SIZE EFFECTS ON FORAGING PATTERNS IN *MACROBRACHIUM* SHRIMP

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Abstract: A change in the size of an organism can select for changes in the behavior of an organism, and vice-versa. Small *Macrobrachium sp.* shrimp can be seen swimming in streams at all times around the Sirena Station in Corcovado National park, while larger shrimp are only visible at night. I compared large and small shrimp foraging behavior under light and dark conditions, and found that small shrimp are more likely to forage in the light. I evaluated two hypotheses to explain the behavior difference between large and small shrimp: (1) smaller shrimp's high metabolic rate requires that they forage during the day, and (2) a tradeoff between the predation risk while foraging and the protection afforded by reaching a greater size through increased foraging. In a 12 hour starvation period, I saw no evidence of differences between metabolic rates of shrimp. A mathematical model of the tradeoff hypothesis evaluated the effects of time spent foraging on probability of surviving to reproductive size under different scenarios of growth rate and predation risk. This exercise failed to identify any plausible scenarios in which small shrimp would maximize the probability of surviving to reproduce by sustaining more risks as a small shrimp to grow quickly through a vulnerable size class.

Key Words: crustacea, foraging behavior, Macrobrachium *shrimp, predation, stream invertebrates*

INTRODUCTION

A change in the size of an organism can select for changes in the behavior of an organism, and vice-versa. Shrimp of the genus *Macrobrachium* are common in streams around the Sirena Biological Station in Corcovado National Park, Costa Rica and can reach up to 15 cm in length. They are thought to be mainly detritivores, but may also function as predators (Brown et. al, 2000). Their foraging patterns probably have consequences for the stream community (Wilson et. al, 2004). Medium and large shrimp appear to be mainly nocturnal, but small individuals apparently forage at all times of the day. It seems paradoxical that the smaller, seemingly more vulnerable shrimp risk foraging more than the larger shrimp.

I propose two hypotheses to explain the difference in foraging behavior between small and large shrimp: (1) Smaller shrimp have greater metabolic requirements (need more grams of food per gram of mass) and needed to forage during the day to stay alive. I tested the prediction that during starvation periods, smaller shrimp will lose a larger proportion of body weight. (2) There is a tradeoff between the predation risk while foraging, and the protection afforded by reaching a greater size (which is contingent upon foraging). The probability of dying in any day has to be reduced by hiding more and foraging less, but the probability of dying before attaining reproductive size might be minimized by foraging more and increasing growth rate through the early vulnerable size classes (even if it means increasing the short term risk of mortality).

METHODS

I collected *Macrobrachium* from 5-meter sections of four small streams around the Sirena Station in Corcovado National Park in February, 2006. I sampled streams at the end of the airstrip, just inside the Pavo and Ollas trails, and one about 1 kilometer up Los Naranjos trail. I grouped the collected shrimp into small (0-3 cm), medium (3-7 cm) and large (7-15 cm) size classes.

I placed one large, one medium, and two small shrimp in a bucket with 50% of its bottom covered with sandy substrate from streams. I kept the bucket in darkness and recorded if shrimp were motionless (hiding) or moving around (foraging) every 15 minutes for 2 hours. I placed the bucket in a constant light source and repeated the process after a half-hour acclimation period.

I randomly chose 3 shrimp from each size class for a starvation trial to test metabolic rate. I measured the changed in body mass following a 12 hour trial, during which test subjects were isolated and activity kept to a minimum.

I developed a speculative model to explore whether decreasing predation risk with increasing size might explain the duration of daily foraging activity in small shrimp. The model simulated shrimp growth from a specified initial mass with growth as a function of time spent foraging:

$$RGR = RGR_{max} - (1/t^2) \qquad \textit{(Eq. 1)}$$

where RGR = the relative growth rate ($g * g^{-1} * d^{-1}$), RGR_{max} = maximum relative growth rate ($g * g^{-1} * d^{-1}$; set at 0.05) and t = the number of hours the shrimp spends foraging. I acknowledge that this functional form may not truly represent the trends in RGR with time spent foraging.

I modeled daily shrimp growth with the equation:

$$M_f = M_i * e^{RGR} \qquad \textit{(Eq. 2)}$$

where the M_f = final mass (g) and M_i = daily initial mass (g; M_i initially set at 0.2 g extrapolated from size of smallest shrimp caught in field).

I modeled daily shrimp mortality as a function of hours spent foraging, which increased mortality, and mass, which decreased mortality:

$$P(D) = k_{min} + (k * t_{forage}) - (k * y * M * t_{forage}) \qquad \textit{(Eq. 3)}$$

where P(D) = probability of shrimp mortality, k = predation rate (shrimp removed from the system per unit time; set at 0.01 for baseline predictions), k_i = initial value of predation rate (set at 0 for baselines predictions) and y = the effect body size has on decreasing predation rate (set at 1 for baseline predictions). I acknowledge that this functional form may not represent actual trends in P(D).

Using the mortality function (Eq. 3), the model calculated the percentage of shrimp that reached a mass necessary to reproduce (set at 0.75 grams based on onset of sexual dimorphism in captured shrimp). I ran the model with the baseline values, and testing the effect of varying y (to 2), RGR_{max} (to 0.1), and k (to 0.02) at three

different starting masses: 0.2 (size at birth based on visual estimation), 0.4, and 0.6 grams (smallest shrimp weighed).

RESULTS

All size classes of shrimp foraged for 81% of the time in the darkness, indicating no difference in foraging patterns. Large and medium shrimp foraged for 12.5% of the time in the light, while small shrimp foraged for 75% of the time in the light. There was no significant relationship between the percentage of mass lost and the initial mass of the shrimp over the 12 hour starvation period (Fig. 2). Within the modeling framework of equations 1-3, I could not find any plausible parameter combinations that predicted high daytime foraging by small shrimp but not large shrimp.

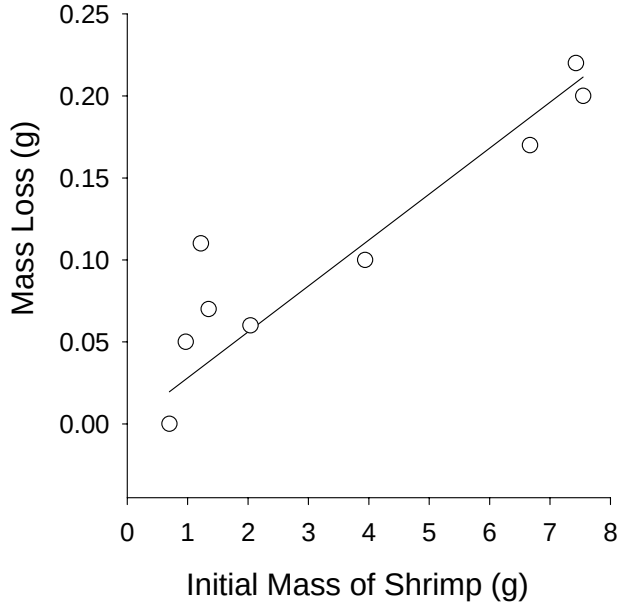

Figure 1. The relationship between the initial mass of Macrobrachium shrimp and mass loss during a 12 hour starvation period.

DISCUSSION

Experimental results confirmed the difference in diurnal foraging behavior between large and small shrimp. When kept in constant light, small shrimp continued to roam about and forage for detritus, while larger shrimp settled down into the substrate and remained motionless. All sizes of shrimp forage actively in the dark, with larger shrimp feeding on both detritus and small organisms, such as fish and tadpoles (Brown et. al, 2000). The behavior of the large shrimp suggests that they are avoiding a diurnal predator, such as large wading birds, while they are not threatened by stream predators that are always resident in the stream, such as fish.

Although it is generally true that small organisms have higher metabolic needs per gram, even the small shrimp that we studied did not die, lose appreciable mass, or show any ill effects from 12 hours of food deprivation. Possibly the smaller shrimp would have lost more mass if the starvation period was longer, and 12 hours of food deprivation might produce mortality if food had been scarce in the weeks before. I was unable to identify a combination of parameters in my speculative model in which small shrimp

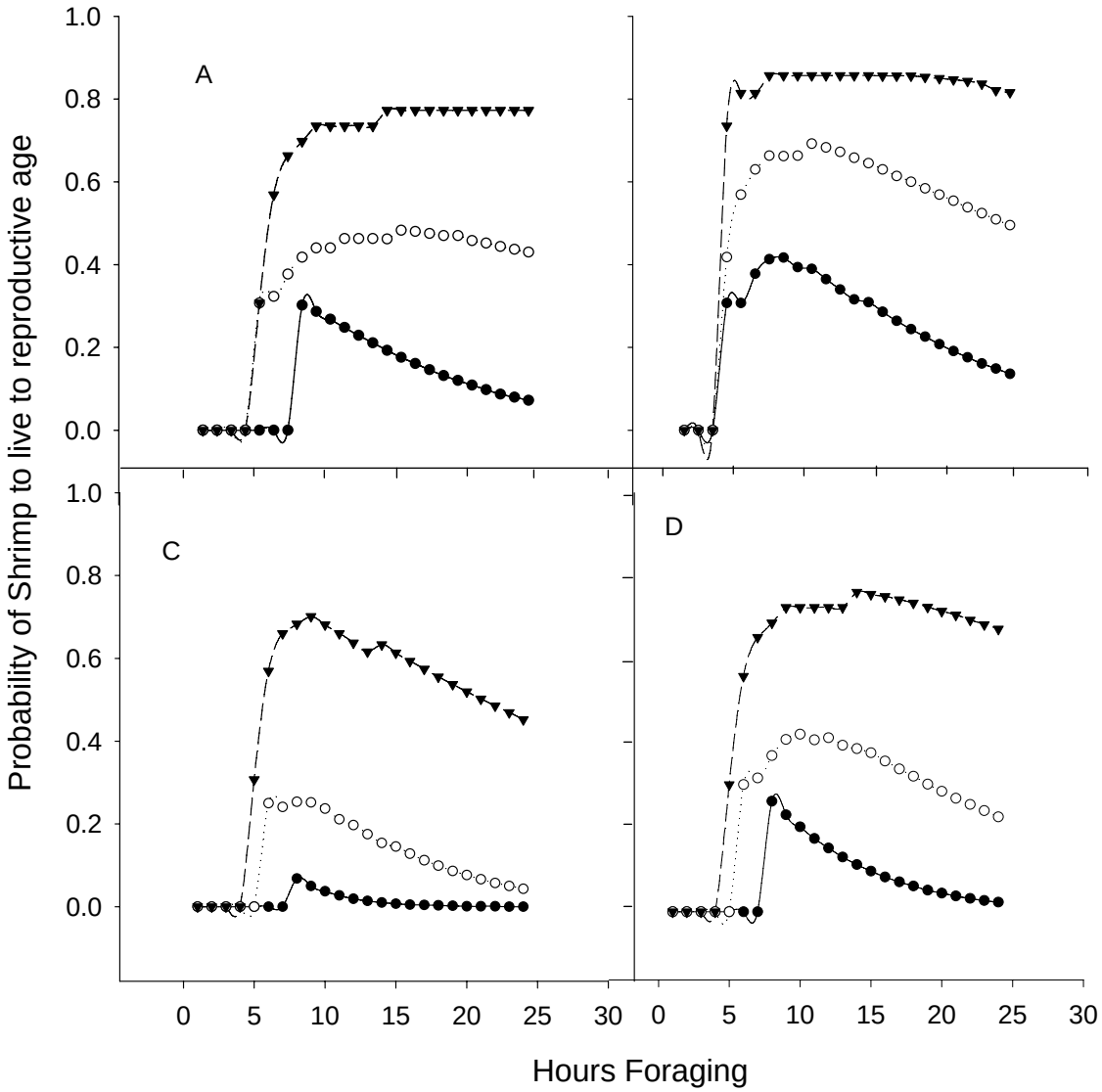

Figure 2. Visual representation of the cost benefit/analysis of the foraging behavior of small (•) medium (o) and large (▼) *Macrobrachium* shrimp. The zenith of each function correspond to the predicted optimum for hours spent foraging. (a)Estimation using baselines values for all parameters. (b) Estimation using increased effects of mass on predation. (c) Estimation using increased predation rates. (d) None of the scenarios within the model could explain the observed behavior of small *Macrobrachium* shrimp.

would benefit from day time foraging. Alternative formulations of the model might favor daytime foraging by small shrimp to reduce their duration of vulnerability.

More research must be performed to determine the mechanism behind the differences in foraging behavior between large and small *Macrobrachium* shrimp. I recommend focusing on community interactions in the stream, examining the different behaviors of predators that feed on large and small shrimp at different times of the day. It is possible that diurnal predators, such as birds, ignore the small shrimp while foraging for the large ones.

LITERATURE CITED

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