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INFLUENCE OF ENVIRONMENTAL CYCLES UPON A SEAGRASS CARIDEAN SHRIMP ASSEMBLAGE

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ABSTRACT. – Seagrass meadows are an ecologically and economically important resource throughout the Indo-Pacific bio-region, but ecological understanding of their faunal assemblages remains largely lacking, with faunal research mostly focussed upon studies of fish. The present study investigated the short-term temporal dynamics of caridean shrimp in relation to diel, tidal and lunar cycles. Such assemblages are important given their link between primary production and higher trophic levels such as fish. Caridean shrimp were found to be at maximal abundance and diversity (Hill's N2) at night and during the waxing moon, increasing by a factor of 4 at night, with assemblage structure significantly influenced by both these factors. Although subtle changes in daily tidal height had little effect upon caridean assemblages, it is thought that the lunar changes that consequentially affect tides (spring to neaps) were key influences upon why caridean shrimp are in greater abundance during the waxing moon. Discussed is the potential for caridean shrimp to undertake inter-habitat migrations in relation to these environmental cycles.

KEY WORDS. – Tidal; Diel; Lunar; Crustacean; Indonesia; Connectivity; Moon; Phases; Indo-Pacific.

INTRODUCTION

Seagrass meadows are an ecologically and economically important resource throughout the Indo-Pacific bio-region (Costanza et al., 1997; de la Torre-Castro & Rönnbäck, 2004). Although numerous studies have described the structural elements of seagrass habitat, the basic functional relationships of the community as a whole remain only partly understood, and then only in few localities (Nakaoka, 2005; Parrish, 1989). This is particularly the case throughout the Indo-Pacific region where seagrass meadows are now experiencing an unprecedented level of damage, deterioration and overexploitation, mostly attributed to human activities (Orth et al., 2006; Waycott et al., 2009; Unsworth & Cullen, 2010). Effective management of seagrass ecosystems requires a greater understanding of their structuring processes (Parrish, 1989).

For the majority of marine taxa, the Indo-Pacific is where faunal diversity is at its highest (Price, 2002), and consequently trophic interactions become more complex. Caridean and dendrobranchiate shrimps commonly dominate tropical seagrass meadows and comprise mixed trophic assemblages that contain both predatory and herbivorous species (Bauer, 1985a, 1985b). Currently, there is limited information regarding such motile macro-invertebrate assemblages residing within seagrass meadows of the Indo-Pacific region. Due to the high biomass and important trophic linkages of shrimp with other marine fauna this is a cause for concern (Barba et al., 2005; Garcia Raso et al., 2006; Greening & Livingston, 1982; Unsworth et al., 2007d). In view of their dominance and diverse trophic roles, seagrass-dwelling shrimps constitute an important link between primary production and higher trophic levels (De Grave et al., 2006; Vonk et al., 2008a). Some species of caridean shrimp also play key roles in the re-mineralisation of seagrass flora (Vonk et al., 2008b). Despite their importance, research on seagrass shrimp assemblages in the Indo-Pacific has only made limited progress beyond species inventory work such as Ledoyer (1969, 1984). Investigation of the relationships between seagrass shrimp fauna and habitat complexity has been undertaken (Mellors & Marsh, 1993; Unsworth et al., 2007b), together with species specific studies upon shrimp burrows (Vonk et al., 2008b). Larger assemblage based studies that seek to understand temporal change have not been conducted.

Connectivity among tropical shallow water habitats influences many fish and crustacean assemblages (Nagelkerken et al., 2000; Mumby et al., 2003): many of these connections have been found to be driven by environmental cycles such as tides and other diel changes (Unsworth et al., 2007a, 2007d). This is because the availability and use of inter-tidal seagrass meadows by faunal assemblages is influenced by three concurrent environmental cycles (diel, lunar and tidal cycles). It might be expected that each flooding tide may bring some small invertebrate fauna into seagrass meadows from adjoining habitats, such as coral reefs, algal meadows or mud flats, when seeking refuge or additional foraging opportunities at high tide in the seagrass meadows (Penn, 1975; Bretsch & Allen, 2006). Additionally some species may be adapted to remain within the meadow, and as the tide floods this fauna may emerge from burrows or flooded pools, and become more active. Changes in diel activity patterns have commonly been observed within shrimp fauna of other regions (De Grave et al., 2006). This diel pattern has been linked to increased nocturnal activity, diurnal net avoidance, nocturnal migration onto meadows from adjacent habitats, habitat patchiness and visual predator avoidance (Bauer, 1985a; Garcia Raso et al., 2006; Greening & Livingston, 1982). Finally, the lunar cycle determines the temporal and spatial availability of intertidal seagrass meadows through the action of the tides. At neap tide, less meadow area is flooded, whilst at spring tide, the seagrass is totally inundated. The influence that this lunar cycle has upon the abundance and assemblage composition of the caridean shrimps remains largely unstudied, particularly how this integrates with diel and tidal cycles. Due to the varying availability of light throughout the different phases of the lunar cycle it may be possible that lunar periodicity occurs, as has been documented in other regions on other fauna (Courtney et al., 1996; De Grave et al., 2006).

An understanding of the influence of environmental cycles upon faunal assemblages within seagrass meadows is critical for developing a greater knowledge of the processes of habitat connectivity commonly structuring their faunal assemblage (Unsworth et al., 2008). This has implications for understanding the role that these assemblages play in supporting higher trophic organisms such as fish, as well as providing the basis for future studies of habitat connectivity.

The present study investigated the influence of environmental cycles upon the caridean shrimp fauna of a seagrass meadow in the Wakatobi National Park, Indonesia. Specific questions addressed relate to how the assemblage is influenced by diurnally changing light levels, tidal and lunar cycles and how this varies on a species level.

MATERIALS AND METHODS

***Study site* –** The present study was conducted between 27 July and 18 August 2006 on the inter-tidal seagrass meadows around the North-West point of Hoga Island, within the Wakatobi National Park (WNP), SE Sulawesi, Indonesia (Unsworth et al., 2007c) (Fig. 1). The WNP is situated in the Tukang Besi archipelago, a remote island group of about 200,000 hectares (Elliot et al., 2001), and is home to approximately 90,000 people. Extensive reef and seagrass systems occur, supporting significant fin- and shell-fisheries (Cullen et al., 2007). The seagrass meadows lie between fringing reefs and the shoreline, and are representative of habitats found across large sections of the Indo–Pacific Ocean (Kirkman & Kirkman, 2002).

Seagrass meadows 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, a sampling site was chosen containing continuous seagrass meadows with high biomass and complexity. This was considered representative of seagrass meadows throughout the WNP (Unsworth, 2010). The sampling site 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 amounts (total cover <5%) of *Cymodocea rotundata* (Ehrenberg and Hemprich ex Ascherson), *Halophila ovalis* (Brown) Hooker f., and occasionally *Halodule uninervis* (Forsskal) Ascherson. Seagrass habitats within the sampling site were continuous from the shore to deeper sub-tidal areas where benthic sediment becomes thin and coral 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 (see Unsworth et al., 2007d). The maximum amplitude of the tide is 2.3 m.

***Shrimp fauna* –** Three independent samples of epifaunal seagrass dwelling shrimp were collected at the sampling site at high and low tide, during both day and night within each of the four phases of the lunar month (new moon, waxing moon, full moon, and waning moon). At the sampling site, the water level as defined as “low tide” was approximately

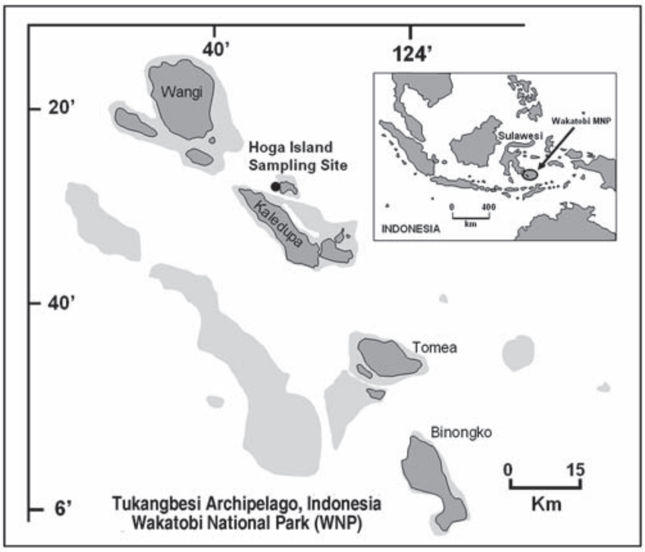

Fig. 1. Location of the study sites on Hoga Island in the Wakatobi National Park (WNP), south-east Sulawesi, Indonesia.

0.5–0.7 m deep, whilst the "high tide" was approximately 1.2–1.8 m deep. These sites are intertidal but during the study period the tidal ranges were not sufficiently large for them to become exposed. Shrimp of the new moon were sampled on the 27 and 28 July, those on the waxing moon were sampled on the 4 August, whilst the full moon and waning moon were sampled on 9, 16 and 17 August respectively. Forty eight samples were taken overall. Samples were considered independent, as they were taken a minimum of 10 m from each other. Each separate sample (regarded as semi-quantitative) was taken using a standardised push net technique (see Bauer, 1985b; De Grave et al., 2006). The net, with a mouth of 0.1 m^2 and 1 mm mesh size, was pushed over the seafloor for 10 m, thus sampling a total volume of 1 m^3 of water. Sampling at high tide was facilitated by the use of a weight belt, snorkel and mask to enable a linear walk to be maintained. All samples were preserved in 70% alcohol and identified in the laboratory.

Data analysis. – Summary statistics were calculated and all mean values are displayed together with their standard errors. Total shrimp abundance and species richness were analysed using three-way general linear models (GLM) ANOVA and Tukey's pairwise comparisons using Minitab (ver. 15). Analysis of differences in shrimp assemblage structure was conducted using multivariate non-metric multidimensional scaling (nMDS) and Bray–Curtis cluster analysis using the computer package PRIMER (ver. 6.1.5) (Clarke & Warwick, 1994). A two-way ANOSIM was used to quantify lunar, tidal and diel effects on shrimp assemblage structure (Clarke & Warwick, 1994).

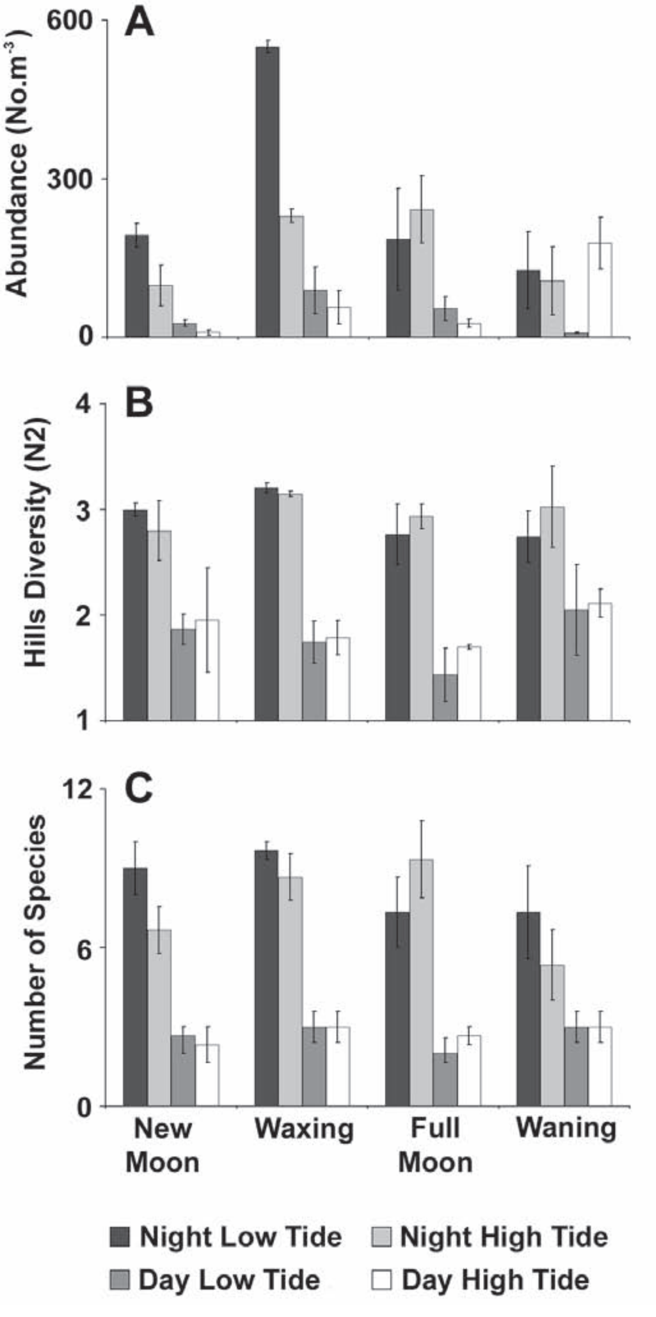

Fig. 2. Mean (+S.E.) shrimp assemblage characteristics at the different sampling times during the lunar, tidal and diel cycle.

RESULTS

Seventeen species of caridean shrimp were recorded during the present study, at a mean density of 136.7 ± 21.1 individuals. m^{-3} (across all states of the tide, time of day and period of the lunar cycle). The fauna was numerically dominated by three species: *Hippolyte* cf. *ventricosa*, *Chlorocurtis jactans*, and *Clytomanningus coutierei* (Table 1).

Total shrimp abundance was found to be significantly influenced by tidal ($F_{1,\ 47}$ = 12.7, p<0.001), lunar ($F_{3,47}$ = 5.96, p<0.01) and diel ($F_{1,47}$ = 55.8, p<0.0001) cycles (Fig. 2); however there was a significant interaction between all three factors (P<0.01). Shrimp abundance increased by approximately a factor of four at night (Day: 56.5 ± 13.6, Night: 216 ± 32.8 individuals.m^{-3}). The lunar cycle resulted in shrimp abundance peaking during the waxing moon (231.5 ± 60.1 individuals.m^{-3}); they were numerically lower at full moon (127.4 ± 36.9 individuals.m^{-3}), waning moon (105.5 ± 29.7 individuals.m^{-3}) and lowest at new moon (82.3 ± 23.9 individuals.m^{-3}). Shrimp abundance was on average 42% higher at low tide than at high tide. Shrimp species richness was found to be significantly higher at night (66% increase) than in the day ($F_{1,47}$ = 114.4, p<0.0001), but was not significantly affected by tidal or lunar changes. Diversity (Hill's N2) was also reduced during daylight relative to night, and had its highest diversity during the waxing moon

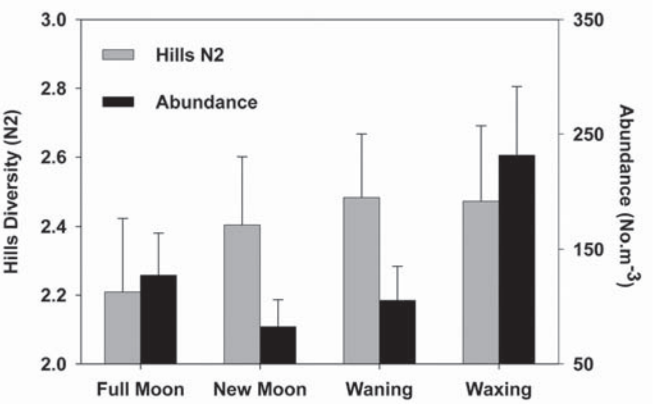

Fig. 3. Mean (+S.E.) shrimp abundance and diversity (Hill's N2) during the lunar cycle.

(Fig. 3). The shrimp assemblage structure changed with environmental cycles. Diel (Global R = 0.15, $p<0.05$) and lunar (Global R = 0.815, $p<0.001$) cycles were both found to significantly influence shrimp assemblage structure, but no influence of the daily tidal cycle was found (Fig. 4). However, ANOSIM pairwise comparisons revealed that significant lunar differences in assemblage structure were only present between waxing and full moon, and the waxing and waning moons.

Of the 17 species, eight were exclusively encountered at night, including three of the more abundant species (*Nikoides danae*, *Processa australiensis*, *Hayashidonus japonicus*). The abundant seagrass specialist, *C. coutierei*, which had a mean abundance of 48.m^{-3} at night, was only recorded at 0.04 m^{-3} in the day. The two most abundant species, *H.* cf. *ventricosa* and *C. jactans*, although most abundant at night, still had at least a third of their night time abundance present in the day (Table 1).

Although the relative abundance of individual species changed with each lunar phase, all of the abundant species were present throughout. Only those species considered rare (i.e., limited low abundance occurrences) were absent from certain sectors of the lunar phase, probably as a result of low sampling returns rather than lunar cycle induced. All of the six most abundant species (*C. jactans*, *H.* cf. *ventricosa*, *C. coutierei*, *N. danae*, *Cuapetes* cf. *ensifrons*, and *P. australiensis*) were observed to have their highest density during the period of the waxing moon, with lowest density occurring during the period of the waning moon. For example, the seagrass/algal specialist, *H.* cf. *ventricosa*, was at least 2.5 times more abundant during the waxing moon than in other phases.

DISCUSSION

This is the first research to integrate the study of lunar, diel and tidal cycles in order to understand the rhythms of a macro-invertebrate assemblage in an Indo-Pacific seagrass meadow. Here we reject our null hypothesis and document that diel, tidal and lunar cycles strongly and interactively influence the abundance and diversity of a caridean shrimp assemblage in an Indonesian, *Thalassia hemprichii* dominated seagrass meadow. The abundance of caridean shrimp increased by a factor of four at night: this was both the result of an increase in the relative abundance of individual species, and an influx of new species into the assemblage.

Fig. 4. Two-dimensional nMDS scaling configuration. Plotted on the figure are 70% Bray-Curtis similarity clusters calculated using PRIMER

The changes in the abundance of organisms residing in these tropical seagrass meadows are not unique, as both fish and small invertebrate assemblages have been found to undertake diel changes in their population structure, with higher abundance and species richness occurring at night (Robertson & Howard, 1978; Robblee & Zieman, 1984; Sogard & Able, 1994; De Grave et al., 2006).

In the marine environment, light plays an important role in faunal habitat utilization by controlling the levels of intra- and inter-specific competition (McIntosh & Towsend, 1994; Pittman & McAlpine, 2001; Aguzzi et al., 2007). Organisms, including small crustaceans and larvae, make migrations between habitats in order to obtain food, or to escape inter-specific predatory pressures (De Grave & Turner, 1997; Aguzzi et al., 2007; Unsworth et al., 2007d).

In the present study, eight species were only observed to be present at night; this included three of the more abundant species (*N. danae, P. australiensis, H. japonicus*). As both *N. danae* and *H. japonicus* could be considered as seagrass specialists (Ledoyer, 1969, 1984), this indicates that their presence at night is not related to inter-habitat migration, but instead related to activity (assuming previous habitat usage characterisation is correct). These shrimp may spend daylight hours hidden within small, isolated coral heads/boulders, or buried within the sand, emerging to feed at night. *Processa australiensis*, although only recorded in seagrass at night, have been recorded living within the coral matrix on the Great Barrier Reef (Preston & Doherty, 1990). The potential for these species to conduct diel migrations between habitats for feeding is entirely plausible and demands further investigation. The other species that were only recorded at night were in such low abundance that no further inferences can be made.

Some species, although more abundant at night, were also recorded during daylight hours, such as the potential seagrass specialist, *C. coutierei* (see Ledoyer, 1969, 1984). The two most abundant species, *H.* cf. *ventricosa* and *C. jactans*, also had reduced daylight abundance. Elsewhere these species have also been recorded within the coral matrix during daylight hours (Preston & Doherty, 1990), although potentially associated with algae, and this could be indicative of diel migratory pathways.

In many marine habitats, fish assemblage structure, diversity and abundance has been found to be influenced by tidal fluxes (Gibson, 2003; Unsworth et al., 2007a). Here we find that subtle tidal differences had only limited influence upon the abundance and assemblage structure of caridean shrimp. This may indicate that any inter-habitat movements

Table 1. Mean (± S.E.; n=6) abundances of shrimp species at the different sampling times of the lunar and diel cycle (averaged across high and low tide) in the Wakatobi National Park, Indonesia.

Species	**Family**	**New Moon Night**		**New Moon Day**		**Waxing Night**		**Waxing Day**		**Full Moon Night**		**Full Moon Day**		**Waning Night**		**Waning Day**		**Total**	
Hippolyte cf. ventricosa H. Milne Edwards, 1837	Hippolytidae	50.8	±14.0	6.8	±2.6	156.8	±31.4	27.7	±12.3	74.2	±33.6	16.2	±6.0	53.7	±23.9	44.0	±19.2	53.8	±9.3
Chlorocurtis jactans (Nobili, 1904)	Pandalidae	61.5	±10.8	11.2	±2.8	130.2	±26.1	44.0	±12.9	60.7	±13	23.8	±10.1	39.7	±13.1	47.2	±24.5	52.3	±7.1
Clytomanningus coutierei (Nobili, 1904)	Processidae	22.7	±4.0			69.2	±12.0	0.2	±0.2	57.7	±16.5			18	±6.3			21.0	±4.6
Nikoides danae (Paulson, 1875)	Processidae	2.7	±1.0			7.5	±2.2			5.7	±1.6			0.8	±0.4			2.1	±0.5
Cuapetes cf. ensifrons (Dana, 1852)	Palaemonidae	0.2	±0.2	0.3	±0.2	7.7	±3.8			4.0	±3.2			0.8	±0.5	0.2	±0.2	1.7	±0.7
Processa australiensis Baker, 1907	Palaemonidae	1.3	±0.5			6.3	±2.9			4.2	±1.2			1.0	±0.6			1.6	±0.5
Kemponia seychellensis (Borradaile, 1915)	Palaemonidae	1.2	±0.8			3.7	±1.2	0.7	±0.3	4.5	±2.1	0.3	±0.3	0.7	±0.3	0.5	±0.5	1.4	±0.4
Processa zostericola Hayashi, 1975	Processidae	1.5	±0.6			3.0	±1.5			0.8	±0.5			1.3	±0.5	0.2	±0.2	0.9	±0.3
Hayashidonus japonicus (De Haan, 1844)	Processidae	2.2	±0.7			3.0	±0.9			0.5	±0.4			0.7	±0.5			0.8	±0.2
Cuapetes sp. A	Palaemonidae	0.3	±0.2			0.8	±0.8	0.5	±0.3			0.3	±0.2			1.7	±1.5	0.5	±0.2
Philocheras plebs (Kemp, 1916)	Crangonidae	0.7	±0.3	0.2	±0.2	0.8	±0.4			1.0	±0.4					0.2	±0.2	0.4	±0.1
Alpheus sp.	Alpheidae	0.3	±0.2	0.2	±0.2	0.8	±0.6			0.5	±0.3							0.2	±0.1
Philocheras wilkinsae De Grave, 2000	Crangonidae	0.3	±0.2			0.2	±0.2			0.3	±0.3			0.2	±0.2			0.1	±0.1
Salmoneus sp.	Alpheidae													0.2	±0.2			0.1	±0.1
Saron sp.	Hippolytidae									0.1	±0.2							0.1	±0.1
Periclimenes soror Nobili, 1904	Palaemonidae													0.2	±0.2			0.1	±0.1
Thor amboinensis (De Man 1888)	Hippolytidae	0.3	±0.3															0.1	±0.1
	Total	146	±29.3	18.7	±5.3	390.0	±72.0	73.0	±25.3	214.2	±53.2	40.7	±12.6	117.2	±43.9	93.8	±43.7	136.7	±21.1

of caridean shrimp are active rather than passive (utilising the tidal movement), however such habitat movements by caridean shrimp may also not be as prevalent as those of other faunal groups. Alternatively, the small size of most caridean shrimps precludes diel movement on a seagrass meadow spatial scale.

Lunar periodicity can have a major influence upon the physiology and behaviour of organisms (Emata, 2003; Peres & Bellwood, 1988; Rahman et al., 2004) and consequently upon a whole species assemblage (Morgado et al., 2003). The present study finds seagrass dwelling shrimp to be influenced by different phases of the lunar cycle, with significantly higher abundance recorded during the waxing moon. These observations correspond to similar patterns observed for the caridean shrimp species *Latreutes fucorum* and *Processa fimbriata* within Caribbean seagrass meadows (De Grave et al., 2006). During the waxing moon relative to the full moon, tidal range is smaller and hence tidal currents are less. Therefore, although small subtle tidal differences throughout a day might not affect these caridean shrimp, we hypothesise that the smaller currents during the waxing moon may facilitate easier movement for shrimp as compared to the spring tides around full moon, allowing greater activity. Abundance of caridean shrimp was also recorded as higher during the waxing moon relative to the waning moon. This observation may be considered surprising given that lunar light intensity during the waning and waxing moons are similar, and that lunar light stimuli is likely to be the major driver of any lunar periodicity. Similar differences in shrimp abundance between waning and waxing lunar periods have been recorded within Caribbean seagrass meadows (De Grave et al., 2006). Currently, no explanation can be offered for this lunar discrepancy, but speculatively it could be related to breeding and/or molting cycles of the species concerned.

In conclusion we find seagrass meadows to be abundant in caridean shrimp fauna, a potentially important prey for numerous economically important fish species (e.g., Lethrinidae and Lutjanidae). These seagrass dwelling caridean shrimp were found to be highly influenced by environmental cycles, particularly diel and lunar cycles. No studies exist to determine whether fish assemblages respond to these changes in prey abundance throughout the lunar cycle; however research in the Wakatobi (in exactly the same location as the present study) has confirmed that seagrass meadows contain a significantly higher abundance of invertebrate feeding fish at night (Unsworth et al., 2007d), suggesting that fish move into seagrass meadows in order to feed on the abundant invertebrates such as caridean shrimp. As shrimp abundance is maximal on the waxing moon it might therefore also be hypothesised that invertebrate feeding fish abudance peaks during this time. Such a hypothesis requires quantification to more fully understand the trophic interactions of the faunal communities of seagrass meadows in the Indo-Pacific. The present study also confirms research from other regions of the globe suggesting that studies of shrimp fauna should consider diel and lunar variation as important factors in the design of sampling regimes.

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LITERATURE CITED

Aguzzi, J., J. B. Company, P. Abelló & J. A. García, 2007. Rhythmic diel movements of pandalid shrimps in the western Mediterranean continental shelf and upper slope. *Journal of Zoology*, **273**: 340–349.

Barba, E., A. Raz-Guzman & A. J. Sanchez, 2005. Distribution patterns of estuarine caridean shrimps in the south-western Gulf of Mexico. *Crustaceana*, **78**: 709–726.

Bauer, R. T., 1985a. Diel and seasonal variation in species composition and abundance of caridean shrimps (Crustacea, Decapoda) from Seagrass meadows on the north coast of Puerto Rico. *Bulletin Marine Science*, **36**: 150–162.

Bauer, R. T., 1985b. Penaeid shrimp fauna from tropical seagrass meadows - species composition, diurnal, and seasonal-variation in abundance. *Proceedings of the Biological Society of Washington*, **98**(1): 177–190.

Bretsch, K. & D. M. Allen, 2006. Tidal migrations of nekton in salt marsh intertidal creeks. *Estuaries and Coasts*, **29**: 474–486.

Clarke, K. R. & R. M. Warwick, 1994. Changes in marine communities: an approach to statistical analysis and interpretation. *Natural Environmental Research Council, Plymouth Marine Laboratory, Plymouth, United Kingdom*.

Costanza, R., R. d'Arge, R. De Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. O'Neill, J. Paruelo, R.G. Raskin, P. Sutton & M. van den Belt, 1997. The value of the world's ecosystem services and natural capital. *Nature*, **287**: 253–260.

Courtney, A. J., D. J. Die & J. G. McGilvray, 1996. Lunar periodicity in catch rate and reproductive condition of adult eastern king prawns, *Penaeus plebejus*, in coastal waters of south-eastern Queensland, Australia. *Marine and Freshwater Research*, **47**: 67–76.

Cullen, L. C., J. Pretty, D. J. Smith & S. P. Pilgrim, 2007. Links between local ecological knowledge and wealth in indigenous communities of Indonesia: Implications for conservation of marine resources. *The International Journal of Interdisciplinary Social Sciences*, **2**: 289–299.

De Grave, S., D. Livingston, & M. R. Speight, 2006. Diel variation in sea grass dwelling shrimp: when to sample at night ? *Journal of the Marine Biological Association of the United Kingdom*, **86**: 5363/5361–5362.

De Grave, S. & J. R. Turner, 1997. Activity rhythms of the squat lobsters, *Galathea squamifera* and *G. strigosa* (Crustacea: Decapoda: Anomura) in south-west Ireland. *Journal of the Marine Biological Association of the United Kingdom*, **77**: 273–276.

de la Torre-Castro, M. & P. Rönnbäck, 2004. Links between humans and seagrasses - an example from tropical East Africa. *Ocean and Coastal Management*, **47**: 361–387.

Elliot, G., B. Mitchell, B. Wiltshire, I. Manan & S. Wismer, 2001. Community participation in marine protected area management: Wakatobi National Park, Sulawesi, Indonesia. *Coastal Management*, **29**: 295–316.

Emata, A.C., 2003. Reproductive performance in induced and spontaneous spawning of the mangrove red snapper, *Lutjanus* *argentimaculatus*: a potential candidate species for sustainable aquaculture. *Aquaculture Research*, **34**: 849–857.

Garcia Raso, J. E., M. J. Martin, V. Diaz, V. Cobos & M. E. Manjon-Cabeza, 2006. Diel and seasonal changes in the structure of a decapod (Crustacea: Decapoda) community of *Cymodocea nodosa* from south-eastern Spain (West Mediterranean Sea). *Hydrobiologia,* **557**: 59–68.

Gibson, R. N., 2003. Go with the flow: tidal migration in marine animals. *Hydrobiologia*, **503**: 153–161.

Greening, H. S. & R. J. Livingston, 1982. Diel variation in structure of seagrass-associated epibenthic macroinvertebrate communities. *Marine Ecology Progress Series,* **7**: 147–156.

Kirkman, H. & J. A. Kirkman, 2002 The management of seagrasses in Southeast Asia. *Bulletin Marine Science,* **71**: 1379–1390.

Ledoyer, M., 1969. Les caridea de la frondaison des herbiers de phanérogames de la région de Tuléar. *Recueil des Travaux de la Station marine d Endoume Supplement*, **8**: 63–115.

Ledoyer, M., 1984. Les caridea (Crustacea: Decapoda) des herbiers de phanérogames marines de Nouvelle-Calédonia (région de Nouméa). *Zoologische Verhandelingen*, **211**: 1–58.

McIntosh, A. R. & C. R. Towsend, 1994. Interpopulation variation in mayfly antipredator tactics: differential effects of contrasting predatory fish. *Ecology*, **75**: 2078–2090.

Mellors, J. E. & H. Marsh, 1993. Relationship between seagrass standing crop and the spatial-distribution and abundance of the Natantian fauna at Green Island, Northern Queensland. *Australian Journal of Marine and Freshwater Research*, **44**: 183–191.

Morgado, F., C. Antunes & R. Pastorinho, 2003. Distribution and patterns of emergence of suprabenthic and pelagic crustaceans in a shallow temperate estuary (Ria de Aveiro, Portugal). *Acta Oecologica,* **24**: S205–S217.

Mumby, P. J., A. J. Edwards, J. E. Arias-Gonza´lez, K. C. Lindeman, P. G. Blackwell, A. Ball, M. I. Gorczynska, A. R. Harborne, C. L. Pescod, H. Renken, C. C. C. Wabnitz, & G. Llewellyn, 2003. Mangroves enhance the biomass of coral reef communities in the Caribbean. *Nature*, **427**: 533–536.

Nagelkerken, I., M. Dorenbosch, W. Verberk, E.C. de la Moriniere & G. van der Velde, 2000. Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. *Marine Ecology Progress Series*, **202**: 175–192.

Nakaoka, M., 2005. Plant-animal interactions in seagrass beds: ongoing and future challenges for understanding population and community dynamics. *Population Ecology*, **47**(3): 167–177.

Orth, R. J., T. J. B. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, J. W. Kenworthy, S. Olyarnik, F. T. Short, M. Waycott & S. L. Williams, 2006. A global crisis for seagrass ecosystems. *Bioscience*, **56**: 987–996.

Parrish, J. D., 1989. Fish communities of interacting shallow-water habitats in tropical oceanic regions. *Marine Ecology Progress Series,* **58**: 143–160.

Penn, J. W., 1975. The influence of tidal cycles on the distributional pathway of *Penaeus latisulcatus* Kishinouye in Shark Bay, Western Australia. *Australian Journal of Marine and Freshwater Research*, **26**: 93–102.

Peres, O. S. & D. R. Bellwood, 1988. Ontogenetic changes in the natural diet of the sandy shore crab, *Matuta lunaris* (Forskal) (Brachyura: Calappidae). *Australian Journal of Marine and Freshwater Research*, **39**: 193–199.

Pittman, S. J. & C. A. McAlpine, 2001. Movements of marine fish and decapod crustaceans: process, theory and application. *Advances in Marine Biology*, **44**: 206–295.

Preston, N. P. & P. J. Doherty, 1990. Cross-shelf patterns in the community structure of coral-dwelling Crustacea in the central region of the Great Barrier Reef. I. Agile shrimps. *Marine Ecology Progress Series*, **66**: 47–61.

Price, A. R. G., 2002. Simultaneous hotspots and coldspots of marine biodiversity and implications for global conservation. *Marine Ecology Progress Series*, **241**: 23–27.

Rahman, M. S., K. Byung-Ho, A. Takemura, P. Chang-Bum & L. Young-Don, 2004. Influence of light-dark and lunar cycles on the ocular melatonin rhythms in the seagrass rabbitfish, a lunar-synchronized spawner. *Journal Pineal Research*, **37**: 122–128.

Robblee, M. B. & J. C. Zieman, 1984. Diel variation in the fish fauna of a tropical seagrass feeding ground. *Bulletin of Marine Science*, **34**(3): 335–345.

Robertson, A. I. & R. K. Howard, 1978. Diel trophic interactions between vertically migrating zooplankton and their fish predators in an eelgrass community. *Marine Biology*, **48**: 207–213.

Sogard, S. M. & K. W. Able, 1994. Diel variation in immigration of fishes and decapod crustaceans to artificial seagrass habitat. *Estuaries*, **17**(3): 622–630.

Unsworth, R. K. F., 2010. Seagrass meadows of the Wakatobi National Park. In: Clifton, J., R.K.F. Unsworth & D.J. Smith, (Eds) 2010. Marine Conservation and Research in the Coral Triangle: The Wakatobi National Park. Nova Publishers, New York: 101–126.

Unsworth, R. K. F., J. J. Bell, & D. J. Smith, 2007a. Tidal fish connectivity of reef and seagrass habitats in the Indo-Pacific. *Journal of the Marine Biological Association of the United Kingdom*, **87**: 1287–1296.

Unsworth, R. K. F., & L. C. Cullen, 2010. Recognising the necessity for Indo-Pacific seagrass conservation. *Conservation Letters* DOI: 10.1111/j.1755-263X.2010.00101.x

Unsworth, R. K. F., S. De Grave, J. Jompa, D. J. Smith & J. J. Bell, 2007b. Faunal relationships with seagrass habitat structure: an example using shrimp from the Indo-Pacific. *Marine and Freshwater Research*, **58**: 1008–1018.

Unsworth, R. K. F., P. Salinas De Leon, S. Garrard, J. Jompa, D. J. Smith, & J. J. Bell, 2008. High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats. *Marine Ecology Progress Series*, **353**: 213–224.

Unsworth, R. K. F., D. J. Smith, A. Powell & F. Hukon, 2007c. The effectiveness of small scale 'No-take Areas' as tools in conservation management of locally exploited coral reef fisheries. *Marine Biology*, **152**: 243–254.

Unsworth, R. K. F., E. Wylie, J. J. Bell, & D. J. Smith, 2007d. Diel trophic structuring of Seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia. *Estuarine Coastal and Shelf Science*, **72**: 81–88.

Vonk, J. A., M. J. A. Christianen & J. Stapel, 2008a. Redefining the trophic importance of seagrasses for fauna in tropical Indo-Pacific meadows. *Estuarine Coastal and Shelf Science*, **79**: 653–660.

Vonk, J. A., D. Kneer, J. Stapel & H. Asmus, 2008b. Shrimp burrows in tropical seagrass meadows: An important sink for litter. *Estuarine Coastal and Shelf Science*, **79**: 79–85.

Waycott, M., C. M. Duarte, T. Carruthers, J. J. Orth, W. C. Dennison, S. Olyarnik, A. Calladine, J.W. Fourqurean, K. L. Heck, R. Hughes, G. A. Kendrick, W. J. Kenworthy, F. Short & S. L. Williams, 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **106**: 12377–12381.