

Diel variation in sea grass dwelling shrimp: when to sample at night?

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The present study investigates hourly variation in nocturnal abundance fluctuations in a tropical, Caribbean sea grass bed. As expected, results indicate that significant diel variation is present. In addition all dominant species show an abundance peak shortly after sunset, with numbers gradually declining throughout the night. It is therefore suggested that nocturnal samples are not only incorporated into any sampling regime, but that nocturnal samples are taken within two hours after sunset.

Tropical sea grass beds and their associated epiphytes form a habitat for a diverse assemblage of organisms, ranging from microflora and fauna through to manatees (Nakaoka, 2005). Although numerous studies have described the structural elements of the sea grass habitat, the basic functional relationships of the community as a whole remain only partly understood (Nakaoka, 2005). In part this is due to a plethora of temporal sampling regimes and differing sampling techniques (e.g. beam trawl, drop net, sweep nets) being employed. This is particularly evident for the epifaunal assemblage, where caridean and dendrobranchiate shrimps dominate (e.g. Greening & Livingston, 1982; Barba et al., 2005; García Raso et al., 2006). In view of this numerical dominance, sea grass dwelling shrimps constitute an important trophic link between primary production and higher trophic levels.

Since the 1980s the diel variation in activity patterns of sea grass dwelling shrimp has been documented several times (Greening & Livingston, 1982; Bauer, 1985; García Raso et al., 2006). During the day, Hippolytidae, such as *Hippolyte obliquimanus* Dana and *Latreutes fucorum* (Fabricius) are abundant (Bauer, 1985), these being species which cling to sea grass blades and are cryptically coloured to reduce vulnerability to visual predators. During the night a more diverse assemblage is present, numerically dominated by Processidae (e.g. Bauer, 1985). This diel pattern has been linked to increased nocturnal activity, diurnal net avoidance, nocturnal migration onto beds from adjacent habitats, habitat patchiness and visual predator avoidance (Greening & Livingston, 1982; Bauer, 1985; García Raso et al., 2006). Regardless of the underlying cause(s), it seems obvious that nocturnal samples need to be incorporated into any ecological study of the epifaunal component of sea grass beds, both tropical and temperate. Nevertheless, studies continue to ignore this temporal fluctuation and often solely concentrate on diurnal sampling regimes. For instance, the study of Barba et al. (2005) on habitat preferences of an estuarine submerged aquatic vegetation shrimp guild only utilized diurnal trawls, although they did acknowledge that the rarity of some species was due to their nocturnal activity peaks.

Perhaps more concerning is the non-standardized temporal way in which nocturnal samples are taken, for instance between sunset and sunrise (Bauer, 1985), or at least 2 h after sunset (García Raso et al., 2005). As it seems conceivable that within the nocturnal phase, specific shrimp species may exhibit

temporally spaced activity peaks, this may unduly influence any diel analysis. Therefore the present study reappraises not only the overall diel differences in shrimp abundance, but pays specific attention to hourly differences within the nocturnal phase itself.

The present study was carried out in a sea grass bed, located off Isla de Cayo Cochino Menor (Caribbean coast of Honduras). The sea grass bed is primarily composed of dense *Thalassia testudinum* Banks ex König stands, with minor quantities of *Syringodium filiforme* Kützting and epiphytic algae, in a water depth of 1.5 m on a sandy substrate. Triplicate samples of epifaunal shrimp species were taken hourly over a 24 h period, by means of a standardized push net technique (Bauer, 1985), on three dates (15, 22, 29 August 2004) corresponding to different phases of the moon cycle (full moon, waning, waxing). Tidal ranges during the three sampling days were 0.58, 0.28 and 0.67 m, respectively. Sunrise and sunset at the time of sampling were approximately at 0530 and 1800 h, respectively, with the 0600 samples regarded as diurnal. Sampling (regarded as semi-quantitative) was by means of a 20×80 cm aperture push net (1 mm mesh size), which was manually pushed along the sediment–sea grass interface for a distance of 15 m, thereby sampling a total of 12 m². Sorting of the catch was done by eye after initial preservation.

During the full moon sampling cycle, a total of 2318 specimens was captured belonging to 14 shrimp species (Table 1), numerically dominated by two Hippolytidae (*Latreutes fucorum*—55.04% of total catch, *Hippolyte obliquimanus*—17.77%) and one species of Processidae (*Processa fimbriata* Manning & Chace—10.12%). During the waxing and waning moon phase sampling cycles, a total of 2285 and 1976 specimens were captured belonging to the same 14 species. *Latreutes fucorum*, *H. obliquimanus* and *P. fimbriata* again dominated, with respective percentages of total catch being 61.66, 11.77, and 10.28 during the waning moon phase and 66.35, 11.23 and 7.74 during the waxing moon phase. In all three sampling cycles, a number of other species only occurred in very low numbers or were only incidentally caught. These are considered as either vagrant species, such as *Periclimenes longicaudatus* (Stimpson) which also occurs in algal beds (Barba et al., 2005) or burrowing species, such as *Alpheus packardii* Kingsley.

Clear differences in diel periodicity were apparent, with both *L. fucorum* and *H. obliquimanus* being significantly more abundant in nocturnal than diurnal samples (Table 1, full moon cycle), especially *L. fucorum* which exhibits a 15-fold increase in

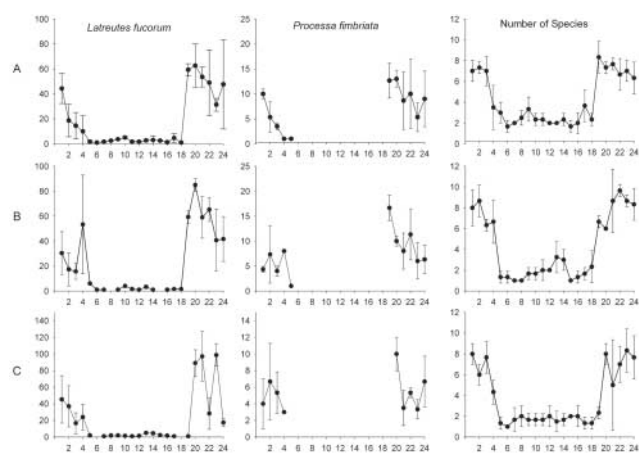


Figure 1. Hourly mean abundance (\pm standard deviation) throughout the diel cycle of *Latreutes fucorum*, *Processa fimbriata* and number of species for (A) the full moon cycle; (B) waning; and (C) waxing moon cycles.

Table 1. Mean values (\pm standard deviation) of total abundance, number of species and species abundance levels for diurnal and nocturnal periods during the full moon sampling cycle, with results from one-way analysis of variance.

	Day	Night	F
Total abundance	5.57 (3.52)	56.94 (46.28)	45.38* _{1,68}
Number of species	2.27 (0.80)	6.58 (2.17)	126.83* _{1,68}
<i>Hippolyte obliquimanus</i> Dana	3.25 (1.99)	8.70 (5.95)	26.91* _{1,67}
<i>Latreutes fucorum</i> (Fabricius)	2.40 (1.58)	35.36 (27.97)	48.50* _{1,66}
<i>Latreutes parvulus</i> (Stimpson)	1.00 (0.02)	4.56 (3.29)	1.13 NS _{1,26}
<i>Thor manningi</i> Chace	1.50 (0.71)	3.20 (1.87)	1.58 NS _{1,25}
<i>Processa bermudensis</i> (Rankin)	–	5.13 (3.12)	–
<i>Processa fimbriata</i> Manning & Chace	–	7.93 (5.62)	–
<i>Leander tenuicornis</i> (Say)	1.00 (0.02)	1.20 (0.42)	0.20 NS _{1,9}
<i>Kemponia americanus</i> (Kingsley)	–	1.00 (0.02)	–
<i>Periclimenes longicaudatus</i> (Stimpson)	–	1.00 (0.02)	–
<i>Periclimenes yucatanicus</i> (Ives)	4.00 (0.02)	–	–
<i>Alpheus packardii</i> Kingsley	–	1.21 (0.58)	–
<i>Sicyonia laevigata</i> Stimpson	–	1.33 (0.50)	–
<i>Tozeuma carolinense</i> Kingsley	1.40 (0.55)	1.00 (0.02)	0.44 NS _{1,4}
<i>Trachycaris restricta</i> (A. Milne-Edwards)	–	1.00 (0.02)	–

*, $P < 0.001$, NS, not significant. [Only species which occurred during both periods were tested.]

abundance (Figure 1). In contrast, both species of *Processa* were only encountered in nocturnal samples (Table 1, Figure 1). A number of other hippolytid species follow the same trend (*Latreutes parvulus* (Stimpson), *Thor manningi* (Chace)), but due to their low frequency are not statistically significant. Similar trends were observed in the other two sampling cycles. Quite logically, given the numerical contribution of the two hippolytid species, total abundance follows the same pattern (Table 1). Equally, species richness is higher during the nocturnal phase (Table 1), clearly linked to the exclusive occurrence of rarer species in nocturnal samples (Table 1). Sampling cycles during waxing and

waning moon phases produced essentially the same results in terms of the diurnal–nocturnal dichotomy of species occurrences and their respective relative abundances.

Although there was no significant difference in hourly mean catch values for any of the species during the hours of darkness (full moon cycle, one-way analysis of variance (ANOVA), all $F < 1.63$, $P > 0.05$), nor for total abundance ($F_{10,22}$ 1.82, $P > 0.05$), or species richness ($F_{10,22}$ 1.40, $P > 0.05$); a gradual decline of catch values (Figure 1) from peak values shortly after sunset for the dominant species was apparent (full moon cycle, nocturnal data only, Pearson's R^2 ; *L. fucorum* -0.42 , *H. obliquimanus* -0.34 , *P. fimbriata* -0.38 , *P. bermudensis* (Rankin) -0.40 , all $P < 0.05$). In all species the first two hours after sunset harboured the highest catch values (e.g. Figure 1A,B). Again, this trend is reflected in total abundance ($R^2 -0.43$, $P < 0.05$). Species richness (Figure 1) exhibits a gradual decline from a minor peak shortly after sunset in the first half of the nocturnal phase, stabilizing in the last half, thus resulting in a non-significant correlation ($R^2 -0.06$). Sampling cycles during the waxing and waning moon phases mirror these trends (Figure 1), with no hourly differences (one-way ANOVA, all $F < 1.72$, all $P > 0.05$), and similar declining trends per species ($-0.32 < R^2 > -0.47$) and total abundance ($R^2 -0.46$, -0.48 , respectively) and no significant decline in species richness ($R^2 -0.03$, -0.05 , respectively).

The results presented here support unequivocally the long established notion of profound diel differences in shrimp abundance values (Greening & Livingston, 1982; Bauer, 1985) and support the contention that community level studies on epifaunal sea grass assemblages should at the very least incorporate nocturnal samples. Further, the results clearly indicate that all dominant species exhibit an activity peak in the first two hours after sunset, with numbers gradually declining throughout the night. It is therefore strongly recommended that future sampling programmes not only incorporate nocturnal samples, but also sample during the first two hours after sunset, which appears to be the optimal sampling time from a community perspective.

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