PREDATION DRIVES SPATIAL-SIZE DISTRUBITON OF SNAIL POPULATIONS IN TWO COASTAL SALT MARSHES

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ABSTRACT

Spatial and size structure are ubiquitous features of natural populations, however our understanding of joint spatial-size distribution is limited. In this study, I tested the hypothesis that spatial gradients in predation pressure in two coastal salt marshes generate spatial size-distributions of *L. irrorata* populations. My results show that predation pressure differs both as a function of distance from tidal creeks that are the source of predators as well as between the marshes. Furthermore, this spatial variation in predation leads to variation in population densities and a nonlinear relationship between size and predation. A simple demographic model illustrates how size-dependent predation alone can explain the spatial-size distribution in *L. irrorata* populations.

INTRODUCTION

Natural populations can be structured in a variety of ways, including size, age, and space. This structure can have huge influences on demography, evolution, and interspecific interactions, and therefore must be considered to build a complete understanding of a variety of population and community processes (Caswell 2001). While the literature on structured populations is massive, most studies focus on a single type of structure. Organisms with complex life cycles provide a possible exception, because different life stages occupy distinct habitats with conspicuous consequences for their ecology (Rudolf et al. 2012). However, other organisms may also be structured in multiple dimensions—for example, populations that show variation in size through space (hereafter referred to as ‘spatial-size distributions’).

In order to characterize the potential importance of spatial-size distributions, it is important to consider the underlying processes that could generate such patterns. For example, predation is often variable through space (Schindler et al. 1994) and is generally strongly size structured (Rudolf 2012). Therefore, one would expect that populations under strong predation would show distinct spatial-size distributions. To explore this possibility, I took advantage of natural spatial gradients in predation produced by tidal cycles in two coastal slat marshes. Salt marshes are characterized by inundation with seawater that overflows from tidal creeks. Predators such as blue crabs (*C. sapidus*) enter the marshes through these creeks during high tide to feed on a variety of organisms including the marsh periwinkle (*L. irrorata*). Previous work has demonstrated significant spatial variation in *L. irrorata* abundance as a function of predation by *C. sapidus* (Schinder et al. 1994) and that predation success is closely linked to *L. irrorata* (Mikulyuk 2013). Therefore, these populations provide an excellent opportunity to explore the potential role of predation in driving spatial-size distributions.

I sampled *L. irrorata* populations at various distances from tidal creeks in two marshes with different levels of ambient predation to test the following predictions: (1) predation pressure decreases with distance from tidal creeks; (2) densities of *L. irrorata* populations decline with predation, and therefore increase with distance from the creek; (3) *L. irrorata* shell size varies with predation pressure, producing variable spatial-size distributions; (4) the patterns observed in (1-3) differ between the two marshes because of differences in overall predation pressure.

FIELD METHODS

This study was conducted in two coastal salt marshes, Odum’s Marsh (OM) and Dean Creek Marsh (DM), on Sapelo Island off the coast of Georgia. Each marsh is associated with a large tidal creek (Lighthouse Creek and Dean Creek, respectively), with a network of smaller creeks permeating the landscape. OM is directly adjacent to Doboy sound, while DM is situated further inland. As *C. sapidus* enter the tidal creeks from the ocean, I expected OM to have higher ambient rates of predation than DM.

During the last week of October 2015, I established approximate transects running perpendicularly to the primary creek for each marsh. In DM, the 5 transects began at the shoreline of Dean Creek and each included 4 plots, for a total of 20 plots. At OM, the transects began along the shoreline of a secondary creek that ran parallel to Lighthouse Creek. Two of the transects included 5 plots, while the third included 3 plots, for a total of 13 plots. In both marshes the plots were located approximately 10m from each other with approximately 20m between transects. The approximate nature of the sampling scheme and the differences between the two marshes were dictated by the presence of patches free of *Spartina* (*L. irrorata’s* host plant) and plots used for long-term sampling that needed to be avoided.

At each plot I collected all *L. irrorata* individuals within a quadrat. I used quadrats of 0.0625m2, 0.25m2, or 1m2, depending on the number of individual in the plot. The *L. irrorata* density was then calculated as the number of individuals per sampling area. For plots that contained too few individuals to provide reasonable size estimates, I collected all *L. irrorata* in a 1m2 quadrat positioned directly adjacent to the originally sampling location with the goal of collected at least 20 individuals (although this was not possible for every plot). Finally, I counted the number of scars on each individual (a measure for predation attempts) and the maximum shell length.

STATISTICAL METHODS

*Creek Distance*

Each of the two marshes was characterized by a network of secondary creeks in addition to the primary creek, all of which might serve as entry points for *C. sapidus* into the marshes and thus could result in complicated spatial variation in predation. To simplify the analysis, I fit linear models to determine whether distance to the nearest creek or the primary creek was a better predictor of *L. irrorata* density. I also included models with intercepts only verify than density does in fact vary with respect to creek distance. I performed the analysis separately for the two marshes to allow for different responses of predation to the unique hydrological features of each marsh. Distance to the nearest creek was a substantially better predictor of density in DM (ΔAIC=21.3), while distance to the primary creek was better for OM (ΔAIC=8.1). Therefore, I created a new variable for creek distance that used distance to the nearest creek for DM and distance to the primary creek for OM. This metric of creek distance was used for all subsequent analyses.

*Scars*

To quantify spatial variation in predation pressure, I fit a linear mixed model with number of scars per individual as a function of creek distance, marsh, length, and two-way interactions. I used log(number of scars plus 1) as the response variable to improve normality and included a random effect for plot. I included length as a covariate because length is closely related to age in organisms with indeterminate growth and the number of scars should increase through the lifespan of each individual. Length and distance were normalized as z-scores to improve estimation of interactions.

*Population density*

To determine whether population density varies through space in response to predation, I fit a linear model with density as a function of creek distance, marsh, and their interaction. Count data typically violate the assumption of normality, however the residuals looked approximately normal and the linear model performed substantially better than a generalized linear model with Poisson-distributed errors (a common way of modeling count data; ΔAIC=107.2).

*Size distribution*

To quantify variation in the size distribution through space, I fit a linear mixed model with individual length as a function of creek distance, marsh, and their interaction with a random effect for plot. Distance was normalized as a z-score to improve estimation of interactions.

RESULTS

The number of scars per individual was higher (χ2 = 4.4899, df = 1; p = 0.0341) and increased more rapidly with size (χ2 = 11.897; df = 1; p < 0.001) in OM than for DM (Fig 1). This indicates higher overall predation rates in OM than in DM. Furthermore, the number of scars declined with distance more rapidly in DM than in OM (χ2 = 6.0561; df = 1; p = 0.0139; main effect of distance not significant). This is also consistent with higher predation rates in OM than in DM, since predation should decline less rapidly when more predators on present in the landscape.

The decline in predation rate with distance from the creek was mirrored by an increase in population density (F = 29.760; df = 1; p < 0.001; Fig 2.). Furthermore, the overall population densities in OM were lower than in DM (F = 27.017; df = 1; p < 0.001) as was the increase in population density with distance (F = 13.479; df = 1; p < 0.001). These results exactly parallel the patterns of predation inferred from the scarring data.

Average *L. irrorata* size was significantly lower in OM than in DM (χ2 = 17.571; df = 1; p < 0.001). While the main effect of distance from the creek was not significant (χ2 = 1.8932; df = 1; p = 0.169), there was a significant interaction between distance and marsh (χ2 = 6.590; df = 1; p = 0.0103). Specifically, the individuals size declined with distance in DM, but increased with distance in OM (Fig 3) indicating that the spatial-size distribution of *L. irrorata* does not follow a simple gradient.

DISCUSSION

In this study, I used the spatial variation of *L. irrorata* density, scarring, and size to evaluate the role of predation in driving the spatial-size distribution in two coastal salt marshes. My results show that ambient predation rates differ between the two marshes, likely because OM is substantially closer to the ocean that is the ultimate source of *C. sapidus*. Furthermore, predation pressure declines with distance from the tidal creeks, although this effect is weaker at OM because of the higher overall levels of predation. Thus, predation pressure varies at both local and landscape scales. In turn, this generates spatial structure in the density of *L. irrorata*, with smaller populations at OM then at DM. In both marshes, population densities increase with distance from the creeks, but this effect is weaker when ambient predation is higher.

Initially, the relationship between predation pressure and the spatial-size distribution of *L. irrorata* seems less clear, with average size decreasing with distance from the creek in DM while the reverse is true of OM. However, this pattern is consistent with a simple nonlinear relationship between size and predation pressure. Because OM has higher predation than DM and predation declines with distance, if Figure 3 was modified such that the x-axis indicated predation the slopes of the relationships for OM and DM would reverse and the data for OM who shift to the right. This would result in a unimodal relationship with the maximum size occurring at an intermediate level of predation.

The hump-shaped relationship between predation and size may be explained by the fact that sizes of *L. irrorata* are likely dependent on individual ages. While large individuals are more likely to survive predation attempts, it is also unlikely that many individuals will survive to such a large size when predation is high. To illustrate how this can produce the observed relationship between size and predation, I built a simple size-structured demographic model. The model has 10 size classes, with transitions between the classes determined by survival probabilities that include size-dependent predation and senescence. These two assumptions lead to a hump-shaped relationship between age-specific survival and size in the presence of predation (Fig 4). I then calculated the long-term size distribution from the dominant eigenvectors of the demographic projection matrix and iterated the procedure for different predation rates. The model shows that under certain parameter values, the relationship between size and predation pressure is hump-shaped. This supports the hypothesis that the particular spatial-size distribution in OM and DM can be explained purely in terms of differences in predation rates (Appendix).

This study illustrates how spatial variation in predation can lead to particular spatial-size distribution, and how this in tern can lead to complex population structure across multiple spatial scales. However, much is still unknown regarding the exact demographic mechanisms that lead to these patterns. For example, the behavior of the model discussed above is extremely sensitive to parameter values and the number of size classes. This is especially true for fecundity, as high reproduction leads to a large positive contribution of large individuals (the parents) to small ones (the offspring), which complicates the analysis of size structure. Furthermore, *L. irrorata* like most animals are mobile and potentially move across the landscape to contribute to observed spatial patterns. Future work should focus on parameterizing biologically responsible demographic models that explicitly consider the potential behavioral responses of individuals to spatial variation in predation.

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FIGURES



Figure 1. Average number of scars per *L. irrorata* individual as function of distance from the creek for OM (blue) and DM (black). The data are averages for each plot to aid interpretability. The lines correspond to predicted means from a linear mixed model fit with individual-level data. The deviation between the line and data for DM is explained by uneven distribution of *L. irrorata* sizes, which is accounted for in the model but not in the calculation of the plot-level averages.



Figure 2. *L. irrorata* density as function of distance from the creek for OM (blue) and DM (black). The lines correspond to predicted means from a linear model.



Figure 3. Snail length as function of distance from the creek for OM (blue) and DM (black). Lines correspond to predicted means from a linear model mixed model.



Figure 4. Age-specific survival probability as a function of size as used in the demographic model. The different lines indicate different levels of predation (solid = 0, dashed = 1, dotted = 2, dashed-dotted = 3).



Figure 5. Average snail size projected from the demographic model, as a function of predation pressure. The scale on the y-axis is arbitrary.

APPENDIX: SIZE-STRUCTURED DEMOGRAPHIC MODEL

To explore the potential for nonlinear relationships between average size and predation, I constructed a size-structured demographic model. The model is abstract and is not intended to provide a biologically plausible description of the *L. irrorata* populations. Rather, it is simply intended to illustrate the potential for the hump-shaped relationship observed in the data.

The model takes the form of a modified Leslie matrix (Caswell 2001), with 10 size classes indexed *i*. I assume that individual size is entirely a function of age, such that the size classes correspond to age classes (with the exception of size class 10; see below). Each individual has some probability of surviving to the next size class *μi* as a function of the current size class *i* and predation pressure *p*. All individuals that survive in a given generation must progress to the next size class. The only exceptions are individuals in age class 10, which corresponds to the maximum size an individual can attain. In this case, surviving individuals return to the same size class. For simplicity, I assume that only individuals in the largest size class can reproduce (with fecundity *f*) and that all offspring belong to size class 1.

If these assumptions correspond to a 10 x 10 transition matrix **A**, then the demography of a single generation is projected as **n***t*+1 **= An***t*, where **n***t* is a vector containing the density of individuals in a particular size class at time *t*. Iterating this equation reveals that **n***t* **= A***t***n**0, where **n**0 is the initial size distribution. The long-term size structure of the population is given by the right eigenvector corresponding to the leading eigenvalue of **A**.

I modeled the size-specific survival probability *μi* using the following relations:

*μi* = logit-1(*b0* - *b1*\**i* - *a*\**p*)

*a = a0\**logit-1(-*a1*\**i*)

where *b0* is a baseline value, *b1* is the strength of senescence (required to yield biologically sensible results), *a0* is the baseline mortality due to predation, *a1* is the decline in the probability of successful predation with size, and *p* is the predation pressure. The logit-1 function is used to constrain probabilities between 0 and 1. Figure 4 plots *μi* against *i* for different levels of *p*, with the following parameter values: *b0* = 3, *b1 =* 0.75, *a0* = 5, and *a1 =* 2. When *p =* 0 the survival probability decline monotonically with size. However, as the strength of predation increases, the survival probability shows an increasingly hump-shaped dependence on size.

To explore how the size distribution changes with predation pressure, I calculated the long-term average size from the right eigenvector of **A**parameterized with different values of *p*. The parameter values for Figure 5 are the same as for Figure 4, with *f* = 1. The behavior of the model is very sensitive to parameter values, and for many combinations it does not predict a hump-shaped relationship between average size and predation pressure. A more thorough analysis of the model is required before any general conclusions can be drawn regarding the effect of predation on the size structure of populations.

ADVICE TO FUTURE SAPELOIDS

1. Both for the class of 2015 and for past years, I think that the most successful Sapelo projects are those that are inspired by the natural history of the system. The original project I designed had a very theoretical motivation that was not directly connected to the unique features of the island. Once I arrived at Sapelo and became familiar with the system, I scrapped my project in favor of the one presented here.
2. Fieldwork is much more fun if you do it with others, and collaboration generally leads to better projects. I was fortunate that several other people were grappling with related issues. In fact, my project could not have existed without their help.
3. Sapelo is defined by a few very strong gradients, most of them connected to the tidal cycle. These produce a variety of spatial patterns that are very fruitful areas for exploration. Experiments are seductive, and can turn out really well if you have a clear idea that you can run with from the start. But field sampling along natural gradients is a quick way to collect lots of data.
4. I really enjoyed working in the marshes. I suspect that the insects were not nearly as bad as in some years, which certainly helped. But even so, I think that would still have elected to work there. The biology of the salt marshes is just so unique, and it’s teeming with cool organisms. Though, I should add that working in Odum’s marsh in 2015 was a bit challenging because of the softness of the sediment. I (with the help of Rob Mooney) spent an entire afternoon more-or-less crawling through the mud to finish my last day of sampling. Though, it did make for a good excuse to bike down to the beach and take a rinse in the ocean (we even saw bioluminescent plankton that only are visible when the water is disturbed).
5. Don’t stress too much. Obviously hard work is important, but more than anything this class provides a great opportunity to experience the ecology of a remarkable ecosystem and the bond with fellow graduate students. Every project from 2015 turned out well (even with many wrong-turns along the way), and people still managed to have a good time.