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ENVIRONMENTAL DETERMINANTS OF SPECIES RICHNESS AND ABUNDANCE IN TROPICAL INTERTIDAL POOLS

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Abstract: Tide pools high in the intertidal zone (i.e., distant from the low tide line) experience more variability in temperature and salinity, because they are isolated from the ocean and exposed to the sun for a longer period of time than lower pools. We hypothesized that few organisms would be able to tolerate the extreme conditions of pools high in the intertidal, and that abundance of organisms and species richness would consequently decrease with increasing distance from the ocean. We assessed abundance and morphotype richness for pools across the intertidal zone. Though abundance and richness decreased with increasing distance from the ocean, it appears that this trend was driven by mobile organisms that move between pools. Furthermore, it appears that the temperature-salinity gradient is probably not the factor driving this trend. Instead, the influence of resource availability may generate the observed patterns.

Key Words: extreme environmental conditions, salinity, temperature, tidal fluctuations

INTRODUCTION

During low tide, variability in tide pool temperature and salinity increases with distance from the ocean (Drake et al. 1993). Tide pools high in the intertidal zone are separated from the ocean and exposed to the sun for the longest period of time, creating high temperatures and rates of evaporation and, consequently, high salinity. This may be particularly pronounced in tropical intertidal habitats. In such environments, some organisms may be unable to tolerate the extreme conditions of these pools and may exhibit a preference for habitat lower in the intertidal zone. Organisms may disperse to these preferred habitats either before the tide recedes or afterwards, by migrating between pools or completely avoiding high pools.

For the clay-underlain intertidal zone of Playa Sirena at Corcovado Na-

tional Park, Costa Rica, we predicted that the pools experiencing more variable and harsh environmental conditions (i.e., those farther from the ocean) would contain fewer organisms and have lower species richness than those pools that are closer to the ocean. We also predicted that this pattern would be less evident at night, when the sun does not drive the temperature-salinity gradient observed during the day.

METHODS

We selected tide pools in a semi-stratified, haphazard fashion at different distances from the tide line in the clay-underlain intertidal zone of the Playa Sirena, Corcovado National Park, Costa Rica. We sampled 25 pools during daytime low tides (1200 - 1600) on 2 and 3 February 2005, and 10 pools during the nighttime low tide (0100 - 0330) on 4 February 2005. No concerted attempt was made to use the same pools for day and night sampling periods, but pools were selected using the same method for both sampling periods. At low tide, all pools were isolated from other pools and from the ocean.

We measured the greatest length, width and depth of each pool to calculate water volume. Pools ranged in surface area from approximately 0.2 to 2.5 m^2 and were between 2.0 and 17.0 cm in depth. Calculated pool volumes ranged from 6 to 220 L. As a reliable proxy for distance from the ocean, which is inherently variable over time, we recorded the distance of each pool from the high tide line, as indicated by the forest edge. We found that tide pool volume did not change with distance from the high tide line for the day ($r^2 = 0.02$, df = 23, P = 0.52) or night ($r^2 = 0.08$, df = 8, P = 0.43) sampling periods. Thus, the sampled pools were comparable in size across the intertidal range.

For each pool, we removed all macro-organisms (i.e., fish, shrimp, snails and crabs) by hand, and counted the number of individuals of each morphotype present. All organisms were returned to their tide pools following counting.

Number of organisms and species richness were log transformed to normalize the data. We examined the effect of time of day on the relationship between organism abundance or morphotype richness and distance from the high tide line using an indicator variables regression. The regression model was:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 + \varepsilon,$$

where Y is the response variable (number of organisms or morphotype richness), X_1 is distance from the high tide line, X_2 is a binary indicator variable coding for time of day (i.e., for day, $X_2 = 1$, and for night, $X_2 = 0$), β_0 is the intercept for the relationship between the response variable and distance at night, β_1 is the slope for the relationship between the response variable and distance at night, β_2 tests the hypothesis that the intercepts of the relationships are equal for day and night, and β_3 tests the hypothesis that the slopes of the relationships are equal for day and night (Neter et al. 1996).

We performed linear regressions to assess the relationship between distance

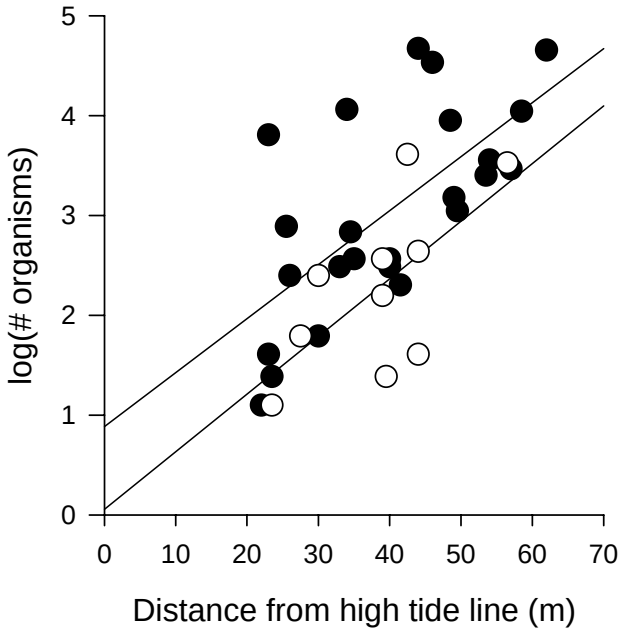

Figure 1. Number of organisms within tide pools increased with distance from the high tide line for day (closed dots) and night (open dots). Lines were fit using least squares linear regression with a binary indicator variable for day and night. Slopes were not significantly different (β_3 = -0.00, P = 0.90), but there was a difference in intercepts (β_2 = 0.68, P = 0.02). $Y_{day} = 0.06x + 0.84$; $Y_{night} = 0.06x + 0.16$.

from the high tide line and the abundance of the six most common morphotypes. Statistical analyses were performed using JMP 5.0.1.

RESULTS

We identified 19 morphotypes in our 35 sampled pools (Table 1). The total number of organisms in each pool increased with distance from the high tide line for both day and night (Fig. 1). Comparisons of this relationship during night and day indicated that slopes were not significantly different. We found a significant difference in intercept between day and night for the relationship between distance from the high tide line and number of organisms (Fig. 1).

Morphotype richness increased with distance from the high tide line during the day and at night (Fig. 2), but the slopes of these relationships did not differ significantly. We found no difference in intercept between day and night for the relationship between distance from the high tide line and morphotype richness (Fig. 2).

We also examined relationships between distance from the high tide line and total abundance (i.e., the sum of abundances for the two sampling periods) for the six most common morphotypes: crab C, crab E, fish A and snails A, B and C. We found a positive relationship between distance from the high tide line and abun-

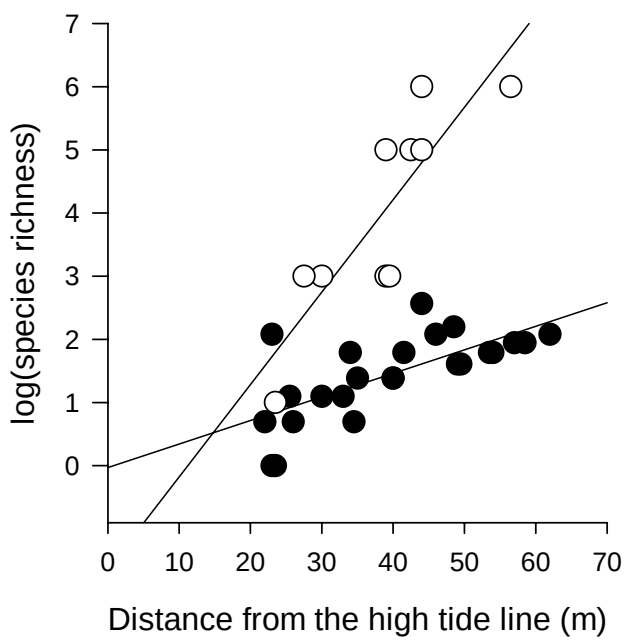

Figure 2. Morphotype richness within tide pools increased with distance from the high tide line for day (closed dots) and night (open dots). Lines were fit using least squares linear regression with a binary indicator variable for day and night. Slopes and intercepts were not significantly different (β_3 = -0.01, P = 0.62; β_2 = 0.12, P = 0.49). $Y_{day} = 0.03x - 0.13$; $Y_{night} = 0.04x - 0.25$.

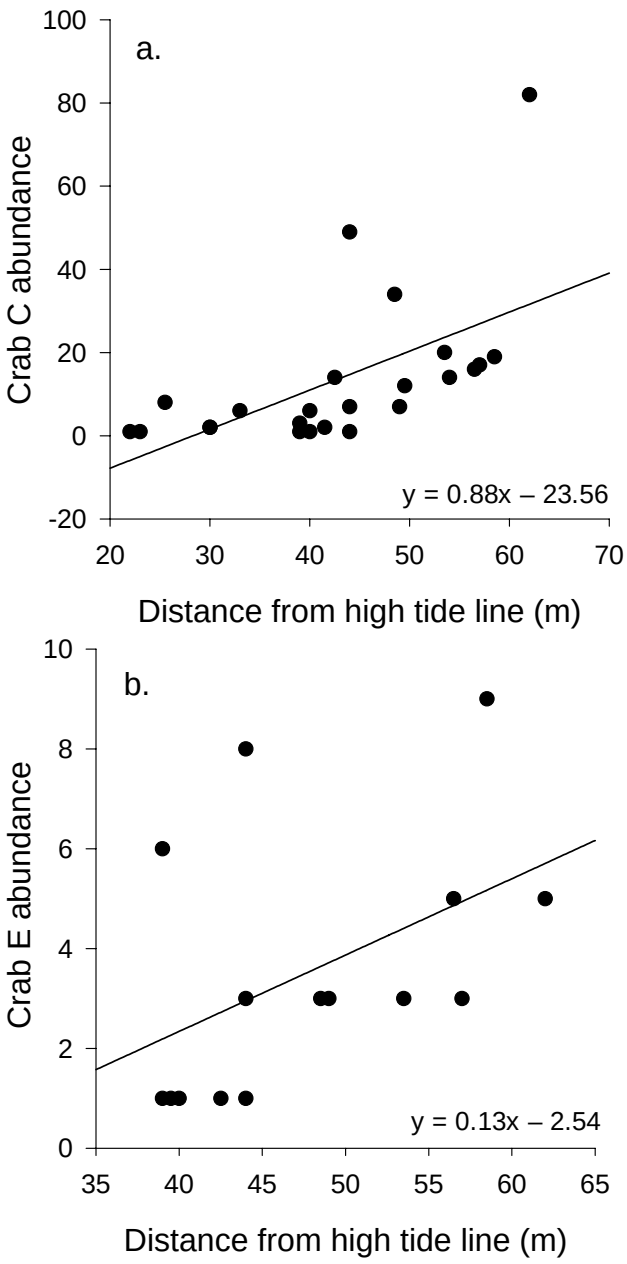

Figure 3. Abundance of (a) crab morphotype C and (b) crab morphotype E increased with distance from the high tide line. Lines were fit using least squares linear regression

dance of crab C (r^2 = 0.33, df = 22, P = 0.01; Fig. 3a) and crab E (r^2 = 0.31, df = 15, P = 0.03; Fig. 3b). There was no relationship between distance and abundance for fish A (r^2 = 0.10, df = 27, P = 0.45), snail A (r^2 = 0.01, df = 12, P = 0.77), snail B (r^2 = 0.04, df = 12, P = 0.47) or snail C (r^2 = 0.19, df = 9, P = 0.18).

Discussion

We found that abundance and species richness of macro-organisms increased with distance from the high tide line during the day. However, contrary to our hypothesis, the same pattern was observed in the night data. Because sun exposure does not differentially affect tide pools at night, an alternative mechanism must drive differences in abundance and species richness across the intertidal zone.

Tides may distribute organisms non-randomly along the intertidal gradient, such that a greater number and diversity of organisms are deposited lower in the intertidal. It is also possible that, during the low tide, when pools are isolated from the ocean, organisms in higher tide pools may die or be preyed upon at higher rates than organisms in lower tide pools. However, these explanations are inconsistent with our observations. We observed very few dead organisms in the sampled pools. We only observed a few bird predators feeding during the sampling period, and these only fed in tide pools outside of our study site. However, it is possible, due to the brevity of the sampling period and the potential influence of our presence on predator behavior, that these observations are not an accurate reflection of actual predation rates in the studied pools.

An alternative explanation is that the more mobile organisms may preferentially distribute themselves along the inter-

tidal gradient, regardless of their original distribution by wave action. This is supported by analysis of the individual distribution patterns of the six most abundant morphotypes and our informal observations of between-pool migration. We found that highly mobile organisms (i.e., crabs C and E) increased in abundance with distance from the high tide line, while organisms with limited mobility between tide pools (i.e., fish A and snails A, B and C) were equally distributed across the intertidal zone. During sampling, we often observed crabs C and E, as well as crabs of other morphotypes, moving from pool to pool. The same observation was never made for fish or snails of any morphotype. This suggests that the more mobile organisms redistribute themselves among pools during low tide. It also suggests that these organisms may prefer pools close to the ocean. The similarity in the patterns of day and night data suggest that this choice is not based upon the extreme temperature or salinity of higher tide pools, but some other factor, such as resource availability.

Table 1. Identification scheme for morphotypes collected in 35 tide pools of the intertidal zone, Playa Sirena, Corcovado National Park, Costa Rica.

Type	Code	N	Diagnostic Features
Fish	A	160	Yellow/tan goby (Gobiidae)
	B	1	Laterally compressed with black longitudinal stripes
	C	1	Laterally compressed with black longitudinal stripes
	D	8	Goby (Gobiidae) with sandy coloration, brown splotches and blue dot below dorsal fin
	E	1	Laterally compressed, round, sandy coloration with brown splotches
Shrimp	A	15	Translucent body, ~ 1-2.5 cm, blue stripes, orange dots on tail
	B	1	Brown with one large claw, < 1 cm
Snail	A	97	Whelk with knobby shell
	B	64	Compressed shell, brown
	C	61	Compressed shell, green spots around spiral, faint red stripes
	D	26	Compressed shell, green spots around spiral
	E	3	Limpet
Crab	A	4	Sandy color, boxy shape
	B	17	Dark color, round shape
	C	360	Hermit crab
	D	23	Dark green color, boxy shape
	E	58	Sandy color, round shape, carapace has 5 teeth, red eyes
	F	8	Purple claws with large bumps
	G	2	Bright orange claws

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THE HITCHHIKER'S GUIDE TO THE LEAF-CUTTER COLONY

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Abstract: Although the minima caste in the leaf-cutter ants, *Atta,* is primarily involved in nest activities, some of these small sized individuals are found outside the nest "hitchhiking" on leaves carried by workers. Their role may be to deter parasitoid phorid flies. We investigated the purpose of these hitchhikers in *Atta colombica* by observing their distribution along trails, the proportion of hitchhikers in the defensive "head up" position on leaves, and the average size of leaves with and without hitchhikers. The ratio of hitchhikers to leaves was greatest closest to the nest, and hitchhikers were as likely to have their heads up as down. Leaves with hitchhikers had a greater surface area than leaves without hitchhikers. These findings are consistent with the hypothesis that hitchhikers could be defending workers against parasitoid phorid flies, which attack near the nest, and may also initiate cleaning and preparation of larger leaves before they enter the nest.

Key Words: Atta, *minima, phorid flies*

INTRODUCTION

In leaf-cutting ants of the genus *Atta*, ants in the minima caste typically carry out nest duties such as nursing young, tending the fungus gardens, and cleaning and scraping each leaf to prepare it for the gardens (Stevens 1983). Minima are also seen on the trail hitchhiking on leaf fragments carried by workers (Wetterer 1996). It has been hypothesized that hitchhikers (minimas riding on leaf pieces being carried by workers on the ant trails) defend workers against parasitoid phorid flies, which are only active during the day (Linksvayer et al. 2002). The hitchhikers will often assume a "head up" defensive position with head and front legs raised ready to detect and deflect incoming phorid flies. Phorid flies have only been observed attacking ants at the entrance to the nest (D. Matlaga, pers. comm.). Hitchhikers in *A. cephalotes* are equally abundant during the day and night, which suggests a purpose other than protection from parasitoid flies, although during the day hitchhikers spend more time in the defensive "head up" position compared to the night (Linksvayer et al. 2002). It has also been proposed that hitchhikers may prepare leaves by early initiation of the cleaning and scraping process (Linksvayer et al. 2002).

In this study, we tested the hypothe-