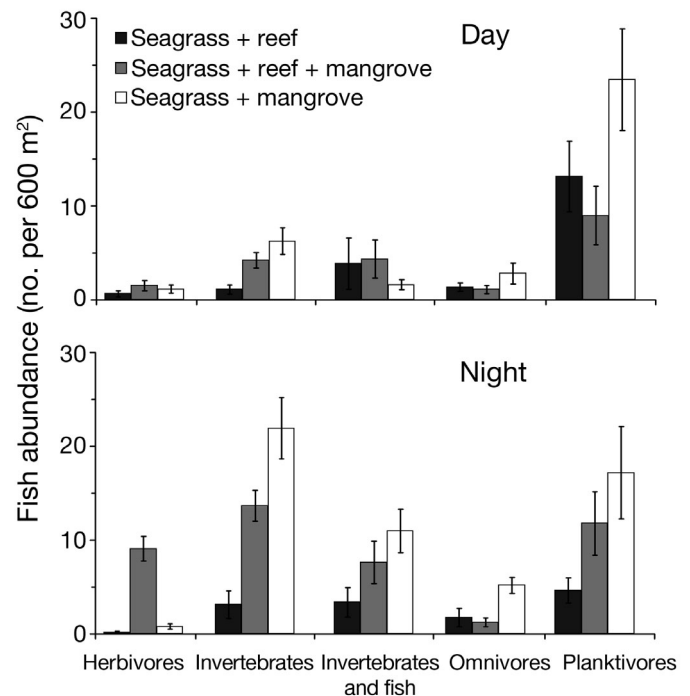

Fig. 4. Mean (±SE, n = 30) abundance of different trophic feeding categories during the day and at night within 3 seagrass habitat types (seagrass + reef, seagrass + reef + mangrove, seagrass + mangrove). All sites are in the Kaledupa subregion of the Wakatobi MNP, Indonesia. Results are averaged over 3 sites and 10 repeat samples using a beach seine net for each habitat for both day and night

Table 4. Mean (±SE, n = 60) abundances during day and night (no. per 600 m²) of the 40 most abundant species (and the abundance of juveniles) in seagrass beds sampled in 3 seagrass habitat types (seagrass + reef, seagrass + reef + mangrove, seagrass + mangrove) in the Kaledupa subregion of the Wakatobi MNP, Indonesia. Densities of seagrass fish observed within mangrove using visual daytime transects are also included. Fish in seagrass were sampled both day and night using a beach seine net. For explanation of categories refer to 'Materials and methods'. Fish were classified as juveniles using maturation data when available (Froese & Pauly 2006) or when necessary on the basis of being less than one-third of the maximum adult length (Nagelkerken & van der Velde 2002)

| | Seagrass + reef | | | | Seagrass + reef + mangrove | | | |
| | Night | | Day | | Night | | Day | |
	All fish	Juvenile fish	All fish	Juvenile fish	All fish	Juvenile fish	All fish	Juvenile fish
Species associated to seagrass near mangrove and reef								
Apogon fuscus Quoy & Gaimard, 1825	0.27 ± 0.12	–	0.03 ± 0.03	–	4.57 ± 1.97	–	–	–
Apogon melas Bleeker, 1848	0.87 ± 0.65	–	–	–	9.43 ± 1.08	–	0.03 ± 0.03	–
Cheilodipterus isostigmus Schultz, 1940	0.13 ± 0.09	–	–	–	1.37 ± 0.34	–	–	–
Cheilodipterus quinquelineatus Cuvier, 1828	0.03 ± 0.03	–	–	–	2.07 ± 1.09	0.27 ± 0.23	1.60 ± 1.53	1.53 ± 1.53
Choerodon anchorago Bloch, 1791	–	–	0.03 ± 0.03	–	0.03 ± 0.03	0.03 ± 0.03	0.50 ± 0.19	–
Halichoeres papilionaceus Valenciennes, 1839	–	–	–	–	–	–	0.87 ± 0.23	–
Lethrinus harak Forsskål, 1775	0.27 ± 0.23	–	0.30 ± 0.60	–	0.27 ± 0.20	–	1.37 ± 0.49	–
Naso vlamingii Valenciennes, 1835	0.10 ± 0.10	0.10 ± 0.10	0.33 ± 0.34	0.33 ± 0.18	8.60 ± 1.19	8.60 ± 1.19	8.73 ± 1.56	8.73 ± 1.56
Plotosus lineatus Valenciennes, 1840	–	0.07 ± 0.04	–	–	1.67 ± 1.67	–	–	–
Siganus virgatus Valenciennes, 1835	–	–	–	–	0.30 ± 0.17	–	0.27 ± 0.16	–
Syngnathoides biaculeatus Bloch, 1785	0.03 ± 0.03	–	0.10 ± 0.08	–	0.90 ± 0.29	–	1.83 ± 0.52	–
Species associated to seagrass near mangrove								
Acreichthys tomentosus Linnaeus, 1758	0.03 ± 0.03	–	–	–	0.30 ± 0.14	0.03 ± 0.03	0.17 ± 0.07	–
Apogon ceramensis Bleeker, 1852	–	–	–	–	0.30 ± 0.17	–	–	–
Atherinomorus lacunosus Forster, 1801	4.40 ± 1.30	0.03 ± 0.03	12.93 ± 11.48	0.17 ± 0.17	7.23 ± 1.61	1.47 ± 0.56	5.57 ± 4.74	1.63 ± 0.94
Caranx ignobilis Forsskål, 1775	0.47 ± 0.23	0.47 ± 0.23	0.10 ± 0.17	0.10 ± 0.08	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.03
Centriscus scutatus Linnaeus, 1758	–	–	0.10 ± 0.07	–	–	–	–	–
Centrogenys vaigiensis Quoy & Gaimard, 1824	–	–	–	–	–	–	–	–
Cheilodipterus macrodon Lacepède, 1802	0.07 ± 0.07	–	0.27 ± 0.34	–	0.47 ± 0.20	–	–	–
Dischistodus fasciatus Cuvier, 1830	0.03 ± 0.03	–	0.07 ± 0.07	0.07 ± 0.07	0.10 ± 0.05	–	0.07 ± 0.07	–
Hyporhamphus dussumieri Valenciennes, 1847	–	–	–	–	0.03 ± 0.03	–	–	–
Lethrinus obsoletus Forsskål, 1775	–	–	–	–	0.13 ± 0.13	–	–	–
Lethrinus ornatus Valenciennes, 1830	–	–	0.03 ± 0.03	–	0.13 ± 0.13	0.03 ± 0.03	0.03 ± 0.03	–
Lethrinus variegatus Valenciennes, 1830	0.27 ± 0.14	–	0.20 ± 0.22	0.03 ± 0.03	0.27 ± 0.18	0.13 ± 0.13	0.13 ± 0.09	–
Liza vaigiensis Quoy & Gaimard, 1825	1.00 ± 0.87	–	0.33 ± 0.55	0.03 ± 0.03	0.10 ± 0.10	0.13 ± 0.13	0.53 ± 0.53	0.03 ± 0.03
Monacanthus chinensis Osbeck, 1765	–	–	–	–	–	–	–	–
Neoniphon argenteus Valenciennes, 1831	0.47 ± 0.18	–	–	–	0.13 ± 0.09	–	–	–
Neoniphon sammara Forsskål, 1775	0.33 ± 0.16	–	–	–	0.13 ± 0.07	–	–	–
Paraplotosus albilabris Valenciennes, 1840	0.07 ± 0.04	–	–	–	–	–	–	–
Parupeneus macronema Lacepède, 1801	–	0.07 ± 0.07	–	–	0.13 ± 0.10	0.07 ± 0.07	0.10 ± 0.08	0.10 ± 0.10
Pseudomonacanthus macrurus Bleeker, 1857	0.23 ± 0.11	–	0.63 ± 0.51	–	0.30 ± 0.19	–	0.63 ± 0.23	–
Scarus sp. 1	–	–	–	–	–	–	–	–
Scolopsis trilineatus Kner, 1868	0.47 ± 0.34	–	–	–	0.47 ± 0.26	–	0.17 ± 0.11	–
Siganus canaliculatus Park, 1797	–	–	–	–	0.17 ± 0.10	–	0.07 ± 0.07	–
No habitat associations								
Apogon hartzfeldii Bleeker, 1852	1.07 ± 0.53	–	–	–	1.37 ± 0.32	–	–	–
Gerres acinaces Bleeker, 1854	0.30 ± 0.17	0.29 ± 0.16	0.37 ± 0.76	0.33 ± 0.24	0.30 ± 0.17	0.27 ± 0.17	0.07 ± 0.07	–
Gerres oyena Forsskål, 1775	0.50 ± 0.21	0.10 ± 0.05	0.27 ± 0.35	0.27 ± 0.13	0.30 ± 0.14	0.27 ± 0.15	0.13 ± 0.09	0.07 ± 0.04
Scolopsis ghanam Forsskål, 1775	0.03 ± 0.03	–	–	–	0.33 ± 0.15	–	0.07 ± 0.07	–
Scolopsis lineatus Quoy & Gaimard, 1824	0.03 ± 0.03	–	0.30 ± 0.64	–	0.03 ± 0.03	0.30 ± 0.12	0.07 ± 0.07	0.07 ± 0.07
Sphaeramia orbicularis Cuvier, 1828	1.10 ± 1.07	–	2.97 ± 3.92	–	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.03	–
Upeneus sundaicus Bleeker, 1855	0.03 ± 0.03	–	0.17 ± 0.17	–	0.07 ± 0.04	–	0.07 ± 0.04	0.03 ± 0.03

Table 4. (continued)

| Species | Seagrass + mangrove | | | | Within mangrove | |
| | Night | | Day | | Day | |
	All fish	Juvenile fish	All fish	Juvenile fish	All fish	Juvenile fish
Species associated to seagrass near mangrove and reef						
Apogon fuscus Quoy & Gaimard, 1825	2.80 ± 0.77	–	–	–	–	–
Apogon melas Bleeker, 1848	0.30 ± 0.16	–	–	–	–	–
Cheilodipterus isostigmus Schultz, 1940	0.10 ± 0.07	0.07 ± 0.04	–	–	–	–
Cheilodipterus quinquelineatus Cuvier, 1828	0.03 ± 0.03	–	0.10 ± 0.05	–	–	–
Choerodon anchorago Bloch, 1791	–	–	–	–	9.67 ± 7.30	4.17 ± 3.10
Halichoeres papilionaceus Valenciennes, 1839	–	–	–	–	0.17 ± 0.17	–
Lethrinus harak Forsskål, 1775	0.27 ± 0.13	0.13 ± 0.10	0.23 ± 0.13	0.07 ± 0.04	6.17 ± 2.40	4.32 ± 1.52
Naso vlamingii Valenciennes, 1835	0.20 ± 0.10	0.20 ± 0.10	–	–	–	–
Plotosus lineatus Valenciennes, 1840	–	0.13 ± 0.08	–	–	–	–
Siganus virgatus Valenciennes, 1835	–	–	–	–	0.08 ± 0.08	–
Syngnathoides biaculeatus Bloch, 1785	0.60 ± 0.20	–	1.33 ± 0.48	–	–	–
Species associated to seagrass near mangrove						
Acreichthys tomentosus Linnaeus, 1758	0.90 ± 0.21	0.20 ± 0.10	1.17 ± 0.79	–	–	–
Apogon ceramensis Bleeker, 1852	12.33 ± 2.24	0.07 ± 0.07	–	–	9.17 ± 5.83	9.18 ± 5.83
Atherinomorus lacunosus Forster, 1801	17.13 ± 4.92	0.93 ± 0.44	22.93 ± 11.20	1.50 ± 0.40	564.00 ± 244.00	154.00 ± 91.40
Caranx ignobilis Forsskål, 1775	0.07 ± 0.07	0.07 ± 0.07	–	–	0.33 ± 0.21	0.33 ± 0.21
Centriscus scutatus Linnaeus, 1758	0.07 ± 0.07	–	0.53 ± 0.23	–	–	–
Centrogenys vaigiensis Quoy & Gaimard, 1824	0.70 ± 0.26	–	0.07 ± 0.04	–	–	–
Cheilodipterus macrodon Lacepède, 1802	0.83 ± 0.33	0.07 ± 0.04	–	–	–	–
Dischistodus fasciatus Cuvier, 1830	–	–	–	–	1.83 ± 1.05	–
Hyporhamphus dussumieri Valenciennes, 1847	0.13 ± 0.13	–	0.37 ± 0.33	0.37 ± 0.33	18.00 ± 14.10	16.17 ± 12.50
Lethrinus obsoletus Forsskål, 1775	0.20 ± 0.10	–	0.07 ± 0.07	0.07 ± 0.07	–	–
Lethrinus ornatus Valenciennes, 1830	2.57 ± 0.73	0.20 ± 0.10	0.40 ± 0.12	0.05 ± 0.04	–	–
Lethrinus variegatus Valenciennes, 1830	0.50 ± 0.26	0.03 ± 0.03	0.10 ± 0.08	–	–	–
Liza vaigiensis Quoy & Gaimard, 1825	0.37 ± 0.30	2.57 ± 0.73	0.20 ± 0.20	0.40 ± 0.12	0.08 ± 0.08	–
Monacanthus chinensis Osbeck, 1765	0.47 ± 0.13	–	0.17 ± 0.07	–	3.58 ± 2.27	1.68 ± 1.67
Neoniphon argenteus Valenciennes, 1831	0.07 ± 0.07	0.07 ± 0.04	–	–	–	–
Neoniphon sammara Forsskål, 1775	0.07 ± 0.04	–	–	–	–	–
Paraplotosus albilabris Valenciennes, 1840	0.13 ± 0.08	–	–	–	–	–
Parupeneus macronemua Lacepède, 1801	0.87 ± 0.31	–	0.30 ± 0.20	–	0.67 ± 0.57	0.66 ± 0.57
Pseudomonacanthus macrurus Bleeker, 1857	1.93 ± 0.47	0.30 ± 0.12	1.07 ± 0.38	0.10 ± 0.08	–	–
Scarus sp. 1	0.10 ± 0.10	–	0.93 ± 0.41	0.03 ± 0.03	–	–
Scolopsis trilineatus Kner, 1868	3.33 ± 0.87	–	3.87 ± 1.15	–	6.83 ± 3.48	0.17 ± 0.17
Siganus canaliculatus Park, 1797	1.23 ± 0.44	–	0.10 ± 0.08	–	6.92 ± 5.03	–
No habitat associations						
Apogon hartzfeldii Bleeker, 1852	0.53 ± 0.19	–	–	–	3.33 ± 3.33	–
Gerres acinaces Bleeker, 1854	0.47 ± 0.25	0.43 ± 0.22	0.37 ± 0.15	0.37 ± 0.15	0.50 ± 0.50	–
Gerres oyena Forsskål, 1775	0.30 ± 0.19	0.23 ± 0.16	0.10 ± 0.08	–	37.30 ± 35.50	2.07 ± 1.18
Scolopsis ghanam Forsskål, 1775	0.30 ± 0.12	–	0.10 ± 0.07	0.10 ± 0.07	3.00 ± 1.22	0.50 ± 0.26
Scolopsis lineatus Quoy & Gaimard, 1824	–	0.30 ± 0.12	–	–	–	–
Sphaeramia orbicularis Cuvier, 1828	4.17 ± 1.11	–	0.07 ± 0.07	–	143.00 ± 142.00	–
Upeneus sundaicus Bleeker, 1855	0.03 ± 0.03	–	0.10 ± 0.07	–	–	–

Table 5. Two-way nested GLM ANOVA for total fish abundance with Tukey's pairwise inter-habitat comparisons of each trophic group during night and day between 3 seagrass habitat types (Sg Cor = seagrass + reef, Sg Cor-mg = seagrass + reef + mangrove, Sg Mg = seagrass + mangrove) in the Kaledupa subregion of the Wakatobi MNP, Indonesia (only significant differences shown). Fish were sampled at 9 sites both day and night using a beach seine net. There were no significant comparisons for herbivorous species

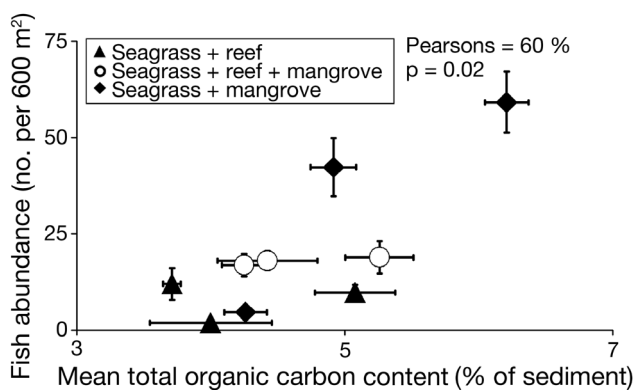|	df	Invertebrates		Fish and invertebrates		Omnivores		Planktivores	
		F	p	F	p	F	p	F	p
Day									
Habitat	2			3.44	<0.05				
Site	1								
Habitat × Site	2								
Significant differences				Sg Cor < Sg Cor-mg					
Night									
Habitat	2	3.75	<0.05	6.17	<0.01	7.52	<0.001	2.92	<0.05
Site	1			5.05	<0.05	9.46	<0.01		
Habitat × Site	2					5.94	<0.01		
Significant differences		Sg Cor < Sg Mg		Sg Cor < Sg Cor-mg Sg Cor < Sg Mg		Sg Cor < Sg Mg		Sg Cor < Sg Cor-mg Sg Cor < Sg Mg	
Total	89								

Fig. 5. Relationship between mean total fish abundance (±SE, n = 20) and mean total organic carbon content (±SE, n = 6) of the sediment (% of sediment) at 9 sites comprising 3 seagrass habitat types (seagrass + reef, seagrass + reef + mangrove, seagrass + mangrove) within the Kaledupa subregion of the Wakatobi MNP, Indonesia. All fish abundance data were obtained using a beach seine net and averaged over both day and night sampling. Pearson's correlation coefficient is shown

Mangroves provide important feeding grounds for fish at high tide (Sheaves 2005) as they contain a large biomass of invertebrate fauna (Robertson 1988). Unlike Caribbean mangroves, Indo-Pacific mangroves are mostly inter-tidal and, thus, represent only temporary habitats (Sheaves 2005). Fish species within mangroves show a high similarity to those within nearby seagrass beds (Table 4) suggesting that many seagrass fish use mangroves for either feeding or shelter on a daily basis. This role is different to the permanently flooded mangrove habitat of the Caribbean commonly used by juvenile reef fish such as Lutjanidae and Haemulidae as a day-time feeding area (Verweij et al. 2006).

There has been recent debate that has highlighted the lack of available information on the complex ecological mechanisms behind faunal inter-habitat connectivity within many regions of the globe (Dahlgren et al. 2006, Layman et al. 2006, Sheaves et al. 2006). This is particularly the case within the Indo-Pacific (Sheaves 2005). This study found that mangroves, when in close proximity to seagrass, are directly connected through fish movement (Table 4) and possibly indirectly connected through the export of organic carbon from the mangrove (Fig. 5). The explanation for these results may be partially obscured by the spatial imbalance within our study design. This study indicates that local environmental conditions may have a large influence on this indirect connectivity as trends in our study were not ubiquitous (Tables 2 & 3). Two of the 6 sites close to mangroves had comparatively low fish abundance, indicating additional factors such as local circulation or habitat structure may be important (Sheaves 2005).

Despite the spatial imbalance of the 3 habitat types (all Sg Cor sites were located around Hoga Island, as mangroves still remain dominant in most coastal areas with low human impact), we do not consider this to be a major reason for our observed results. No evidence exists to suggest that biological factors (e.g. recruitment processes) vary enough within the region to place an artefactual bias upon Hoga Island. For example, reef monitoring found persistently high fish diversity of similar assemblage composition throughout the entire Wakatobi MNP (including sample sites around the islands of Kaledupa and Hoga) (Halford 2003).

Due to the strong relationship we found between sedimentary organic carbon content and fish abundance,

we hypothesise that the supply of organic carbon to the food web (possibly from adjacent mangrove) may stimulate the food web of adjacent habitats (Fig. 5). This premise requires further investigation. The inconsistency in the conclusion of this study and those from Tanzania (Dorenbosh et al. 2006) may reflect localised circulation patterns influencing mangrove out-welling to nearby seagrass (as well as the diel sampling regime of the present study). This study indicates that mangroves may have cascade effects on the food webs of adjacent habitats, but this requires further study.

Partitioning fauna into trophic categories provides a useful tool for understanding the ecological structure in fish assemblages (Khalaf & Kochzius 2002, Unsworth et al. 2007). Abundant planktivorous fish were found in all habitat types, but in much higher densities within seagrass beds close to mangroves, yet far from reefs (Fig. 4). This trophic group was dominated by one species, *Atherinomorus lacunosus*, which also had very high abundance within nearby mangrove habitats. The high nutrient cycling within mangrove habitats (Nedwell et al. 1994) may stimulate both zooplankton and phytoplankton assemblages providing abundant food for species such as *A. lacunosus* to feed on at high tide.

Herbivorous fishes, dominated by Siganidae spp. and juvenile Acanthuridae spp., were in much higher densities within seagrass beds close to mangroves and reefs (Fig. 4). Siganids found in this study commonly use reef habitat and were also found in mangroves indicating the requirement for regular feeding migrations. The absence of many Acanthuridae spp. individuals from the mangroves suggests that their presence in high numbers in seagrass beds close to mangroves and reefs is for nursery shelter and feeding. In addition mangroves adjacent to seagrass beds may serve as refuges from predation for small fishes that forage in seagrasses.

Many questions have been raised about the role of mangroves in supporting juvenile reef fish in the Indo-Pacific (Laroche et al. 1997, Sheaves 2005), with many studies providing contradictory information, which is presumably due to local environmental variability (Laroche et al. 1997, Laegdsgaard & Johnson 2001, Lugendo et al. 2005). We found evidence that mangroves do have a role in supporting juvenile fish, both directly by providing habitat and indirectly as part of an ecosystem of connected habitats. Close proximity of mangroves to seagrass was observed to result in the juvenile fish populations of seagrass beds being 6 times greater than in those distant from mangroves (Fig. 2). This supports the findings of Dorenbosch et al. (2006) and may be the result of feeding ground availability and shelter from predation provided by the complex mangrove root systems.

Juvenile fish found within Indo-Pacific mangroves have often been considered to be of little commercial importance (Laroche et al. 1997, Lugendo et al. 2005). Our study did not find high concentrations of high value juvenile reef fish within mangroves, but did find high densities of juvenile fish species of high importance to local subsistence fisheries (e.g. *Lethrinus harak*, *Choerodon anchorago*, *Siganus canaliculatus*) (May 2005). Additionally, we found that 7 of the 10 most abundant juvenile fish families within seagrass are of commercial importance (May 2005, Froese & Pauly 2006). Six of these 10 species were in higher abundance in seagrass associated with mangroves, which indicates that mangrove habitat is important to the majority of juvenile seagrass fish species (Table 4).

In conclusion fish abundance, richness, trophic structure and assemblage composition of seagrass beds were found to be significantly influenced by the proximity of adjacent mangrove and coral reef habitats. Seagrass beds and mangroves were found to be an important habitat for juvenile fishes and when in a 3-way continuum with nearby reefs provided a greater fish nursery function. This research supports the need for ecosystem-level management of shallow water tropical habitats, but also suggests that management requires knowledge of local level processes and habitat interactions, along with water circulation to successfully enhance or conserve fish assemblages.

LITERATURE CITED

Alongi DM (1990) Abundances of benthic microfauna in relation to outwelling of mangrove detritus in a tropical coastal region. Mar Ecol Prog Ser 63:53–63

Boto KG, Bunt JS (1981) Tidal export of particulate organic matter from a northern Australian mangrove system. Estuar Coast Shelf Sci 13:247–255

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/ Tutorial. PRIMER-E, Plymouth

Clarke KR, Warwick RM (1994) Changes in marine communities: an approach to statistical analysis and interpretation. National Environmental Research Council, Plymouth Marine Laboratory, Plymouth

Cocheret de la Morinière E, Pollux BJA, Nagelkerken I, Hemminga MA, Huiskes AHL, van der Velde G (2003) Ontogenetic dietary changes of coral reef fishes in the mangrove–seagrass–reef continuum: stable isotopes and gut-content analysis. Mar Ecol Prog Ser 246:279–289

Costanza R, d'Arge R, De Groot R, Farber S and others (1997) The value of the world's ecosystem services and natural capital. Nature 287:253–260

Dahlgren CP, Kellison GT, Adams AJ, Gillanders BM and others (2006) Marine nurseries and effective juvenile habitats: concepts and applications. Mar Ecol Prog Ser 312: 291–295

de la Torre-Castro M, Rönnbäck P (2004) Links between humans and seagrasses — an example from tropical East Africa. Ocean Coast Manage 47:361–387

Dorenbosch M, Grol MGG, Nagelkerken I, van der Velde G (2006) Different surrounding landscapes may result in different fish assemblages in east African seagrass beds. Hydrobiologia 563:45–60

Dorenbosch M, Verberk WCEP, Nagelkerken I, van der Velde G (2007) Influence of habitat configuration on connectivity between fish assemblages of Caribbean seagrass beds, mangroves and coral reefs. Mar Ecol Prog Ser 334:103–116

English S, Wilkinson C, Baker V (1997) Survey manual for tropical marine resources. Australian Institute of Marine Science, Townsville

Folk RL (1966) A review of grain-size parameters. Sedimentology 6:73–93

Froese R, Pauly DE (2006) FishBase (04/2006). Available at www.fishbase.org

Gell FR, Whittington MW (2002) Diversity of fishes in the Quirimba Archipelago, northern Mozambique. Mar Freshw Res 53:115–121

Guest M, Connolly R, Loneragan N (2003) Seine nets and beam trawls compared by day and night for sampling fish and crustaceans in shallow seagrass habitat. Fish Sci 64:185–196

Halford A (2003) Fish diversity and distribution. In: Pet-Soede L, Erdmann MV (eds) Rapid ecological assessment Wakatobi National Park. World Wildlife Fund and The Nature Conservancy Joint Publication, Bali, p 53–64

Hutomo M, Peristiwady T (1996) Diversity, abundance and diet of fish in the seagrass beds of Lombok Island, Indonesia. In: Kuo J, Phillips RC, Walker DI, Kirkman H (eds) Seagrass biology: proceedings of an international workshop. Faculty of Science, University of Western Australia, Perth, p 205–212

Kenworthy WJ (2000) The role of sexual reproduction in maintaining populations of *Halophila decipiens:* implications for the biodiversity and conservation of tropical seagrass ecosystems. Pac Conserv Biol 5:260–268

Khalaf MA, Kochzius M (2002) Changes in trophic community structure of shore fishes at an industrial site in the Gulf of Aqaba, Red Sea. Mar Ecol Prog Ser 239:287–299

Kochzius M (1999) Interrelation of ichthyofauna from a seagrass meadow and coral reef in the Philippines. In: Séret B, Sire J (eds) Proceedings of the 5th International Indo-Pacific Fish Conference, Nouméa, 1997. Société Française d'Ichtyologie, Paris

Laegdsgaard P, Johnson CR (2001) Why do fish utilise mangrove habitats? J Exp Mar Biol Ecol 257:229–253

Laroche J, Baran E, Rasoanandrasana NB (1997) Temporal patterns in a fish assemblage of a semiarid mangrove zone in Madagascar. J Fish Biol 51:3–20

Layman CA, Dahlgren CP, Kellison GT, Adams AJ and others (2006) Marine nurseries and effective juvenile habitats. Mar Ecol Prog Ser 318:307–308

Lee SY (1995) Mangrove out-welling — a review. Hydrobiologia 295:203–212

Lugendo BR, Pronker A, Cornelissen I, de Groene A and others (2005) Habitat utilisation by juveniles of commercially important fish species in a marine embayment in Zanzibar, Tanzania. Aquat Living Resour 18:149–158

May D (2005) Folk taxonomy of reef fish and the value of participatory monitoring in Wakatobi National Park, south-east Sulawesi, Indonesia. South Pac Comm Trad Mar Resour Manage Knowl Info Bull 18:18–35

Meziane T, Tsuchiya M (2000) Fatty acids as tracers of organic matter in the sediment and food web of a mangrove/intertidal flat ecosystem, Okinawa, Japan. Mar Ecol Prog Ser 200:49–57

Mumby PJ, Edwards AJ, Arias-González JE, Lindeman KC and others (2003) Mangroves enhance the biomass of coral reef communities in the Caribbean. Nature 427:533–536

Nagelkerken I, van der Velde G (2002) Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curaçao (Netherlands Antilles)? Mar Ecol Prog Ser 245:191–204

Nagelkerken I, Dorenbosch M, Verberk W, Cocheret de la Morinière E, van der Velde G (2000) Day–night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. Mar Ecol Prog Ser 194:55–64

Nagelkerken I, Kleijnen S, Klop T, van den Brand R, Cocheret de la Morinière E, van der Velde G (2001) Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Mar Ecol Prog Ser 214:225–235

Nakamura Y, Sano M (2004) Overlaps in habitat use of fishes between a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan: importance of the seagrass bed as juvenile habitat. Fish Sci 70:788–803

Nakamura Y, Horinouchi M, Nakai T, Sano M (2003) Food habits of fishes in a seagrass bed on a fringing reef at Iriomote Island, southern Japan. Ichthyol Res 50:15–22

Nedwell DB, Blackburn TH, Wiebe WJ (1994) Dynamic nature of the turnover of organic carbon, nitrogen and sulphur in the sediments of a Jamaican mangrove forest. Mar Ecol Prog Ser 110:223–231

Orth RJ, Carruthers TJB, Dennison WC, Duarte CM and others (2006) A global crisis for seagrass ecosystems. BioScience 56:978–996

Pollux BJA, Verberk WCEP, Dorenbosch M, Cocheret de la Morinière E, Nagelkerken I, van der Velde G (2007) Habitat selection during settlement of three Caribbean coral reef fishes: indications for directed settlement to seagrass beds and mangroves. Limnol Oceanogr 52:903–907

Robertson AI (1988) Abundance, diet and predators of juvenile banana prawns, *Penaeus merguiensis*, in a tropical mangrove estuary. Aust J Mar Freshw Res 39:467–478

Sheaves M (2005) Nature and consequences of biological connectivity in mangrove systems. Mar Ecol Prog Ser 302:293–305

Sheaves M, Baker R, Johnston R (2006) Marine nurseries and effective juvenile habitats: an alternative view. Mar Ecol Prog Ser 318:303–306

Sogard SM, Powell GVN, Holmquist JG (1989) Utilization by fishes of shallow, seagrass covered banks in Florida Bay: 2. Diel and tidal patterns. Environ Biol Fishes 24:81–92

Unsworth RKF, Wylie E, Bell JJ, Smith DJ (2007) Diel trophic structuring of seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia. Estuar Coast Shelf Sci 72:81–88

Verweij MC, Nagelkerken I, de Graaff D, Peeters M, Bakker EJ, van der Velde G (2006) Structure, food and shade attract juvenile coral reef fish to mangrove and seagrass habitats: a field experiment. Mar Ecol Prog Ser 306:257–268