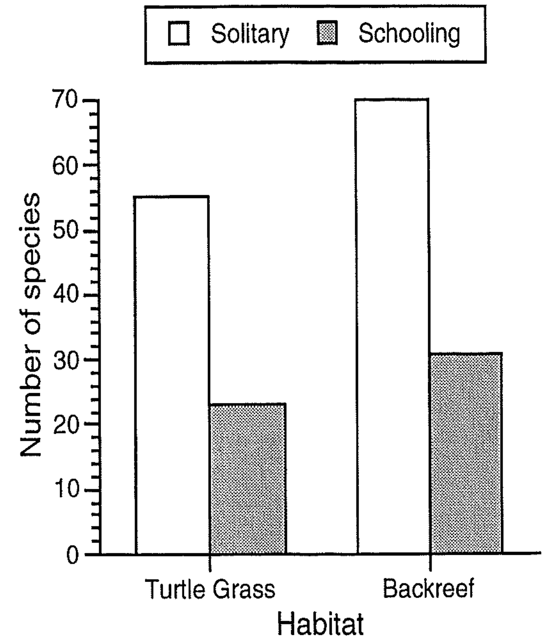

FIG. 3. The proportions of schooling and solitary fish species did not differ between backreef and turtle grass habitats in Discovery Bay, Jamaica, W.I.

Time of day influenced schooling behavior as well as species composition and richness. Most species that schooled were also observed as solitary individuals, suggesting that schooling is not a fixed behavior and it may vary with age or environmental conditions. The proportion of schooling species was higher during the day than the night. This may be because daytime schooling reduces predation by visual predators. Alternatively, damselfish activity may influence schooling behavior. Territorial damselfish defend their algal turfs during day, therefore schooling may be a strategy for overwhelming these defenses and exploiting these resources. However, schooling behavior did not appear to differ between habitat type. This behavioral strategy may be equally important and effective in both habitats.

Fish community structure, species richness and fish behavior were strongly influenced by time of day. Surprisingly, only species richness differed between habitat type. These results imply that temporal shifts in community structure may better facilitate resource partitioning and predator avoidance among tropical fish species. Detailed study of how foraging strategies and predation risk differ between day and night would improve our understanding of the mechanisms that contribute to daily variations in fish activity.

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Zooplankton diel variation on a Caribbean back-reef

Kimberly A. Iwamoto, Jay T. Lennon, and Katharine E. Simon

Abstract: Many zooplankton have evolved a diel vertical migration pattern in which they take refuge in the benthos during the day to avoid visual predators and emerge to feed in the water column at night when predation pressure is lower. In a study of the daily patterns of zooplankton abundance at Discovery Bay, Jamaica, we found that all taxa were more abundant in night than day samples, but the differences were only significant for copepods, decapod larvae, and total zooplankton. Copepods were by far the most abundant taxon in both day and night samples and were responsible for the vast majority of the increase in total zooplankton abundance from day to night. In addition, medium-sized copepods were disproportionately abundant at night, which could be due to stage-based population structure, different diel behavior for each size class, or ontogenetic shifts in migration behavior.

Key Words: copepod, zooplankton size, diel vertical migration, size selective predation

Introduction

Many zooplankton undergo diel vertical migrations in which they remain in the benthos during the day but emerge at night to feed in the water column. It is thought that these daily migrations help zooplankton avoid visual predators that are more active during the day. Thus, we predicted that the density of zooplankton in the water column would be greater at night than during the day. In addition, zooplankton size may influence vulnerability to visual predators. If large zooplankton are easier to see during the day than smaller ones, they may experience stronger selective pressure to perform diel vertical migrations. Therefore, we predicted that within taxa, small individuals should be more abundant in the water column during the day and large individuals would be more abundant at night.

Methods

We collected five replicate zooplankton samples during the day (16:00-17:00) and night (22:00-23:00) on 28 February 2003 near the reef crest in the west-back reef of Discovery Bay, Jamaica, W. I. We sampled zooplankton by towing a plankton net (153 µm mesh, 26 cm diameter) for 40 m back and forth along a 20 m transect at a depth of 20-40 cm. The volume of water filtered in each replicate sample was ~1.06 m^3. Zooplankton were preserved with 10% formalin. We counted zooplankton in gridded Petri dishes using dissecting microscopes. We categorized zooplankton taxa into 11 categories: copepods, amphipods, isopods, decapods, polychaete worms, larval fish, ostracods, medusae, cumacean shrimp, chaetognatha, and larvaceans. We determined zooplankton body sizes for copepods (< 0.5 mm, 0.5 – 1.0 mm), decapod larvae (1.0 – 2.0 mm, and > 2.0 mm), polychaetes (< 1 mm, 1 – 2 mm, and > 2 mm), isopods (< 1 mm, 1 – 2 mm, and > 2 mm), amphipods (< 1 mm, 1 – 2 mm, and > 2 mm), and fish (< 2 mm, 2 – 4 mm, and > 4mm) using a clear plastic ruler under the Petri dish.

We used Student's t-test to determine the effect of time of day on the density of different zooplankton taxa. We corrected p-values (P_{VAR}) using a Welch's ANOVA when the assumption of equal variance was violated (Brown-Forsythe test). We used a two-way ANOVA to test for the main effects of time, size, and their interaction on zooplankton density. We adjusted our p-values using a Bonferroni correction to make sure that we did not increase the likelihood of rejecting the null hypothesis when it was in fact true (type II error). The Bonferroni-corrected p-value equals α (0.05) divided by the number of statistical tests peformed. We did not run statistical tests for zooplankton taxa that had either day or night densities that were below detection limits.

Results

In general, zooplankton densities were greater at night than during the day. However, these differences were only statistically significant for copepods, decapods, and total zooplankton (Table 1, Fig 1). Cumacean shrimp, chaetognaths, and larvaceans were only detected in night samples (Table 1). There was a significant time x day interaction on copepod density (Fig. 2; $F = 42.3$, $df = 2, 9$; $P < 0.0001$;), due to high densities of medium-sized copepods (0.5 – 1 mm) at night. There was no main effect or interaction of size on zooplankton density for any of the other taxa.

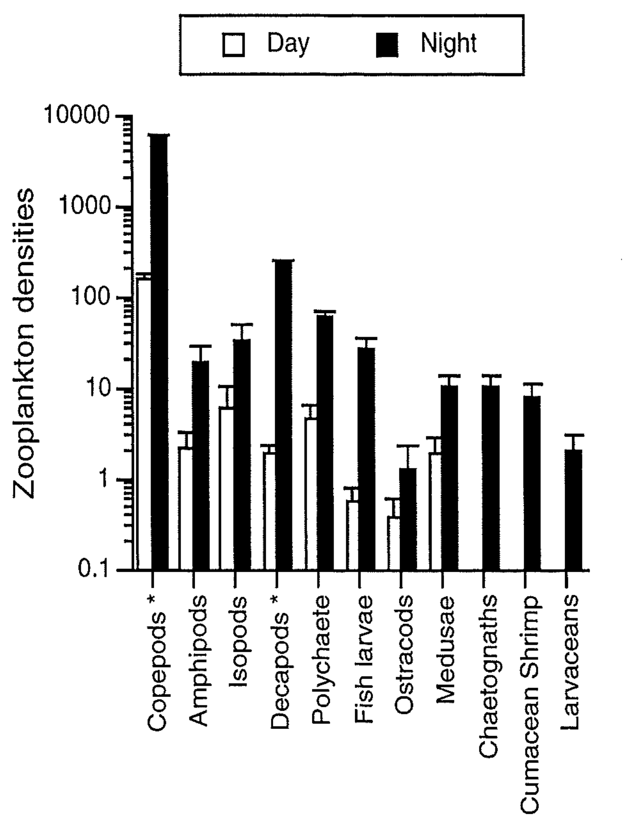

FIG. 1. The density (number / m^{3}) of zooplankton taxa (mean ± SE) for day (n = 5) and night (n = 5) samples taken on the backreef of Discovery Bay, Jamaica. * indicates taxa for which density was significantly different between night and day samples. Note logarithmic scale.

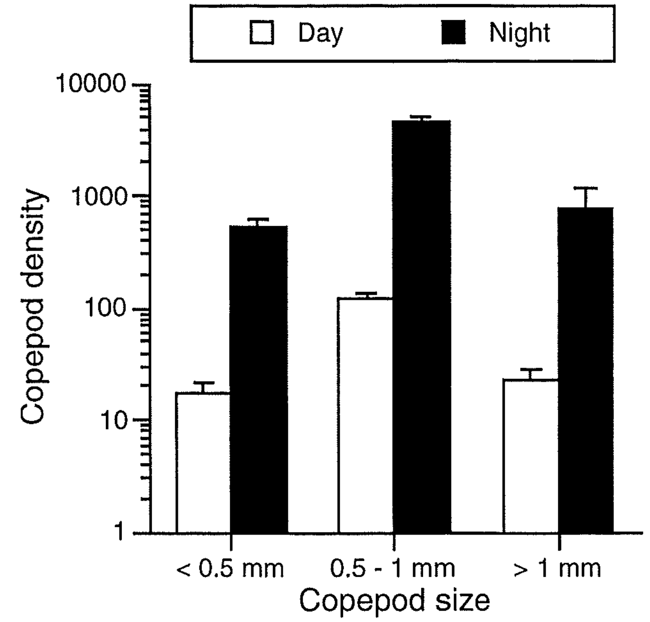

FIG. 2. The density (number / m^{3}) of copepods (mean ± SE) in three size categories for day and night samples taken on the backreef of Discovery Bay, Jamaica. There was a significant time by size interaction ($F = 42.26$, $df = 2, 1, 2$, $P < 0.0001$). Note logarithmic scale.

Discussion

As predicted, zooplankton were more abundant at night than during the day, probably because demersal zooplankton migrated into the water column at night. Copepods and decapods were the only taxa that had significant differences in diel densities (Table 1, Fig. 1). Copepods were by far the most abundant taxon in both day (48%) and night (94%) samples, and were responsible for the vast majority of the increase in total zooplankton abundance from day to night. Some zooplankton did not exhibit significant migratory patterns (Table 1, Fig. 1), which may reflect variation in taxon-specific predation pressure. Alternatively, our snapshot night sample may have missed the migration patterns of other zooplankton. For example, Ohlhorst (1982) reported that polychaetes reach peak abundance one hour after sunset, while isopods show peak abundance two hours after sunset. Higher temporal resolution in sampling design would reveal whether taxa besides copepods and decapods exhibit significant shifts

Table 1. A comparison of zooplankton density (mean m^{-3} ± SE) between day (n = 5 tows) and night (n = 5 tows) samples on the west-back reef of Discovery Bay, Jamaica. Student's t-tests were used to determine the effect of time of day. P_{VAR} were determined using Welch's ANOVA test when the differences in variance were high. P values were compared to an adjusted value calculated using the Bonferroni correction for nine tests run ($P = 0.00568$). Statistical tests could not be run for cumacean shrimp, chaetognaths, or larvaceans because their daytime densities were 0. * indicates significant results ($P < 0.00568$).

Taxa	Density (m^{-3})		t	P	P_{VAR}
	Day	Night			
Copepoda	160.9 ± 17.13	5858.1 ± 282.22	20.15	<0.0001*	-
Amphipoda	2.3 ± 0.97	19.3 ± 9.12	1.85	0.10	-
Isopoda	6.2 ± 4.05	32.3 ± 16.14	1.57	0.16	-
Decapoda	1.9 ± 0.42	235.7 ± 24.21	9.66	<0.0001	0.0006*
Polychaeta	4.5 ± 1.92	58.9 ± 10.68	5.01	0.001	0.0063
Fish larvae	0.6 ± 0.23	27.4 ± 8.41	3.18	0.013	0.033
Ostracoda	0.4 ± 0.23	1.3 ± 1.10	0.84	0.43	-
Medusae	1.9 ± 1.08	10.4 ± 2.97	2.69	0.028	-
Cumacean Shrimp	0.0 ± 0.00	7.9 ± 3.64	-	-	-
Chaetognatha	0.00 ± 0.00	10.19 ± 3.91	-	-	-
Larvacean	0.00 ± 0.00	2.08 ± 0.96	-	-	-
Total zooplankton	335.1 ± 44.14	6264.2 ± 230.21	25.2	<0.0001*	-

in vertical migration behavior.

We also found evidence for size-based differences in diel densities within the copepods. There was a disproportionately large increase in medium-sized copepods at night (0.5 – 1 mm) compared to the small- (<0.5 mm) and large-sized (> 1 mm) copepods (Fig. 2). We suggest three possible explanations for this pattern. First, differences in the stage-based population structure could be influencing diel zooplankton densities. Under this scenario, all copepods would migrate in proportion to the relative number of individuals in a given size class. In fact, our results support this hypothesis given that the factor increase in densities between night and day are somewhat comparable (30, 38, and 34 times more individuals at night in small, medium, and large size classes, respectively). Second, it is possible that different size zooplankton have different diel behaviors. For example, copepods may migrate to different depths or locations at different times of the day. Finally, there may be ontogenetic shifts in migration behavior if there is strong selective predation on specific copepod size classes. Under this scenario, small and large copepods would migrate less than the medium copepods. Future FSP projects might examine which of these mechanism (or others) account for size-based variability in zooplankton diel behavior.

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