

## Diel trophic structuring of seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia

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### Abstract

The faunal communities of seagrass beds throughout SE Asia are highly threatened by continued overexploitation, yet their ecology is poorly understood. Developing a greater understanding of the faunal linkages between seagrass beds and associated coastal habitats can facilitate more informed ecosystem level management. The present study used beach seine netting to sample seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia, to investigate diel migrations of fish into and out of seagrass beds. These fish assemblages were found to be diverse relative to other studies within the region, with many species being economically important to local subsistence fisheries. The abundance, species richness and trophic structure of these fish assemblages changed with time of day indicating that fish populations are in a dynamic state. Mean fish abundance increased by  $\approx 45\%$  from day to night (Day:  $8.61 \pm 0.13$  fish  $100\text{ m}^{-2}$ ; Night:  $15.6 \pm 1.4$  fish  $100\text{ m}^{-2}$ ) while mean species richness increased from  $6.6 \pm 1.9$  per seine haul to  $11.4 \pm 0.2$ . Increasing abundance and diversity of fish at night suggests migration onto these habitats from nearby habitats such as reefs, mangroves or deep water; and/or increased activity of those fish resident within seagrass habitats. Division of species into trophic categories enabled the trophic structure of changing fish assemblages to be examined. Assemblages were dominated during both the day and night by invertebrate and fish feeders; however, a major diel change in trophic structure occurred in the abundance of omnivores. During the day omnivores were abundant, but they were replaced at night by exclusive invertebrate feeders. We therefore propose that diel changes in seagrass fish assemblages are predominantly structured by food availability, although other factors such as increased night-time shelter provision were also found to be important albeit to a much lesser extent.

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### 1. Introduction

The diverse faunal communities of seagrass beds throughout SE Asia are threatened by continued overexploitation of living marine resources such as fish, molluscs and sea cucumbers (Kuriandewa et al., 2003). Understanding the linkages between coastal habitats will facilitate more informed ecosystem level management, whilst knowledge of fish movements and migrations will assist fishery managers in developing measures

appropriate for sustainable fish exploitation. Fish movements are utilised by local fishers across SE Asia who use Fyke nets (fish fences) set into tidal currents or between seagrass beds and reefs to catch fish. It is important for the future sustainable management of seagrass beds that habitat connectivity is fully understood (Parrish, 1989; Fortes, 1990).

Fish assemblages residing in tropical seagrass beds of the Caribbean and Australia undergo diel changes in their population structure, with higher abundance and species richness occurring at night (Robertson, 1980; Robblee and Zieman, 1984; Sogard et al., 1989; Gray et al., 1998; Nagelkerken et al., 2000; Griffiths, 2001). This is usually the result of either inward migrations of fish from associated habitats, such as coral

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reefs, or increased activity of resident fish that hide for various reasons at different times of the day (Sogard et al., 1989; Kochzius, 1999; Nagelkerken et al., 2000). Fish have been found in many locations to shelter on, or near, the reef during the day and then forage the surrounding habitats including seagrass at night (Parrish, 1989). Such a premise remains widely untested within SE Asia, where data is only available from studies dealing with species composition and relative abundance during the day (Marasabessy and Hukom, 1989; Dolar, 1991). Much of the literature concerned with seagrass fish ecology, like the majority of tropical seagrass research, has been conducted within the Caribbean (e.g. Nagelkerken et al., 2002; Mumby et al., 2004) and therefore the global scale applicability of hypotheses relating to seagrass ecology, along with the factors structuring the associated fish assemblages are not possible, indicating the need for more regional based studies. Seagrass beds and coral reefs within SE Asia have a much higher floral and faunal diversity than the Caribbean and therefore potentially different structuring processes. Despite calls by Parrish (1989) for an increased study of fish migrations there is still a poor understanding of the causation of diel changes in SE Asian seagrass fish assemblages.

Seagrass beds offer important feeding sites for fish (Weinstein and Heck, 1977; Heck and Orth, 1980) due to the high invertebrate biomass they support (De Troch et al., 2003; Nakamura and Sano, 2005). Seagrass fish assemblages are commonly dominated by fish that feed on abundant small crustaceans (e.g. Hutomo and Peristiwady, 1996; Nakamura et al., 2003). Food availability has been found to explain the distribution of fish within seagrass beds (Jenkins and Hamer, 2001; Grenouillet et al., 2002). In contrast, research in the Red Sea indicates that invertebrate feeders do not always dominate seagrass beds indicating the need for regional understanding of the trophic structure of seagrass fish assemblages. Surveys by Khalaf and Kochzius (2002) found 79.9% of fish in seagrass were planktivores, 5.5% fed on both fish and invertebrates, 5% were omnivorous and only 2.5% fed exclusively on invertebrates. Although several studies (e.g. Marasabessy and Hukom, 1989; Dolar, 1991) have reported on the diversity and abundance of seagrass fish assemblages within SE Asia their trophic structure remains undocumented.

Shelter, in addition to food, is an important factor controlling fish distribution in shallow water seagrass beds, as the reduced predation risk at night may encourage fish species to move into seagrass habitats to feed. In SW Australia, fish were found to move in response to avian piscivores (Hyndes et al., 1996; Young et al., 1997), whilst in the Caribbean many reef fish species sought shelter in seagrass beds from large piscivorous fish (Nagelkerken et al., 2000). The regularity and magnitude of any migrations between seagrass beds and associated coral reefs in SE Asia are unknown as are any explanations for such movements.

In the present study we investigated day-night shifts in the structure of seagrass bed fish assemblages within the Wakatobi Marine National Park, Indonesia, an area characterised by high fish diversity (Halford et al., 2003). Research tested the following null hypotheses: (1) seagrass fish assemblages show

no change in abundance and diversity between day and night; (2) no diel changes in trophic structure of the fish assemblage exist; (3) seagrass beds are not subjected to influxes of fish that commonly reside in reef habitats.

## 2. Materials and methods

This study was conducted during July and August 2005 on the inter-tidal seagrass beds around Hoga Island, which is located in the Wakatobi Marine National Park (Fig. 1). The seagrass beds lie between fringing reefs and the shoreline and are representative of habitats found across large sections of the Indo-Pacific and Indian Oceans (Holbrook et al., 2002; Salita et al., 2003; Nakamura and Sano, 2004). The Wakatobi Marine National Park (MNP) is situated in the Tukang Besi archipelago, a remote island group of about 200,000 hectares, off SE Sulawesi in Indonesia (Elliot et al., 2001). The MNP is home to approximately 90,000 people and has extensive reef and seagrass systems that support heavily exploited fin and shell fisheries (May, 2003).

### 2.1. Study sites

Four sites (Hoga Beach [S 05°28'35.3"; E 123°45'40.0"], Boat Bay [S 05°28'36.3"; E 123°45'47.7"], Mushroom Bay [S 05°28'32.8"; E 123°45'51.3"] and Bounty Bay [S 05°28'30.6"; E 123°45'53.6"]) were sampled around Hoga Island (Fig. 1). All sites were on the south side of the island as no comparable sites of inshore seagrass existed on the northerly coast. Seagrass habitats within the sampling sites were continuous from the shore to deeper subtidal areas where benthic sediment becomes thin and corals habitats begin to dominate. The area is subjected to a daily tidal cycle that comprises two high tides, a half low and a full low tide. The maximum amplitude of the tide is 2.3 m (Fig. 1).

All sites were within 400 m of a fringing coral reef; however, none of the sites were considered to be directly influenced by mangroves as they were all approximately 3 km from the nearest mangrove forest and separated by a deep-water channel. Seagrass beds within the region can be variable in biomass and habitat complexity as a result of variable floral assemblages. To reduce any potential error due to this variability, we investigated seagrass beds with high biomass and complexity and we considered representative of seagrass beds throughout the Wakatobi MNP (Unsworth, personal observation). All sites were of a similar depth profile reaching 3 m (relative to mean high water spring mark) at 200 m from the shore.

The sampling sites were determined on the basis of an initial assessment exercise where a 0.25 m<sup>2</sup> metal quadrat was used to identify four sites comprising similar seagrass floral assemblages that were representative of the locality. All sites had >70% seagrass cover comprising a mixed floral assemblage but dominated by two species, *Thalassia hemprichii* (Ehrenberg) and *Enhalus acoroides* (L.f.) Royle. These assemblages also contained minor floral coverage (total cover <5%) of *Cymodocea rotundata* (Ehrenberg and Hemprich ex Ascherson),

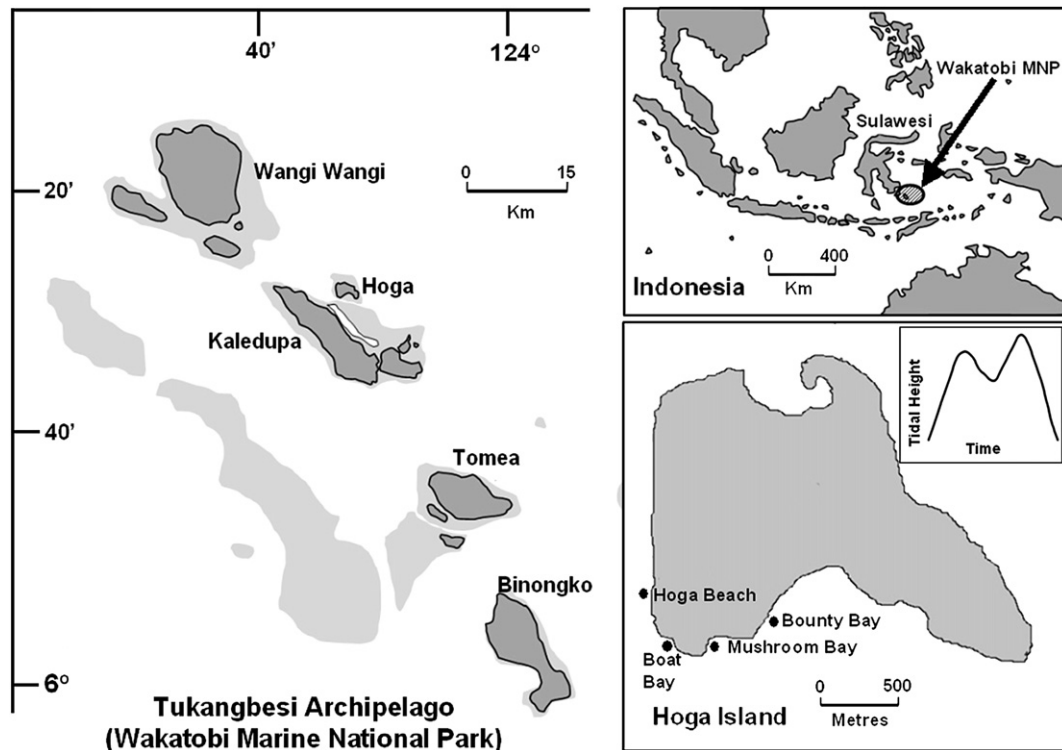


Fig. 1. The location of the four study sites, Hoga Beach, Boat Bay, Mushroom Bay and Bounty Bay in the Tukang Besi Archipelago (Wakatobi Marine National Park), Indonesia, with the local daily tidal regime inset on right.

*Halophila ovalis* (Brown) Hooker f., occasionally *Halodule uninervis* (Forsskal) Ascherson.

## 2.2. Diel beach seining

Beach seine netting was used (after Cocheret de la Moriniere et al., 2003) to sample diel variation in the near shore seagrass fish populations. The disadvantages of beach seine netting have been discussed by English et al. (1997) and Nagelkerken et al. (2001). The major concerns are that seine nets under-sample fast swimming and pelagic fish species such as Jacks and Travallies, and also small fish such as gobies and blennies (Gell and Whittington, 2002). Additionally, during daylight hours large fish may also have greater avoidance ability. Despite these drawbacks, this approach remains the only non-destructive method for sampling night-time fish populations. The non-destructive nature of seine netting has been challenged (Gray and Bell, 1986); however, observations made of the net being pulled through the seagrass beds coupled with its small size found no evidence of damage to the seagrass. Other possible methods could include beam trawls or night visual transects, but Guest et al. (2003) found that seine nets are more appropriate for determining the relative proportion of species in a seagrass habitat and estimating the density of most species.

In order to standardise tidal effects seine netting was conducted at  $\approx 1 \pm 0.2$  m above chart datum during both day and night. This was the most appropriate water height for the seine net to work effectively. Day seines were carried out between 09:00 and 16:00 h, while all night-time seines were conducted between 19:00 and 01:00 h. The net was 10 m

long and 1.1 m high with a 1.1 m  $\times$  1.1 m cod end in the middle. The net mesh size was 1 cm and stretched mesh size was 1.1 cm. The net was carried 30 m into the seagrass (from start of seagrass) and dragged into the shore by four people, thereby sampling an area of approximately 300 m<sup>2</sup>. All fish caught were identified to species level where possible and then returned to the sea at least 100 m away from the sampling site. Adjacent seine hauls were not conducted consecutively in order to maintain sample independence. Five day and five night seine hauls were carried out at each of the four sites as a preliminary assessment determined that this sampled 95% of all species. These were all carried out during spring tide periods.

## 2.3. Statistical analysis

Total fish abundance and species richness data was found to be heteroscedastic and deviated from a normal distribution. Transformation could not rectify this distribution, therefore two-way PERMANOVA was used to analyse for differences in fish abundance and species richness between sites and times of day. This method is not reliant upon the assumptions of a GLM ANOVA and tests the simultaneous response of one or more variables to one or more factors in an ANOVA design on the basis of any distance measure using permutation methods (Anderson, 2001; McArdle and Anderson, 2001). PERMANOVA enabled a conventional “ANOVA style” univariate two-way analysis to be conducted using the concepts and assumptions of a multivariate method.

Analysis of differences in fish assemblage structure was conducted using multivariate non-Metric Multidimensional

Scaling ordination (MDS) and Bray–Curtis cluster analysis using the computer package PRIMER (Clarke and Warwick, 1994). The Bray–Curtis similarity index was applied on square-root transformed data (to down-weight the influence of rare and extremely abundant species) generating a rank similarity matrix, which was then converted into an MDS ordination (Clarke, 1993). To check on the adequacy of the low-dimensional approximations seen in cluster and MDS the use of PRIMER v6.1.5 enabled clusters to be superimposed upon the MDS ordination (Clarke and Gorley, 2006). A two-way ANOSIM was used to investigate differences identified from MDS and cluster (Clarke and Warwick, 1994). SIMPER analysis was used to ascertain the fish species that contributed most to the dissimilarity between sites and time of day.

To analyse patterns in the trophic status of fish assemblages between day and night, all species were characterised into feeding categories based upon information from a number of sources including Hutomo and Peristiwady (1996), Khalaf and Kochzius (2002), Nakamura et al. (2003) and Froese and Pauly (2006). Due to the tendency for fish species inhabiting seagrass beds to exhibit patterns of ontogenetic dietary shifts (Cocheret de la Moriniere et al., 2003), categories for trophic status were determined on the basis of as many data sources as were available. This allowed diets to be categorised

on the basis of gut analysis of both juveniles and adults rather than for fish at different stages of development.

### 3. Results

A total of 81 fish species were recorded across all sites (Tables 1 and 2). The four most abundant species were *Atherinomorus lacunosus* ( $5.06 \pm 1.03$  fish  $100 \text{ m}^{-2}$ ), *Cheilodipterus quinquelineatus* ( $1.39 \pm 0.83$  fish  $100 \text{ m}^{-2}$ ), *Apogon hartzfeldii* ( $1.23 \pm 0.43$  fish  $100 \text{ m}^{-2}$ ) and *Sphaeramia orbicularis* ( $0.95 \pm 0.36$  fish  $100 \text{ m}^{-2}$ ) (Table 1). The Apogonidae family were the most abundant fish family. Many rare species were reported, with abundances of less than  $0.01$  fish  $100 \text{ m}^{-2}$  (30 species in total). A mean number of  $12.13 \pm 1.72$  fish  $100 \text{ m}^{-2}$  were found with a mean species richness of  $8.75 \pm 1.9$  per seine haul.

Beach seine netting showed mean fish abundance to be  $\approx 45\%$  greater at night ( $15.6 \pm 1.4$  fish  $100 \text{ m}^{-2}$ ) than during the day ( $8.61 \pm 0.13$  fish  $100 \text{ m}^{-2}$ ), species richness also increased from  $6.6 \pm 1.9$  to  $11.4 \pm 0.2$  per seine haul. This trend was found at all sites except Boat Bay where more fish ( $\approx 15\%$ ) were found during the day (Fig. 2). PERMANOVA demonstrated significant differences for both fish abundance ( $F = 0.1815$ ;  $p < 0.02$ ) and species richness ( $F = 0.3023$ ;  $p < 0.001$ ) between night and day; however, no significant

Table 1  
Mean ( $\pm$ SE,  $n = 20$ ) fish abundance per  $100 \text{ m}^2$  beach seine haul for the 30 most abundant species in seagrass beds sampled at day and night averaged across four sites. Species are also assigned one of five trophic categories: omnivore (O), herbivore (H), invertebrate feeder (I), invertebrate and fish feeder (IF) or planktivore (P). Species are also assigned one of three diel usage categories: night users (N), day users (D) and ubiquitous users (U)

	Overall	$\pm$ SE	Day	$\pm$ SE	Night	$\pm$ SE	Trophic group	Diel usage
<i>Atherinomorus lacunosus</i> (Forster, 1801)	5.06	$\pm 1.03$	4.92	$\pm 1.74$	5.23	$\pm 0.91$	IF	U
<i>Cheilodipterus quinquelineatus</i> (Cuvier, 1828)	1.39	$\pm 0.83$	2.21	$\pm 1.52$	0.42	$\pm 0.14$	IF	U
<i>Apogon hartzfeldii</i> (Bleeker, 1852)	1.23	$\pm 0.43$	0.01	$\pm 0.01$	2.68	$\pm 0.84$	I	U
<i>Sphaeramia orbicularis</i> (Cuvier, 1828)	0.95	$\pm 0.36$	1.14	$\pm 0.59$	0.72	$\pm 0.36$	P	U
<i>Rhabdamia</i> sp.	0.73	$\pm 0.62$	1.33	$\pm 1.14$	0.00	$\pm 0.00$	I	D
<i>Acreichthys tomentosus</i> (Linnaeus, 1758)	0.57	$\pm 0.15$	0.74	$\pm 0.26$	0.37	$\pm 0.11$	O	U
<i>Gerres oyena</i> (Forsskål, 1775)	0.48	$\pm 0.14$	0.40	$\pm 0.16$	0.58	$\pm 0.23$	O	U
<i>Liza vaigiensis</i> (Quoy and Gaimard, 1825)	0.27	$\pm 0.18$	0.04	$\pm 0.04$	0.55	$\pm 0.38$	O	U
<i>Scolopsis trilineatus</i> (Kner, 1868)	0.27	$\pm 0.09$	0.04	$\pm 0.03$	0.53	$\pm 0.18$	I	U
<i>Plotosus lineatus</i> (Thunberg, 1787)	0.26	$\pm 0.20$	0.00	$\pm 0.00$	0.57	$\pm 0.45$	IF	N
<i>Scolopsis lineatus</i> (Quoy and Gaimard, 1824)	0.24	$\pm 0.06$	0.28	$\pm 0.09$	0.20	$\pm 0.07$	IF	U
<i>Lethrinus harak</i> (Forsskål, 1775)	0.23	$\pm 0.06$	0.08	$\pm 0.05$	0.42	$\pm 0.11$	IF	U
<i>Apogon hoevenii</i> (Bleeker, 1854)	0.23	$\pm 0.06$	0.01	$\pm 0.01$	0.48	$\pm 0.11$	I	U
Unknown Juvenile	0.18	$\pm 0.08$	0.18	$\pm 0.13$	0.18	$\pm 0.08$	P	U
<i>Apogon</i> sp. C	0.18	$\pm 0.06$	0.00	$\pm 0.00$	0.40	$\pm 0.12$	I	N
<i>Neoniphon</i> sp.	0.16	$\pm 0.05$	0.00	$\pm 0.00$	0.35	$\pm 0.10$	I	N
<i>Lethrinus variegatus</i> (Valenciennes, 1830)	0.13	$\pm 0.05$	0.06	$\pm 0.03$	0.22	$\pm 0.09$	I	U
<i>Cheilodipterus artus</i> (Smith, 1961)	0.12	$\pm 0.06$	0.14	$\pm 0.10$	0.10	$\pm 0.04$	IF	U
<i>Stegastes</i> sp. A	0.12	$\pm 0.08$	0.22	$\pm 0.14$	0.00	$\pm 0.00$	H	D
<i>Hyporhamphorus affinis</i> (Günther, 1866)	0.10	$\pm 0.06$	0.15	$\pm 0.12$	0.03	$\pm 0.02$	IF	U
<i>Ablabys taenianotus</i> (Cuvier, 1829)	0.08	$\pm 0.03$	0.01	$\pm 0.01$	0.17	$\pm 0.06$	IF	U
<i>Apogon</i> sp. A	0.08	$\pm 0.05$	0.00	$\pm 0.00$	0.17	$\pm 0.10$	I	N
<i>Acreichthys hajan</i> (Bleeker, 1852)	0.07	$\pm 0.02$	0.06	$\pm 0.03$	0.08	$\pm 0.03$	O	U
<i>Caranx ignobilis</i> (Forsskål, 1775)	0.07	$\pm 0.05$	0.00	$\pm 0.00$	0.15	$\pm 0.10$	IF	N
<i>Dischistodus perspicillatus</i> (Cuvier, 1830)	0.07	$\pm 0.03$	0.00	$\pm 0.00$	0.15	$\pm 0.07$	H	N
<i>Pomacentrus</i> sp. B	0.06	$\pm 0.04$	0.00	$\pm 0.00$	0.13	$\pm 0.08$	H	N
<i>Halichoeres</i> sp.	0.05	$\pm 0.03$	0.10	$\pm 0.06$	0.00	$\pm 0.00$	I	D
<i>Parapercis cylindrica</i> (Bloch, 1792)	0.05	$\pm 0.03$	0.08	$\pm 0.05$	0.02	$\pm 0.02$	O	U
<i>Syngnathoides biaculeatus</i> (Bloch, 1785)	0.05	$\pm 0.02$	0.06	$\pm 0.03$	0.03	$\pm 0.02$	IF	U
<i>Stolephorus indicus</i> (van Hasselt, 1823)	0.05	$\pm 0.03$	0.01	$\pm 0.01$	0.08	$\pm 0.05$	P	U

Table 2

Other species caught and identified during the study

<i>Canthigaster compressa</i> (Marion de Procé, 1822)	<i>Gobiidae</i> sp.	<i>Cheilodipterus quinquelineatus</i> (Cuvier, 1830)
<i>Dischistodus fasciatus</i> (Cuvier, 1830)	<i>Omobranchus</i> sp.	<i>Choerodon anchorago</i> (Bloch, 1791)
<i>Pseudomonacanthus macurus</i> (Bleeker, 1857)	<i>Stegastes</i> sp. B	<i>Engraulidae</i> sp.
<i>Bothus pantherinus</i> (Rüppell, 1830)	<i>Hemiglyphidodon plagiometopon</i> (Bleeker, 1852)	<i>Lutjanus decussatus</i> (Cuvier, 1828)
<i>Lethrinus semicinctus</i> (Valenciennes, 1830)	<i>Gerres filamentosus</i> (Cuvier, 1829)	<i>Plectorhinchus orientalis</i> (Bloch, 1793)
<i>Apogon melas</i> (Bleeker, 1848)	<i>Gerres subfasciatus</i> (Cuvier, 1830)	<i>Taeniura lymma</i> (Forsskål, 1775)
<i>Lutjanus ehrenbergii</i> (Peters, 1869)	<i>Scaridae</i> sp.	<i>Sphyræna</i> sp.
<i>Amblygobius phalaena</i> (Valenciennes, 1837)	<i>Hippocampus taeniopterus</i> (Bleeker, 1852)	<i>Siganus canaliculatus</i> (Park, 1797)
<i>Bothus mancus</i> (Broussonet, 1782)	<i>Corythoichthys haematopterus</i> (Bleeker, 1851)	<i>Dascyllus aruanus</i> (Linnaeus, 1758)
<i>Lethrinus xanθοcheilus</i> (Klunzinger, 1870)	<i>Fistularia commersonii</i> (Rüppell, 1838)	<i>Abudefduf septemfasciatus</i> (Cuvier, 1830)
<i>Syngnathidae</i> sp.	<i>Scolopsis mongramma</i> (Cuvier, 1830)	<i>Dischistodus pseudochrysopeicius</i> (Allen and Robertson, 1974)
<i>Arothron manilensis</i> (de Procé, 1822)	<i>Scolopsis affinis</i> (Peters, 1877)	<i>Dischistodus prosopotaenia</i> (Bleeker, 1852)
<i>Calotomus spinidens</i> (Quoy and Gaimard, 1824)	<i>Scolopsis temporalis</i> (Cuvier, 1830)	<i>Synanceiidae</i> sp.
<i>Bothus</i> sp.	<i>Apogon</i> sp. B	<i>Pterois</i> sp.
<i>Upeneus sundaicus</i> (Bleeker, 1855)	<i>Fowleria punctulata</i> (Rüppell, 1838)	<i>Apogon</i> sp. E
<i>Ctenochaetus</i> sp.	<i>Mulloidichthys vanicolensis</i> (Valenciennes, 1831)	<i>Parupeneus macronema</i> (Lacepède, 1801)
<i>Istigobius ornatus</i> (Rüppell, 1830)	<i>Labridae</i> sp.	<i>Pomacentrus</i> sp. A

difference was found between sites for fish abundance or richness. The interaction between sites and time of day for all abundance and richness analysis were not significant.

Many species (Table 1) were present in the seagrass only during day or only during night, for example *Neoniphon* sp. was nocturnally present, whilst *Dischistodus pseudochrysopeicius* was only found during the day. Of the top 30 most abundant species, four were only found during day whilst nine species occurred exclusively at night (Table 1). Of those species omnipresent, ten had a higher abundance during the night whilst five had a higher abundance during the day. The most abundant species sampled (*Atherinomorus lacunosus* and *Cheilodipterus quinquelineatus*) had high abundances during the day and night.

Superimposed Bray–Curtis clusters onto the MDS ordination (Fig. 3) showed differentiation between night and day fish assemblages. Day samples were scattered around a clustered group of night samples showing day fish assemblages to be more variable. The low similarity levels of the clusters (20%)

illustrated that differences between day and night assemblages were present although they were small. ANOSIM confirmed these differences to be significant (global  $r = 0.48$ ;  $p < 0.01$ ). SIMPER analysis showed the highest dissimilarity (>5% dissimilarity contribution) to be as result of *Atherinomorus lacunosus*, *Apogon hartzfeldii*, and *Acreichthys tormentosus*. *Gerres oyena*. *A. lacunosus*, *Acreichthys tomentosus*, *G. oyena* and *Cheilodipterus quinquelineatus* were the most representative (>5% similarity contribution) species of the day-time fish assemblage (determined from SIMPER), while *A. lacunosus*, *A. hartzfeldii*, *Apogon hoevenii* and *Sphaeramia orbicularis* were most representative of the night-time fish assemblage.

Of the 81 species caught, 26 (32.1%) species had a diet of invertebrates and fish, 24 (29.6%) ate exclusively invertebrates, 16 (19.7%) species were omnivorous, 4 (4.9%) were planktivorous, whilst 11 (13.5%) species were found to be herbivorous. Therefore the majority of the fish species were predators either of the category “fish and invertebrate feeders” or just

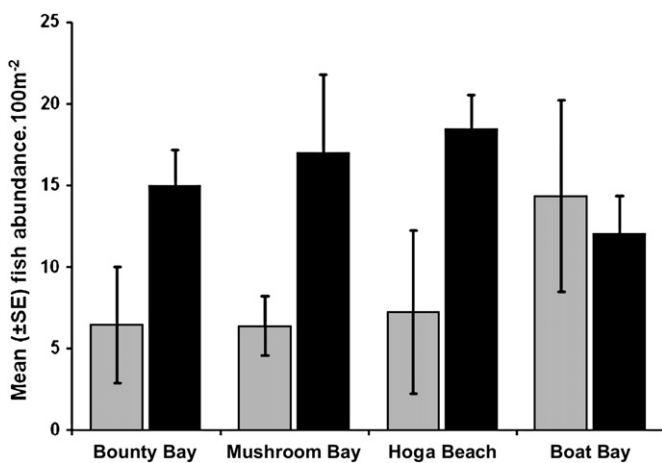


Fig. 2. Mean ( $\pm$ SE,  $n = 5$ ) fish species abundance per 100 m<sup>2</sup> in seagrass beds during day (light bars) and night (dark bars) at four sites (Hoga beach, Boat Bay, Mushroom Bay and Bounty Bay) within the Wakatobi Marine National park, Indonesia, collected using a beach seine net.

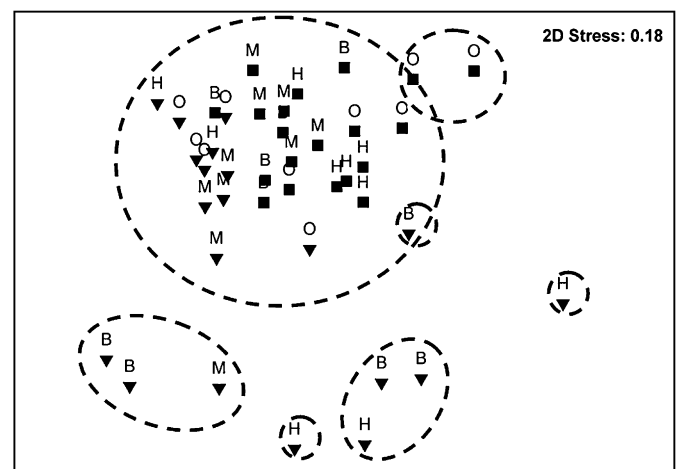


Fig. 3. MDS configuration with superimposed Bray–Curtis similarity clusters at the 30% level for sample comparison of fish species abundance in the Wakatobi Marine National park, Indonesia, in Seagrass beds at day ( $\blacktriangledown$ ) and night ( $\blacksquare$ ) using a beach seine net. Four sites were used: Hoga Beach (H), Bounty Bay (B), Boat Bay (O) and Mushroom Bay (M).

“invertebrate feeders” (50 species, 61.7%) whilst herbivores and planktivores were only minor contributors. The majority of individuals caught were of the category “fish and invertebrate feeders” (Fig. 4). Trophic structure of the fish assemblages changed significantly between day and night (Fig. 4). The major change that occurred was in the number of exclusive invertebrate feeders and omnivores. During the day omnivores made up  $34.2 \pm 7.0\%$  of the population, but this decreased significantly to  $8.6 \pm 2.0\%$  ( $F = 9.15$ ;  $p < 0.01$ ) at night. During the night-time there was a significant increase ( $F = 24.74$ ;  $p < 0.001$ ) in the proportion of exclusive invertebrate feeders from  $10.5 \pm 3.1\%$  to  $31.4 \pm 3.8\%$ , whilst the invertebrate and fish feeders comprised  $\approx 50\%$  of the population during the day and night. The percentage of herbivores more than doubled ( $1.1 \pm 0.5\%$  to  $2.8 \pm 0.9\%$ ) from day to night, although this group remained only a small proportion of the overall assemblage. The proportion of planktivores increased from day to night but this difference was not significant due to the large variability at both day and night.

#### 4. Discussion

This study determined that seagrass bed fish differ in their abundance, diversity, and both their assemblage and trophic structures from day to night, indicating that they are in a dynamic state. This is the first study to demonstrate the influence of diel cycles on the trophic composition of fish assemblages in a SE Asian seagrass system. Based on the evidence of diel changes in fish trophic structure, we propose diel changes in SE Asian seagrass fish assemblages are structured by a number of factors including food availability and the provision of shelter. We also propose increasing abundance and diversity of fish at night suggests a diel migration onto these habitats from nearby coral reefs.

##### 4.1. Diel migrations

Night-time fish assemblages within seagrass beds of the Wakatobi were dominated by three species of Apogonidae,

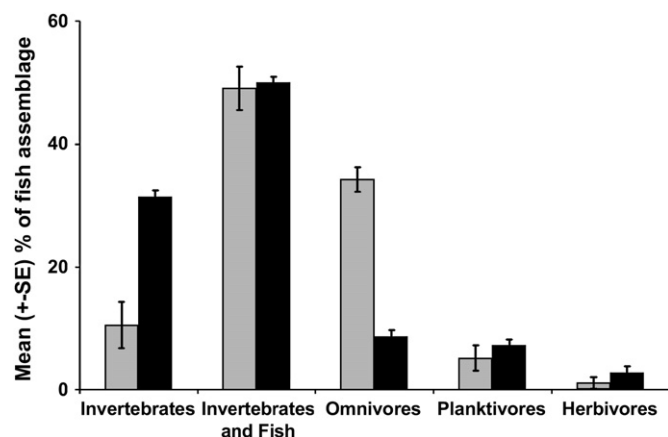


Fig. 4. Mean ( $\pm$ SE,  $n = 20$ ) proportions of different trophic feeding categories at day (light bars) and night (dark bars) averaged across four seagrass beds around the Island of Hoga Wakatobi Marine National Park, Indonesia.

all of which have been recorded on local coral reefs (Halford, 2003). This indicates that the most dominant night-time seagrass fish species migrate from nearby coral habitats on a diel basis, similar findings have been reported from the Philippines (Kochzius, 1999). These fish migrations may not be just restricted to diel movement as at least 15 of the most abundant 30 species (unrelated of diel usage category) reported have also been recorded from local coral reef habitats (Halford, 2003). Therefore movements may also be related to tidal and lunar cycles. We found the majority of abundant fish species to be resident within seagrass beds during both day and night; however, the abundance of most of these species increased during the night-time, probably to take advantage of the increased food availability and shelter from predators (Robblee and Zieman, 1984). Foods, such as epibenthic crustaceans, whilst available in the day, have been found to nocturnally increase in abundance, both locally (Unsworth et al., unpublished data) and in other localities (Guest et al., 2003). Such increases are thought to trigger feeding migrations of many fish species onto seagrass beds at night (Robertson, 1980). We suggest that diel migrations, resulting from food availability, are most likely to be the dominant factor influencing the diel movement of fish between coral reefs and seagrass beds.

##### 4.2. Change in trophic structure

The trophic structure of the fish assemblage changed from containing a high proportion of omnivorous fish during the day to a night-time assemblage with a much larger proportion of exclusive invertebrate feeders. The proportionally small abundance of herbivorous fish within the day assemblage also increased at night. The exclusive nocturnal increase in invertebrate feeders relative to all other trophic groups suggests this is independent from the provision of shelter provided by seagrass beds at night. Our study suggests that the reported increase is the result of the greater availability of invertebrate food resources that have been widely reported at night within seagrass beds from other biogeographic regions (Bauer, 1985; Howard, 1987; Sogard and Able, 1994; Guest et al., 2003). The small increase in herbivores, however, is unlikely to be effected by increased food resources as both seagrass and the abundant attached algae are available day and night. Although many of these species such as *Dischistodus perspicillatus* are considered seagrass residents they also inhabit mixed seagrass, coral and algal habitats and may remain in such habitats during the day, utilising holes in the sediment or hiding in dense foliage (Griffiths, 2001). Shelter in seagrass dominated habitats at night may cause such species to move further inshore. The overall low abundance of herbivorous fish, particularly those belonging to the family Siganidae, is unexpected as these fish usually dominate seagrass beds throughout Indonesia (Tomascik et al., 1997). This result may be due to the large distance between local mangroves (3 km) and the seagrass study sites reducing the influence of organic matter on food webs relative to seagrasses close to mangroves. Increased organic matter from mangroves has consequences for

increasing algal epiphyte communities to which Siganidae are known to be particularly dependent (Dolar and Lepiten, 1991). Research has found increasing evidence that seagrass bed utilisation by fauna may be more related to elevated food levels than to the shelter provided by these complex habitats (Bologna and Heck, 1999; Bostrom and Mattila, 1999; Jenkins and Hamer, 2001). The present research suggests that food resources are important in structuring fish assemblages in these seagrass beds in Indonesia, but that this trend is not ubiquitous for all fish species, with some species being highly influenced by the provision of shelter from predation at night (e.g. herbivores). These findings corroborate those of comparable research in eastern Australia (Robertson and Howard, 1978; Robertson, 1980) and the Caribbean (Nagelkerken et al., 2000) that found diel changes in seagrass fish assemblages to be structured by food availability and the provision of shelter.

Invertebrate feeders and mixed invertebrate and fish feeders dominated the trophic structure of the fish assemblages. Such separation of a seagrass fish assemblage into separate trophic groups has not commonly been conducted, so few comparable studies exist. The present study, that of Nakamura et al. (2003) in Japan and the work of Khalaf and Kochzius (2002) in the Red Sea have shown that seagrass beds do not contain geographically consistent trophic assemblages suggesting factors such as tidal movements and currents may have high local or regional significance.

#### 4.3. Species assemblages

Seagrass beds of the Wakatobi MNP comprised species rich fish assemblages, with this richness being relatively high for one small location within the marine park ( $\approx 3 \text{ km}^2$ ). These diverse fish assemblages have large value to the local communities as a high proportion of the species (>30 species) are utilised by subsistence fisheries (May, 2005). Studies in other areas of the Indo-Pacific have found fewer species over much larger spatial scales (Nakamura and Sano, 2004; Dorenbosch et al., 2005).

Criticisms of seine netting are the under-sampling of gobies and blennies, fast swimmers and pelagic fish (Gell and Whittington, 2002). The present study contained all these fish groups, yet underwater visual census in the area (Unsworth, personal observation) suggests that the present study may suffer from similar bias and cannot be considered an absolute sample of the fish assemblage. For complete sampling of the fish population a combination of sampling methods may be necessary such as the additional use of underwater visual census.

This study showed *Atherinomorus lacunosus* and four species of Apogonidae to be the most abundant fish, and that many species were rare indicating uneven, yet species rich fish assemblages. Other studies within Indonesia have found different fish assemblages to the present study (Marasabessy and Hukom, 1989; Kuriandewa et al., 2003). Differences between these studies indicates that there are large changes in seagrass fish assemblages over reasonably small spatial scales within Indonesia, which may reflect local environmental conditions, other available food and shelter resources (e.g.

mangroves) (Skilleter et al., 2005) as well as the health and diversity of associated reef systems. Connectivity between these two habitats is bidirectional; therefore it is important to consider that faunal assemblages residing in both of these habitats will have large influence upon each other.

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