

## ABSTRACT

Title: EFFECTS OF ABIOTIC STRESS AND PREDATOR  
REFUGE ON TERRESTRIAL PREDATOR-PREY  
INTERACTIONS

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A major goal of ecology has been to understand how abiotic stress modifies species interactions, including predation. In marine habitats, a well-supported hypothesis holds that stress reduces the importance of predation because predators are more vulnerable to stress than prey, but this hypothesis has not been well-tested in terrestrial systems. The effect of refuge from stress on predation level has been studied even less, particularly in terrestrial systems. My research examines the effects of two types of stress, and refuge from them, on predation in a terrestrial salt-marsh food web.

I investigated the stress of winter weather and asked first, whether the top predator used a particular marsh habitat as a winter refuge, second, how inter-year variation in winter severity affected refuge use, and third, how refuge use affected the predator's spatial distribution later in the year (Chapter 1). I found that spring predator density was higher within the refuge than outside, a difference that increased following colder winters. Consequently, predators were forced to re-colonize the rest of the marsh from the winter refuge, creating a long-lasting density gradient with

lower densities farther from the refuge. In contrast, prey densities were not affected by winter temperatures, and were higher outside the refuge. This prey distribution may have facilitated predator colonization of non-refuge habitats.

I investigated the stress of tidal inundation on marsh predators and prey, and their use of vegetation above water as a refuge from submersion. I found that densities of two key predators were more highly correlated with refuge availability than with tidal intensity. Notably, this correlation with refuge increased during the highest tides of the month. In contrast, distribution of the most abundant herbivore was not correlated with refuge availability (Chapter 2). These results suggested that tides impacted predators more than herbivores, but that refuge negated tidal effects on predators. To test these hypotheses, I eliminated tidal inundation from experimental field mesocosms while allowing control mesocosms to experience normal tides (Chapter 3). I found that tides caused substantial mortality at all trophic levels, but affected predators significantly more than herbivores and decreased predation levels.

EFFECTS OF ABIOTIC STRESS AND PREDATOR REFUGE ON  
TERRESTRIAL PREDATOR-PREY INTERACTIONS

By

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Research directed by Professor Robert F. Denno (1945 - 2008)

## **Dedication**

I would like to dedicate this dissertation to Bob Denno, my PhD advisor, for his time, energy, expertise and patience. Also for the stimulating, diverse, demanding, enjoyable lab he nurtured, and especially for the amazing good will and humor he demonstrated in dealing with me as I overestimated my own knowledge and took too long to appreciate his.



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## Table of Contents

Dedication .....	ii
Acknowledgements .....	iii
List of Tables .....	v
List of Figures .....	vi
CHAPTER 1: A seasonal shift in habitat suitability enhances an annual predator subsidy .....	1
Abstract .....	1
Introduction .....	2
Methods .....	5
Results .....	11
Discussion .....	13
Figures .....	20
CHAPTER 2: Predators take refuge to mitigate the impact of abiotic stress on a terrestrial food web .....	25
Abstract .....	25
Introduction .....	26
Methods .....	29
Results .....	34
Discussion .....	37
Figures .....	43
CHAPTER 3: Abiotic stress differentially impacts higher trophic levels despite a predator refuge .....	49
Abstract .....	49
Introduction .....	50
Methods .....	53
Results .....	59
Discussion .....	61
Figures .....	67
Tables .....	73
Appendices .....	75
Appendix 1.1 .....	75
Appendix 1.2 .....	76
Appendix 1.3 .....	80
Appendix 1.4 .....	83
Appendix 2.1 .....	87
Appendix 3.1 .....	89
Literature cited .....	91

## List of Tables

**Table 3.1.** Mean densities for adults and nymphs of *Tytthus* and *Prokelisia*, pooled over all sample dates, for tide-free and tidal treatments. Tidal treatment means combine data from open control plots and tidal mesocosms. Treatment ratios equal tide-free means divided by tidal means. P values are from repeated-measures F tests for equality of treatments.

**Table 3.2.** Predator-to-prey ratios for all predator-prey combinations, averaged over all dates when both predators and prey were present. The “Treatment effect” column divides the ratio in tide-free mesocosms by the ratio in tidal treatments. P values are from repeated-measures F tests for equal ratios in tide-free and tidal treatments.

## List of Figures

**Figure 1.1.** Gradients in *Pardosa* density with increasing distance from *S. patens*. (A) August 16, 2002, following a mild winter, there was no significant gradient ( $F_{1,19} = 2.35$ ,  $P = 0.14$ ). (B) August 26, 2003, following a much colder winter, *Pardosa* were significantly more abundant closer to *S. patens* ( $F_{1,21} = 23.61$ ,  $P < 0.0001$ ).

**Figure 1.2.** Effect of mean winter temperature on the slope of *Pardosa* (A) and planthopper (B) density gradients the following summer. Each data point represents the gradient slope from a single sample date ( $\pm 1$  SE), such as those in Figs 1A and 1B. Slopes for *Pardosa* (A) were significantly less steep following milder winters (temperature  $\times$  distance from *S. patens*  $F_{1,460} = 6.49$ ,  $P = 0.011$ ). Winter temperature had no effect on planthopper gradients (B) (temperature  $\times$  distance from *S. patens*  $F_{1,459} = 0.14$ ,  $P = 0.71$ ).

**Figure 1.3.** Effect of habitat and time on the size of over-wintered *Pardosa* during the spring, pooled data from all years. Solid circles and line show square-root transformed sizes ( $\pm 1$  SE) in *S. patens*, open circles and dashed line in *S. alterniflora*. Size was significantly larger in *S. alterniflora* ( $F_{1,53} = 26.15$ ,  $P < 0.0001$ ), and the difference between the habitats increased from March to June (time  $\times$  habitat  $F_{1,28} = 10.22$ ,  $P = 0.0034$ ).

**Figure 1.4.** The effect of winter severity on spring densities of *Pardosa* (A) and planthopper nymphs (B). Solid circles and line show observed densities and regression in *S. patens*, open circles and dashed line in *S. alterniflora*. Increasing winter temperature had a greater effect on *Pardosa* density (A) in *S. alterniflora* than in *S. patens* (temperature  $\times$  habitat  $F_{1,218} = 4.56$ ,  $P = 0.034$ ). Winter temperature had no effect on planthopper density (B) in either habitat ( $F_{1,203} = 0.24$ ,  $P = 0.62$ ).

**Figure 1.5.** Effect of cage treatment (un-manipulated *S. patens*, *S. alterniflora* with augmented thatch, or *S. alterniflora* with low thatch) on *Pardosa* survivorship after being caged throughout the winter. Mean ( $\pm 1$  SE) number of *Pardosa* recovered per cage: *S. patens* = 8.5 ( $\pm 1.5$ ), added-thatch = 8.2 ( $\pm 2.2$ ), low-thatch = 4.0 ( $\pm 1.3$ ). Probability that *S. patens* mean  $\leq$  thatch-removed mean or thatch-added  $\leq$  thatch-removed = 0.012 based on 20,000 randomisations.

**Figure 2.1.** Three marsh habitats occupied by *Spartina alterniflora*. Creek-side vegetation is substantially taller than meadow grass, and as a result, more vegetation extends above tide water in the creek-side habitat than in the other two. This vertical refuge is least available in low-elevation meadows.

**Figure 2.2.** Square-root-transformed number  $\pm$  SEM of *Pardosa* remaining in each of the inundation treatments, out of the 15 originally stocked. Letters indicate significant differences.

**Figure 2.3.** Mean density  $\pm$  SEM of *Pardosa* (A, D), *Tytthus* (B, E), and *Prokelisia* planthoppers (C, F) in low-elevation plots (A, B, C) and in high-elevation plots (D, E, F). An asterisk signifies that a mean density was significantly less than a long-stem density, determined by rejecting one of the one-sided *a priori* null hypotheses  $H_0$ : long-stem density  $\leq$  short-stem density or  $H_0$ : long-stem density  $\leq$  no-stem density ( $\alpha = 0.05$ ). “Long-stem” plots supplemented *Spartina* with 50 cm vertical stems of *Phragmites*, providing arthropods with the opportunity to climb above rising tidewaters. Stems in “Short-stem” plots were 20 cm high, approximately the height of the *Spartina* canopy. Short-stem and no-stem plots provided no refuge from tides. Tides in high-elevation meadows are shallow and infrequent, making vertical refuge unnecessary.

**Figure 2.4.** Mean values  $\pm$  SEM for the three habitats, pooled across the four sample dates of the field survey, for vertical refuge (A), predatory *Pardosa* density (B), predatory *Tytthus* density (C), herbivorous planthopper density (D), and predator-to-prey ratio (E).

**Figure 2.5.** Response of *Pardosa* density (A), *Tytthus* density (B), and planthopper density (C) to availability of vertical refuge and to tide height. Tide height was treated as discrete, with two values, “modest” and “highest”. Open circles and dashed lines show data and regression solutions for the two samples collected during relatively modest high tides. Closed circles and solid lines show data and regression solutions for the two samples taken during the highest monthly tides. P values are displayed within the plots. Significant interactions mean that slopes differ with tide height.

**Figure 2.6.** Fractions of *Tytthus* collected in each of the three habitats, corrected for the number of sample points in each habitat. The three fractions add to 1.0 on each date. Samples taken on July 13 and August 10 followed the highest tides of July and August, and the fraction of *Tytthus* collected in low-elevation meadows fell by roughly two-thirds on those days, while the fraction collected in the creek-side habitat rose.

**Figure 3.1.** One tide-free mesocosm and one tidal mesocosm during a low tide (A) and a somewhat higher tide (B). White plastic bottles provide flotation for the tide-free mesocosm, and upright boards keep it in place while floating. Pictures were taken in June, when creek-side *Spartina* was approximately half the height it would attain by August.

**Figure 3.2.** Effect of treatment on densities of (A) *Pardosa*, (B) *Tytthus*, (C) *Grammonota*, (D) *Prokelisia*, and (E) *Trigonotylus*. Densities were square-root transformed before analysis. Error bars display standard errors of the means. Treatments that do not share a letter are significantly different ( $\alpha = 0.05$ ).

**Figure 3.3.** Mean ( $\pm$  standard error of the mean) of log-transformed densities of the three trophic levels in tidal and tide-free treatments. Slopes for the regression lines are significantly different (trophic level by treatment interaction  $F_{1,1263} = 48.53$ ,  $P < 0.0001$ ), showing that densities of higher trophic levels were reduced more by tidal inundation than those of herbivores.

**Figure 3.4.** *Pardosa* treatment ratios (mean density in tide-free mesocosms divided by mean density in tidal treatments) for all dates on which *Pardosa* were present in both treatments. *Pardosa* treatment ratios increased over the course of both seasons of the experiment. No other species ratio changed consistently with time.

**Figure 3.5.** Nymphs per adult for *Prokelisia* (A) and *Tytthus* (B) in tide-free and tidal treatments for all dates on which both nymphs and adults were present. Error bars show standard errors of the ratio means.

**Figure 3.6.** Percent nitrogen and carbon in *Spartina* cordgrass samples taken from the three treatments on 22 May 2006. Error bars show standard errors of mean percentages. Percentages did not differ significantly among treatments.

# **CHAPTER 1: A seasonal shift in habitat suitability enhances an annual predator subsidy**

## **Abstract**

Entry of substantial numbers of natural enemies from outside a habitat can have profound impacts on food web structure in the recipient habitat, but underlying mechanisms are poorly understood, including the role of relative predator fitness in source and recipient habitats. I studied a naturally-occurring annual movement of the salt-marsh spider *Pardosa littoralis* across habitats in an attempt to clarify factors enhancing and impeding movements of predator populations. Marsh vegetation is dominated by two cordgrass species, *Spartina patens*, a complex-structured grass with a well-developed litter layer, and *Spartina alterniflora*, a sparse-structured grass with little thatch accumulation. *Pardosa* hunts across both habitats and can drastically reduce densities of planthoppers and leafhoppers, the most abundant marsh herbivores. I found an annual subsidy of *Pardosa* from *S. patens*, extending hundreds of meters into *S. alterniflora* made possible by a winter refuge provided by *S. patens*. As a result, the strength of the subsidy is correlated with the severity of the preceding winter, with the largest subsidies following the coldest winters. Higher *Pardosa* fitness in the recipient habitat following winter, as indicated by higher growth rates associated with greater prey availability, enhanced the strength of this subsidy. Conversely, lower structural complexity in *S. alterniflora*, which is associated with higher rates of cannibalism in this spider, may impede the subsidy. The mechanistic underpinnings of the predator subsidy demonstrated here can improve our

understanding of subsidies in other contexts, such as conservation biological control. In addition, identifying such subsidies is key to preserving food webs in recipient habitats when source habitats are threatened.

## **Introduction**

Over the last decade, empirical studies have demonstrated that flows of energy, material and organisms across ecosystem boundaries can strongly influence the structure and dynamics of food webs (Polis et al. 1998, Nakano and Murakami 2001, Marczak et al. 2007). Moreover, subsidies entering at different trophic levels (e.g. detritus vs. predators) can have very different effects on the recipient habitat (Polis et al. 1997, Huxel et al. 2002). In particular, subsidies of natural enemies can alter food web dynamics (Polis et al. 2000, Holt 2002, Murakami and Nakano 2002), including the prevalence of trophic cascades in recipient habitats (Polis and Strong 1996, Schmitz et al. 2000, Finke and Denno 2004, Leroux and Loreau 2008). Despite the potential importance of enemy subsidies, we know little about their prevalence in natural and managed systems, the spatial scales over which they occur (Döbel and Denno 1994, Pfiffner and Wyss 2004), or factors that promote and constrain them (Bell et al. 2006). In particular, we know little about how the relative fitness of natural enemies in source and recipient habitats contributes to movement between them (Polis et al. 1997).

An application of natural enemy subsidies is found in conservation biological control, which seeks to encourage such subsidies to crop fields by manipulating habitats in and around fields to serve as sources of predators and parasitoids to crops



(Landis et al. 2000, Collins et al. 2002, Banks 2004). This approach has produced notable successes (Lys and Nentwig 1994, Landis et al. 2000, Midega and Kahn 2003), but failure has also been common (Landis et al. 2000). The altered habitats, such as weed strips, wildflower borders and beetle banks have supported enhanced natural enemy abundance, but on occasion have contributed no additional enemies to the crop (Samu et al. 1999, Frere et al. 2007, Koji et al. 2007), have increased enemy density only in their immediate vicinity (Frank and Nentwig 1995, Samu et al. 1999), or have acted as sinks, reducing enemy density in crop fields (Corbett and Plant 1993, Corbett 1998, Rypstra et al. 1999). Mechanisms contributing to success and failure remain obscure, especially factors affecting the propensity for natural enemy movement (Bell et al. 2006).

I used *Spartina* salt marshes on the Atlantic coast of North America as a model system to understand natural enemy movement and habitat-dependent fitness. These marshes consist of two distinct, adjacent habitats: the cordgrass *Spartina patens*, with a well-developed layer of dead thatch at ground level, and *Spartina alterniflora*, with less thatch and a more open architecture. Plant-based food webs in the two habitats are largely distinct, with few species in common (Denno 1977). Although species differ, the most abundant herbivores in both webs are sap-feeding planthoppers and leafhoppers (Denno et al. 1996). The wolf spider *Pardosa littoralis* (henceforth *Pardosa*) is exceptional in being common to both habitats, and can drastically reduce densities of sap feeders (Döbel and Denno 1994). Therefore an influx of *Pardosa* to *S. alterniflora* habitats has the potential to radically modify food web structure.

Previous studies have found *Pardosa* largely restricted to *S. patens* and high-elevation *S. alterniflora* meadows during the spring, and assumed a winter refuge in those habitats (Denno et al. 2005). The distribution and timing of herbivore outbreaks on the marsh has been explained partly by distance from the winter refuge and the time required for *Pardosa* migration to other habitats (Denno et al. 2005). Here I extend that work by testing whether the winter refuge actually consists of only a portion of the high marsh, the *S. patens* habitat, and by examining the contributions of winter severity and prey availability to the intensity, duration and extent of the *Pardosa* subsidy to the rest of the marsh. Specifically, my objectives were to: (1) document *Pardosa* population movement into *S. alterniflora* by sampling *Pardosa* density along transects through the two habitats throughout the summer, (2) assess the relative fitness of *Pardosa* in *S. patens* and *S. alterniflora* by comparing their body sizes in the two habitats throughout the season, (3) investigate the winter refuge provided by *S. patens* by examining the correlation between winter severity and spring *Pardosa* abundance in the two habitats over six years, and (4) assess winter survival rates in the two habitats and the effect of thatch on survival by caging *Pardosa* throughout the winter in *S. patens*, in *S. alterniflora* with augmented thatch and in *S. alterniflora* with little thatch. Body size can be used as an indicator of fitness because female size positively correlates with clutch size in *Pardosa* (Buddle 2000). In addition, cannibalism can be particularly high among wolf spiders (Wise 2006) and *Pardosa* cannibalism is generally asymmetric, with larger spiders killing smaller individuals (Langellotto and Denno 2006).

## Methods

### *The study system*

Fieldwork was conducted on an extensive intertidal salt marsh in the Great Bay-Mullica River estuarine system in Tuckerton, Ocean County, New Jersey. Marsh vegetation is dominated by two cordgrass species, *S. alterniflora* and *S. patens*, which grow in expansive pure stands with markedly different structures. *S. patens* is a low-profile grass with a well-developed thatch layer that maintains its structure through the winter, whereas *S. alterniflora* is a coarse-culmed grass with a sparser layer of thatch (Redfield 1972). The most abundant herbivores in both habitats are planthoppers and leafhoppers (Denno et al. 1996), many of which overwinter as nymphs, providing their predators with some level of prey throughout the year (Döbel and Denno 1994).

Generalist wolf spiders (Araneae: Lycosidae), particularly *Pardosa littoralis*, are the major predators of planthopper nymphs and adults on mid-Atlantic coastal marshes (Döbel et al. 1990, Döbel and Denno 1994). Planthoppers are an important resource for *Pardosa*, constituting 60% of their diet (Döbel et al. 1990). *Pardosa* are univoltine in New Jersey. Reproduction begins in May or June and continues into August. Hatchlings grow throughout the summer and fall, and overwinter as late instar juveniles. Overwintered individuals moult to adults and mate during the spring (Döbel et al. 1990). *Pardosa* population structure in these marsh habitats changes radically with the onset of reproduction. Abundance increases more than ten-fold during the first month of reproduction (D. Lewis unpublished data), while mean size

declines accordingly. Consequently, experiments described below examine spring (pre-reproduction) and summer *Pardosa* populations separately.

### *Experimental design*

#### *Pardosa* population movement into *S. alterniflora*

In order to document the movement of *Pardosa* from *S. patens* to *S. alterniflora* during the summer, two sampling transects two kilometres apart were established in August 2002. The first transect consisted of four sample locations in *S. patens* and nine in *S. alterniflora*, the second consisted of three locations in *S. patens* and 14 in *S. alterniflora*. (Aerial photos in Appendix 1.1). Locations in *S. alterniflora* ranged from 3 to 390 meters from the nearest *S. patens*, and were chosen for similarity in grass height, culm density and thatch accumulation. In addition, all sample sites in *S. alterniflora* were located in high-marsh meadows to make tidal inundation as similar as possible among sites. Transects were sampled in August and October 2002, and monthly for the next four years (2003-2006) starting when *Pardosa* reproduction began. Sampling therefore began in June of 2003, May of 2004, and July of 2005 and 2006. Insects and spiders at all sites were collected using a D-vac suction sampler (D-Vac Company, Ventura, California, USA), with each sample consisting of nine non-overlapping four-second placements of the D-vac head (21 cm diameter) over the cordgrass. This duration, chosen to fall within the range of published sampling effort (Good and Giller 1991, Elliott et al. 2006, Brook et al. 2008), was used consistently to provide reliable estimates of spatial and temporal arthropod distributions, rather than absolute density estimates. Arthropods were

preserved in alcohol, and density per square meter was calculated at each sample location for *Pardosa* and their planthopper prey.

To test whether *Pardosa* density in *S. alterniflora* declined with distance from *S. patens*, *Pardosa* densities in *S. alterniflora* were square-root transformed to achieve normality and homogenous variances. For each sample date, transformed *Pardosa* densities were regressed against distance from *S. patens*. To test whether the strength of that density gradient depended on winter severity, data from all five years were pooled, and transformed *Pardosa* densities were regressed against distance from *S. patens*, mean temperature of the preceding winter, and their interaction. Since the same sites were sampled on all dates, repeated measures regression was performed using Proc Mixed (SAS 2002) with compound symmetry as the covariance structure. Since spatial autocorrelation among units can violate the assumption of independence, residuals were tested for spatial independence using variogram modelling (Fortin and Dale 2005). Mean temperature was chosen as an admittedly crude measure of winter severity because it allowed me to make unambiguous predictions. Other factors such as cold snaps, wind, and snow cover undoubtedly affect *Pardosa* density, but I had no basis for predicting their relative importance.

Despite my efforts to select sample sites with similar elevations, there was a difference of 14.3 cm between the highest and lowest sites, and a significant negative correlation between a sample site's elevation and distance from *S. patens* (Spearman rank correlation  $P = 0.0054$ ). I therefore included elevation along with sample date as random effects in the regression. Site elevations were determined using a Wild NA30 automatic level (Leica Heerbrugg AG, Heerbrugg, Switzerland).

*Pardosa* fitness in the two habitats as indicated by body size

In order to assess the relative fitness of *Pardosa* in *S. patens* and *S. alterniflora*, I measured carapace widths of over-wintered *Pardosa* collected in both habitats during the spring, before the onset of *Pardosa* reproduction, and juvenile *Pardosa* collected during the summer. Measurements were made under a microscope using a VIA-170 video image marker-measurement system (Boeckeler Instruments, Inc., Tucson, Arizona, USA). Mean *Pardosa* size was calculated for each combination of sampling location and date, and then square-root transformed to achieve normality and homogeneity of variance.

The relative fitness of juveniles collected in these samples was evaluated by regressing the square root of mean *Pardosa* size against habitat, date, and their interaction. An interaction between habitat and date would indicate a more rapid size change in one habitat than in the other. I do not know how long *Pardosa* resided in the habitat where they were collected, but inter-habitat movement would obscure any size difference, making this a conservative test of relative fitness.

To assess the relative fitness of over-wintered *Pardosa* before the onset of reproduction, I sampled transects in March and June from 2003 through 2006. I sampled an additional group of fifteen sample sites, six in *S. patens* and nine in *S. alterniflora*, in March and June from 2001 through 2006. *Spartina alterniflora* sites in this group were between 30 and 70 meters from *S. patens*, and the whole group was at least one kilometre from either of the transects. Differences in *Pardosa* size in the two habitats were evaluated by performing a repeated measures general linear model

(Proc Mixed) on the square root of mean *Pardosa* size with habitat, sample month, and their interaction as independent variables.

#### *The effect of winter severity on spring Pardosa density*

In order to assess the existence of a winter refuge provided by *S. patens*, I examined the correlation between winter severity and spring *Pardosa* abundance in the two habitats. Data from all March and June samples from 2001 through 2006 were used to calculate density per square meter of *Pardosa* and their planthopper prey at each sample site.

Repeated-measures regression was performed separately on densities of *Pardosa* and planthopper nymphs with mean temperature of the preceding winter, habitat, and their interaction as independent variables using Proc Mixed (SAS 2002). As above, a significant interaction would show that winter severity had different effects in the two habitats. Densities of *Pardosa* were square-root transformed as before, whereas densities of planthopper nymphs were log-transformed.

#### *The role of habitat structure on winter survival*

To test whether winter *Pardosa* survival rates were higher in *S. patens* than in *S. alterniflora* and to evaluate the role of thatch in survival, *Pardosa* were caged on the marsh throughout the winter in one of three treatments: un-manipulated *S. patens*, *S. alterniflora* with added thatch, and *S. alterniflora* with low thatch density. Each treatment was replicated six times. Cylindrical cages consisted of a PVC pipe frame (91 cm in diameter, 44 cm high) covered with fibreglass screen. There was no screen

on cage bottoms, and cages were buried 4 cm into the marsh surface. Before installing the *S. alterniflora* cages, thatch was raked from the grass. This removed most dead leaves not well-attached to living culms, resulting in thatch density much lower than in most meadows, but higher than that found around mud flats. After installation, 650 g dry-weight *S. alterniflora* thatch was placed around the base of living plants in added-thatch treatments. This resulted in approximately three times mean *S. alterniflora* thatch density (Finke and Denno 2006), near the highest naturally-occurring density. No thatch was added to low-thatch treatments after raking.

Although thatch is less abundant in *S. alterniflora* than in *S. patens*, there is extensive variation in thatch accumulation within *S. alterniflora*, from as low as 10 g/m<sup>2</sup> near mud flats to as high as 1500 g/m<sup>2</sup> in some meadows (Redfield 1972, Warren and Niering 1993), so my low-thatch and added-thatch treatments roughly bracket naturally-occurring thatch densities in *S. alterniflora*. Thatch removal in *S. patens* was not practical because its thatch remains tightly attached to living plants. Sham raking in *S. patens* treatments was deemed unnecessary because cage installation and subsequent defaunation, described below, caused greater disturbance to the arthropod community than raking.

On November 28, 2006 cages were defaunated using a D-vac, after which all arthropods except spiders were returned to cages. To ensure that *Pardosa* survival could be affected by habitat structure, but not by prey availability, an area of open marsh equal to three times the cage area was vacuumed for each cage and all non-spider arthropods were added to the cage. Thirty field-collected *Pardosa* were then added to each cage and cages were sealed. The initial density of 30 *Pardosa* per cage,



or 42 *Pardosa*/m<sup>2</sup>, is similar to the mean fall density of 49 *Pardosa*/m<sup>2</sup> in *S. patens* and higher than the mean density of 11 *Pardosa*/m<sup>2</sup> in *S. alterniflora* (D. Lewis, unpublished data). On March 27, 2007 all cages were opened and surviving *Pardosa* were counted.

Numbers of surviving *Pardosa* could not be transformed to achieve normality, so a non-parametric randomization test was done to test the hypothesis that *Pardosa* survival in low-thatch cages was lower than in *S. patens* cages and also lower than in added-thatch cages. Numbers of *Pardosa* recovered from each of the 18 cages were randomly reassigned to the three treatments 20,000 times and a P value was calculated as the fraction of times that randomised data were at least as extreme as the observed data. “At least as extreme” meant that (1) the *S. patens* total minus the low-thatch total was greater than or equal to the observed difference and (2) the added-thatch total minus the low-thatch total was greater than or equal to its observed difference (Manly 1997). I used Levene’s test to determine whether an adjustment for non-homogeneous variances would be necessary (Manly and Francis 2002).

## Results

A significant gradient of *Pardosa* density in *S. alterniflora* was found during 15 of the 21 days on which transects were sampled in the years 2002 through 2006. In all significant gradients, *Pardosa* were more abundant close to *S. patens* than farther away. Figure 1.1B from August 2003 is typical, whereas figure 1.1A from August 2002 shows one of the six days on which the gradient was absent. The gradient was steeper following colder winters (temperature  $\times$  distance from *S. patens*  $F_{1,460} = 6.49$ ,

$P = 0.011$ . See Appendix 1.2 for complete regression tables.) (Fig. 1.2A). There was no significant difference in *Pardosa* density between the two transects ( $F_{1,592} = 0.03$ ,  $P = 0.86$ ), and no spatial autocorrelation among regression residuals (see Supplementary material, Appendix 1.3). Planthoppers, on the other hand, exhibited significant density gradients in only three of the samples, all with higher densities farther from *S. patens*, opposite from the *Pardosa* gradients (Fig. 1.2B). Densities of both planthopper adults and nymphs were higher in *S. alterniflora* than in *S. patens* during the summer (adults  $F_{1,73} = 43.56$ ,  $P < 0.0001$ ; nymphs  $F_{1,73} = 11.15$ ,  $P = 0.0013$ ).

During spring, over-wintered *Pardosa* were larger in *S. alterniflora* ( $F_{1,53} = 26.15$ ,  $P < 0.0001$ ), and the difference increased from March to June (date  $\times$  habitat  $F_{1,28} = 10.22$ ,  $P = 0.0034$ ) (Fig. 1.3). During the summer, juvenile *Pardosa* were larger in *S. alterniflora* than in *S. patens* ( $F_{1,35} = 25.27$ ,  $P < 0.0001$ ).

Milder winters were correlated with higher spring *Pardosa* densities in both habitats ( $F_{1,218} = 16.64$ ,  $P < 0.0001$ ), but the effect was significantly greater in *S. alterniflora* than in *S. patens* (temperature  $\times$  habitat  $F_{1,218} = 4.56$ ,  $P = 0.034$ ) (Fig. 1.4A). In contrast, spring densities of planthopper nymphs, the most abundant prey for spiders during winter and spring, did not respond to winter temperature ( $F_{1,203} = 0.24$ ,  $P = 0.62$ ) (Fig. 1.4B). Planthopper nymphs were significantly more abundant in *S. alterniflora* than in *S. patens* ( $F_{1,68} = 7.77$ ,  $P = 0.007$ ).

The *Pardosa* survival rate when caged throughout the winter in *S. alterniflora* with little thatch was less than half that when caged in *S. alterniflora* with added thatch or in un-manipulated *S. patens* ( $P = 0.012$ ) (Fig. 1.5). Levene's test found no

significant difference among treatment variances ( $F_{2,15} = 1.68$ ,  $P = 0.22$ ) so no adjustment was necessary. Prey availability in cages was not a factor in these results. At the end of the experiment, planthopper nymph densities in low-thatch cages were significantly higher than in open *S. alterniflora* ( $T_{15} = 4.45$ ,  $P = 0.0005$ ). Planthopper densities in added-thatch cages were also higher than in open plots but the difference was not significant ( $T_{15} = -1.91$ ,  $P = 0.07$ ), whereas planthopper densities in *S. patens* cages were 29% lower than in open *S. patens*. Therefore, lower *Pardosa* survivorship in low-thatch cages was not caused by lower prey availability.

## Discussion

I found strong evidence for an annual subsidy of predatory *Pardosa* wolf spiders from *S. patens* into *S. alterniflora*. The subsidy appears to be driven by an annual shift in fitness among habitats, with higher winter survival in *S. patens*, followed by higher spring and summer growth rates in *S. alterniflora*.

As mean winter temperature declined, *Pardosa* density declined in both habitats, but the decline was significantly smaller in *S. patens* than in *S. alterniflora* (Fig. 1.4A). Abundant thatch in *S. patens* was key in creating this winter refuge, as shown by the fact that *Pardosa* caged throughout the winter in *S. alterniflora* with little thatch had survival rates less than half those of *Pardosa* caged in *S. alterniflora* with ample thatch or in *S. patens* (Fig. 1.5). Habitats similar to *S. patens*, including tussock-forming grasses and leaf litter have previously been shown to increase arthropod winter survival (Luff 1965, Edgar and Loenen 1974, Collins et al. 2002). Planthopper nymphs, the most abundant prey during winter months, were

significantly more available in *S. alterniflora*, outside the refuge habitat, and were not affected by winter temperatures in either habitat (Fig. 1.4B), indicating that prey availability did not contribute to the winter refuge.

Summer movement into *S. alterniflora* created a gradient of *Pardosa* density, with higher densities close to *S. patens* (Fig. 1.1B). The gradient was steepest following the coldest winters, when spring *Pardosa* densities differed most between the two habitats, and was absent following the two mildest winters (Fig. 1.2A). Prey distribution in *S. alterniflora* did not explain the *Pardosa* density gradient. Prey gradients were rare and when present were in the direction opposite from the *Pardosa* gradient (Fig. 1.2B).

#### *Mechanistic basis for the predator subsidy*

I propose that two mechanisms promote this *Pardosa* population movement whereas a third mechanism impedes it. The promoting mechanisms are first, directed movement towards *S. alterniflora* due to fitness advantages, and second, random diffusion coupled with higher *Pardosa* densities in *S. patens*. The impeding mechanism is *Pardosa*'s affinity for the structural complexity of *S. patens*.

After winter has ended, the fitness advantage for *Pardosa* may shift to *S. alterniflora* because of its higher planthopper prey density during the spring (Fig. 1.4B) and summer. Additionally, *S. alterniflora*-inhabiting planthopper species are known to possess weaker behavioural defences against spider predation than *S. patens*-inhabiting species (Denno et al. 2003), increasing the mismatch in prey availability. Since spiders in the field are widely thought to be food limited (Wise

2006, but see Gunnarsson 2007, Reed and Nicholas 2008), higher prey availability could lead to higher fitness in *S. alterniflora*. For example, higher prey abundance can increase the fraction of *Pardosa* females producing egg sacs (Denno et al. 2002). The larger *Pardosa* body size I found in *S. alterniflora* (Fig. 1.3) is likely another result of higher prey availability. Increased female size positively correlates with clutch size in *Pardosa* (Buddle 2000): another indication of higher fitness in *S. alterniflora*. *Pardosa*'s rapid aggregation in response to local prey increases (Döbel and Denno 1994, Denno et al. 2002) demonstrates an ability to take advantage of local concentrations of abundant prey resources. Higher fitness during spring and early summer also may result from lower levels of cannibalism in *S. alterniflora* because of lower *Pardosa* density in that habitat. This fitness advantage diminished or reversed later in the summer as density in *S. alterniflora* increased.

In addition to directed movement, the *Pardosa* subsidy may be driven by random diffusion coupled with higher spring densities in *S. patens*. Completely random movement can be a successful dispersal strategy in systems where the relative suitability of habitats changes (Armsworth and Roughgarden 2005). Spiders of the genus *Pardosa* are known to exploit disturbed, changeable habitats and to efficiently colonize new habitat patches (Marshall et al. 2006), aided by their propensity to emigrate from even highly suitable habitats (Buddle and Rypstra 2003, Marshall et al. 2006). This mechanism contributes less to the subsidy later in the summer as densities in the two habitats become more similar.

Movement caused entirely by higher fitness in *S. alterniflora* and random diffusion would be expected to continue until *Pardosa* density in *S. alterniflora* was

higher than in *S. patens*. There is some evidence that this occurred: although mean *Pardosa* density in the entire *S. alterniflora* habitat remained lower than in *S. patens*, density within 35 meters of *S. patens* exceeded *S. patens* density in midsummer during three of the five years of the survey.

More complete movement of the *Pardosa* population into *S. alterniflora* may be impeded by a third mechanism: the tendency of wolf spiders to aggregate in thatchy habitats such as *S. patens*, possibly as a refuge from cannibalism (Langellotto and Denno 2006, Rypstra et al. 2007). Wolf spiders (Lycosidae) are among the most cannibalistic of spider families (Wise 2006) and cannibalism is especially common among *Pardosa* hatchlings (Langellotto and Denno 2004). Cannibalism increases with increasing conspecific density (Wagner and Wise 1997, Buddle et al. 2003), so as density rises in *S. alterniflora*, *Pardosa* may face a trade-off between faster growth in *S. alterniflora* and lower mortality risk in *S. patens*. Therefore this third mechanism may substantially slow further population movement to *S. alterniflora*.

#### *Alternate explanation for density gradients*

Although density gradients have been used to indicate migration (e.g. Collins et al. 2002), it is reasonable to ask whether these gradients can be explained by a mortality gradient without inter-habitat movement. Reproduction intensity, as measured by densities of the smallest *Pardosa*, was significantly higher in *S. patens* than in *S. alterniflora* in May, June and July, and was not significantly different in August. Simultaneously, *Pardosa* density increased faster in *S. alterniflora* than in *S. patens*. (Documentation in Appendix 1.4). Therefore, in the absence of inter-habitat

movement, mortality must be much lower in *S. alterniflora*, but must increase with distance from *S. patens*. Furthermore, that mortality gradient must vary with the severity of the preceding winter. I am not aware of any set of mechanisms that could produce such gradients, but cannot rule them out without further study.

#### *Alternate explanation for size difference*

I suggest that larger *Pardosa* body size in *S. alterniflora* is caused by higher growth rates made possible by higher prey density. However, other mechanisms can cause body size to differ between habitats. For example, high rates of cannibalism can increase mean size because survivors are generally larger than their victims (Buddle et al. 2003, Kiss and Samu 2005). However, cannibalism rate is positively correlated with conspecific density (Wagner and Wise 1997, Buddle et al. 2003), so should be lowest during the spring, when *Pardosa* abundance is at its low point for the year. On the marsh, the largest size difference and the largest increase in difference between habitats was observed during the spring (Fig. 1.3). In addition, *Pardosa* body size in the spring tended to be lower in both habitats during years when *Pardosa* density was high, so cannibalism is unlikely to be the cause of the size discrepancy (Appendix 1.4). Higher reproduction rates in *S. patens* could contribute to smaller mean body size in that habitat during part of the summer, but would not explain the size difference before the onset of reproduction.

Finally, although I am not aware of evidence supporting size-dependent mobility among Lycosids, it is conceivable that larger individuals move farther and are thus over-represented among colonists of *S. alterniflora*. This would increase

mean *Pardosa* size in *S. alterniflora* without increased growth rate, but there is only limited support for this mechanism in my data. This mechanism would cause larger size differences following colder winters, when colonization is more important, but the size discrepancy was not correlated with winter temperature (Appendix 1.4). This mechanism would also cause a size gradient, with larger individuals farther from *S. patens*, and such a gradient did exist during the summer (Appendix 1.4). Since this summer gradient lends some support for the mechanism, I cannot rule it out at this time, and I note that it depends on inter-habitat movement.

### *Implications*

Here I have described an annual predator subsidy penetrating hundreds of meters into the recipient habitat. The resulting predator density gradient was most intense and long-lasting following the most severe winters. This pattern held over multiple years despite significant inter-year variation in prey abundance, overall predator density, and timing of predator reproduction. This study supports the theoretical prediction that a predator subsidy can be fostered by a winter refuge coupled with greater suitability of the recipient habitat in spring and summer (Corbett and Plant 1993, Corbett 1998).

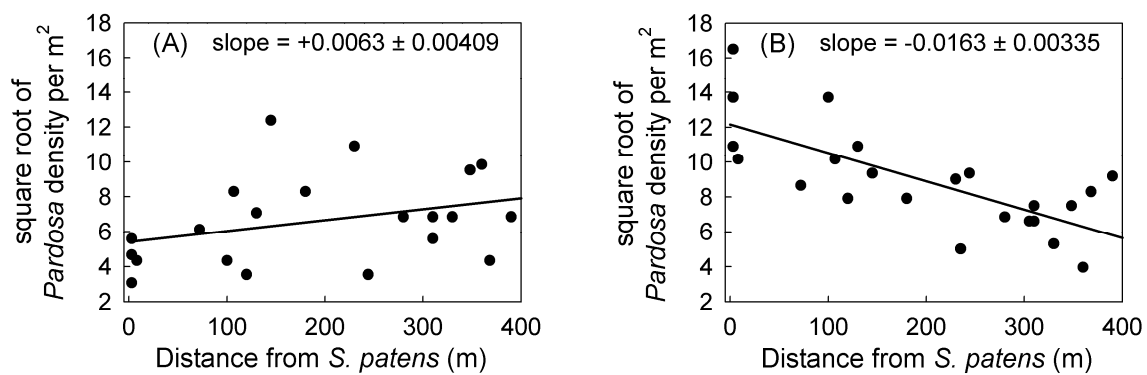
This research increases our understanding of mechanisms underlying natural enemy subsidies, including the role of refuge from abiotic stress, the role of relative fitness in donor and recipient habitats, and the effects of temporal change in those factors. Previous studies have found evidence for subsidies of terrestrial arthropod predators, including dragonflies (Wikelski et al. 2006), lacewings (Perry and Bowden



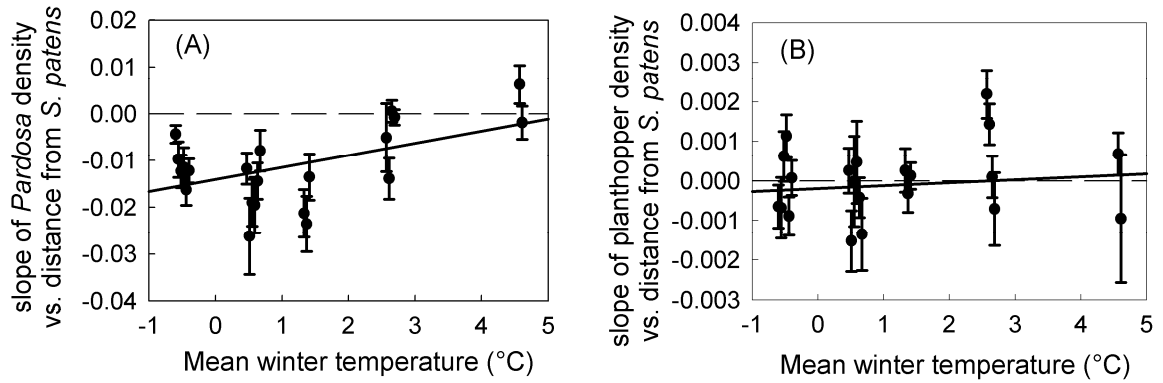
1983), carabids (Chapman et al. 2005) and another *Pardosa* species (Morse 1997), but the current study is unique in that it integrates the spatial extent of the subsidy, factors promoting and constraining the subsidy, and fitness consequences for the predator.

The paradigm for biological control through habitat manipulation is that natural enemies move from altered habitats close to and within crop fields into the crops themselves. My results suggest that such movement is more likely when enemy fitness and structural complexity are higher in crop fields than in refuge habitats. This confirms the importance of complexity noted by other researchers (Rypstra et al. 1999, Samu et al. 1999, Marshall et al. 2000). It has been noted that enemies immigrating from the surrounding landscape can make an important contribution to pest control (Schmidt et al. 2004, Tschardt et al. 2007), but it is sometimes assumed that cursorially-dispersing predators are relatively unimportant in large-scale movements (Griffiths et al. 2008). My observation that *Pardosa* disperse hundreds of meters from their winter refuge shows that they can be an important part of landscape subsidies.

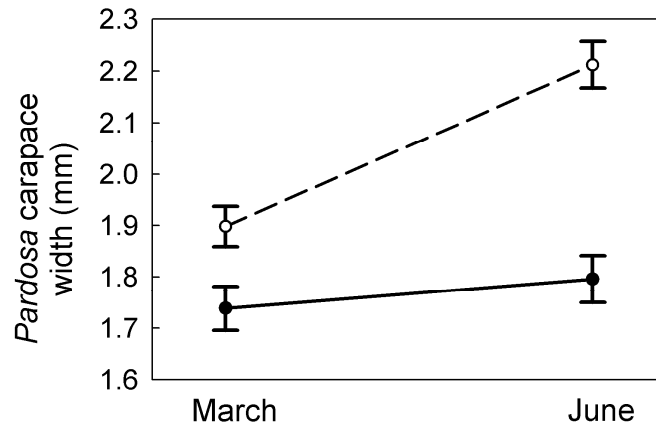
## Figures



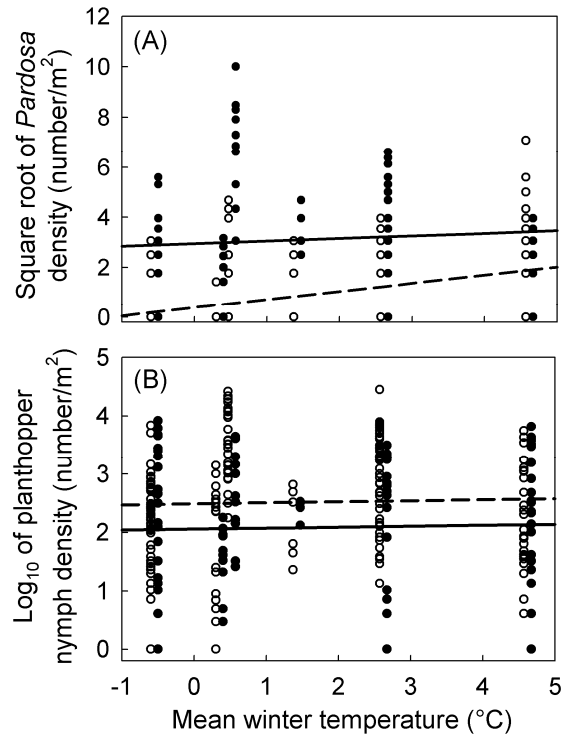
**Figure 1.1.** Gradients in *Pardosa* density with increasing distance from *S. patens*. (A) August 16, 2002, following a mild winter, there was no significant gradient ( $F_{1,19} = 2.35$ ,  $P = 0.14$ ). (B) August 26, 2003, following a much colder winter, *Pardosa* were significantly more abundant closer to *S. patens* ( $F_{1,21} = 23.61$ ,  $P < 0.0001$ ).



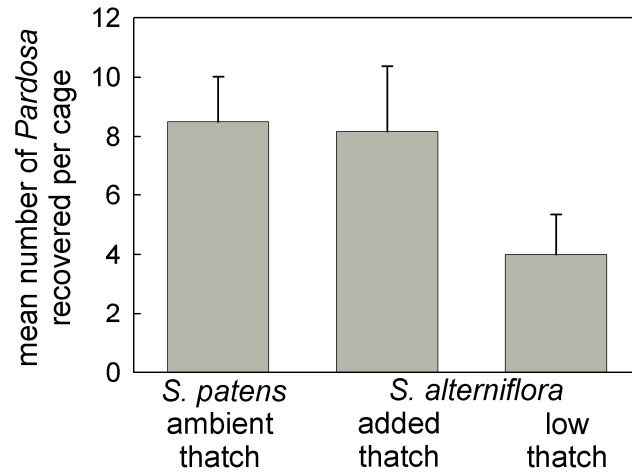
**Figure 1.2.** Effect of mean winter temperature on the slope of *Pardosa* (A) and planthopper (B) density gradients the following summer. Each data point represents the gradient slope from a single sample date ( $\pm 1$  SE), such as those in Figs 1A and 1B. Slopes for *Pardosa* (A) were significantly less steep following milder winters (temperature  $\times$  distance from *S. patens*  $F_{1,460} = 6.49$ ,  $P = 0.011$ ). Winter temperature had no effect on planthopper gradients (B) (temperature  $\times$  distance from *S. patens*  $F_{1,459} = 0.14$ ,  $P = 0.71$ ).



**Figure 1.3.** Effect of habitat and time on the size of over-wintered *Pardosa* during the spring, pooled data from all years. Solid circles and line show square-root transformed sizes ( $\pm 1$  SE) in *S. patens*, open circles and dashed line in *S. alterniflora*. Size was significantly larger in *S. alterniflora* ( $F_{1,53} = 26.15$ ,  $P < 0.0001$ ), and the difference between the habitats increased from March to June (time  $\times$  habitat  $F_{1,28} = 10.22$ ,  $P = 0.0034$ ).



**Figure 1.4.** The effect of winter severity on spring densities of *Pardosa* (A) and planthopper nymphs (B). Solid circles and line show observed densities and regression in *S. patens*, open circles and dashed line in *S. alterniflora*. Increasing winter temperature had a greater effect on *Pardosa* density (A) in *S. alterniflora* than in *S. patens* (temperature  $\times$  habitat  $F_{1,218} = 4.56$ ,  $P = 0.034$ ). Winter temperature had no effect on planthopper density (B) in either habitat ( $F_{1,203} = 0.24$ ,  $P = 0.62$ ).



**Figure 1.5.** Effect of cage treatment (un-manipulated *S. patens*, *S. alterniflora* with augmented thatch, or *S. alterniflora* with low thatch) on *Pardosa* survivorship after being caged throughout the winter. Mean ( $\pm 1$  SE) number of *Pardosa* recovered per cage: *S. patens* = 8.5 ( $\pm 1.5$ ), added-thatch = 8.2 ( $\pm 2.2$ ), low-thatch = 4.0 ( $\pm 1.3$ ).

Probability that *S. patens* mean  $\leq$  thatch-removed mean or thatch-added  $\leq$  thatch-removed = 0.012 based on 20,000 randomisations.

## **CHAPTER 2: Predators take refuge to mitigate the impact of abiotic stress on a terrestrial food web**

### **Abstract**

The consumer stress model (CSM) predicts that when abiotic stress varies spatially, the impact of natural enemies on their prey decreases in the most stressful locations. This occurs because enemies are generally more mobile than prey, are able to escape stressful situations, and so have experienced weaker pressure to adapt to stress. However, if a refuge from stress is available to predators within stressful habitats, spatial separation of predators from prey could be minimized, fundamentally altering the stress-predation relationship. The role of refuge from stress for predators has rarely been investigated in natural systems, even though it is central to the practice of conservation biological control through habitat manipulation. I examined the effect of tidal stress on distributions of predators and prey in a salt-marsh food web consisting of the most abundant insect herbivore and its two most important predators. I also investigated the role of vegetation extending above tide water as a vertical refuge from submersion and its effect on predation. I found that densities of predators, but not prey, increased in experimental field plots with augmented vertical refuge. In un-manipulated surveys, densities of both predators were positively correlated with the amount of refuge, and that correlation increased as tide heights increased. In lower marsh elevations, where tidal effect was greatest, refuge availability was positively correlated with predator/prey ratio and negatively correlated with herbivore density. Therefore in this marsh system, the spatial pattern

of predation is affected by the distribution of stress, as predicted by CSM, but also by the distribution of refuge from stress.

## **Introduction**

Ecologists have long recognized the importance of abiotic factors in shaping community structure (Connell 1975, White and Pickett 1985, Bertness and Callaway 1994), and have made several attempts to predict the relative effects of abiotic stress on different trophic levels. One hypothesis, the consumer stress model (CSM), notes that animals at higher trophic levels tend to be more mobile than their prey, can therefore escape stressful situations, and so have experienced weaker selection pressure than prey to develop adaptations to stress (Menge and Sutherland 1987). CSM concludes that predator density declines as stress increases, diminishing the importance of predation (Connell 1975, Menge and Sutherland 1987). This hypothesis successfully describes the relationship between stress and predation in the rocky intertidal, where marine organisms experience stress from exposure to air during low tide, and where predation decreases in upper elevations, where exposure is more frequent (Menge and Olson 1990, Peckarsky et al. 1990, Mattila 1997). Several classic studies have demonstrated that mobile predators abandon those areas during low tides, allowing much higher densities of bivalve prey in the upper intertidal than at lower elevations (Connell 1961, Petes et al. 2008).

Implicit in CSM is the assumption that widespread stress has a greater effect on predation than more localized stress because predators must move farther to



escape it. Refuge within stressful areas can therefore lessen the effects of stress by allowing predators to remain closer to prey (Menge and Olson 1990). This concept underlies some approaches to conservation biological control which attempt to increase predation in crop fields by supplying predators with refuge from stress in or near fields (Griffiths et al. 2008). For example, grassy ridges have been established within crop fields to provide refuge for predators from the stress of winter weather as well as from farming practices such as plowing, spraying and harvest (Thomas et al. 1992). This approach has increased predation in some cases (Collins et al. 2002), but not others (Lemke and Poehling 2002). Given the importance of conservation biological control, it is surprising that predator refuge from stress has rarely been studied in natural systems. To my knowledge, all such studies have taken place in aquatic habitats. For example, some marine predators maintain high feeding rates at wave-exposed sites by using crevices or algal canopies as refuge from wave shock (Menge and Olson 1990). Predation by invertebrate predators in freshwater streams can remain high during high-flow disturbances when low-flow refugia are available (Lancaster 1996, Felten et al. 2008).

I used a salt marsh on the Atlantic coast of North America as a model system to evaluate the effects of tidal stress and refuge availability on a terrestrial food web composed of insect herbivores and their predators. Submersion in saltwater is stressful and even fatal for insects and spiders (Boomsma and Isaaks 1982), so stress increases at lower elevations of the intertidal, where inundation is more frequent and long-lasting. However, terrestrial animals may avoid submersion by climbing

vegetation extending above tide water (Foster and Treherne 1976, Hovel et al. 2001). Vegetation in this marsh is dominated by the cordgrass *Spartina alterniflora* Loisel (Denno 1983), which takes on two different growth forms at different elevations. At the lowest elevations, along the banks of tidal creeks, robust tall-form *S. alterniflora* can reach heights of over two meters due to nutrient inputs from creek water, whereas at higher elevations, short-form *S. alterniflora* is only 10-40 cm high (Redfield 1972, Bertness 1991). As a result vertical grass refuge is abundant at the lowest elevations, where tidal stress is greatest, but quite scarce in adjacent low-elevation meadows (Fig. 2.1).

Herbivore density increases at lower elevations, with outbreak densities most common at the lowest, more stressful elevations, along tidal creek banks (Bowdish and Stiling 1998). Grass nutritional quality plays a key role in creating this herbivore density gradient, as frequent tidal flooding increases the nitrogen content of marsh grass at lower elevations (Ornes and Kaplan 1989, Bowdish and Stiling 1998).

Spiders are important marsh predators and previous studies have noted a positive correlation between spider density and elevation, assumed to be caused by tidal flooding (Döbel et al. 1990). In this research I investigated the role tidal flooding plays in modifying distributions of both predators and prey, possibly enhancing or diminishing the herbivore gradient caused by grass quality. I asked whether tidal stress tends to spatially decouple predators from their prey, as predicted by CSM, and whether predator use of vertical refuge minimizes that decoupling.

My specific objectives were to: (1) establish predator use of vertical refuge to escape submersion, (2) experimentally confirm that the response of predators and prey is to vertical refuge *per se*, rather than to some associated factor, and (3) observe correlations of predators and prey with vertical refuge in the field, and test whether such correlations increase during the highest monthly tides. Few studies have tested whether stress separates terrestrial predators from prey, as assumed by CSM, and fewer still have examined the role of predator refuge in natural systems. With this study I aim to increase our understanding of how refuge from abiotic disturbance can affect the importance of top-down forces on herbivores.

## **Methods**

### *The study system*

Research was conducted on a tidal salt marsh just north of the Rutgers University Marine Station near Tuckerton, Ocean County, New Jersey, USA (39° 30.8' N, 74° 19.0' W). The most abundant herbivores of *Spartina alterniflora* are planthoppers of the genus *Prokelisia* (Denno 1976, Vince and Valiela 1981). Two of the most important predators of these planthoppers are the wolf spider *Pardosa littoralis*, a generalist predator, and the mirid bug *Tytthus vagus*, a specialist predator of *Prokelisia* eggs (Döbel and Denno 1994, Finke and Denno 2002). In addition to preying on planthoppers, *Pardosa* is a very effective intraguild predator of *Tytthus* (Denno et al. 2002, Finke and Denno 2002), and this interaction can result in diminished predation of planthoppers (Finke and Denno 2002, 2003). A variety of

parasitoids also attack *Prokelisia* planthoppers on this marsh, but they are less effective in suppressing planthopper populations than invertebrate predators (Denno & Peterson 2000).

### *Experimental design*

#### *Pardosa's use of vertical refuge*

To determine *Pardosa's* response to rising tides in the presence and absence of vertical refuge, I measured *Pardosa* emigration from potted *Spartina* plants (25 cm high in 25 cm diameter pots) subjected to one of three tidal inundation treatments (complete submersion, half submersion or no submersion), achieved by placing plants at different levels on platforms in a tidal creek (Fig. A, appendix 2.1). Each treatment was replicated eight times. Prior to placement in the creek, I removed all arthropods from pots using a D-vac suction sampler (D-Vac Company, Ventura, California, USA). I then stocked each pot with 15 field-collected *Pardosa*, resulting in 300 *Pardosa* per square meter, within the range of naturally-observed densities (Döbel and Denno 1994). I placed pots on platforms during low tide, where they remained until the tide peaked, at which time I counted the number of *Pardosa* remaining in each pot. I carried out experiments on July 17, 30 and 31, 2001. I performed a square-root transformation on the number of *Pardosa* remaining in each plot and analyzed treatment effects using repeated measures ANOVA. Repeated measures resulted from using all pots three times.

### *Predator response to artificial vertical refuge*

To confirm that predators, and possibly prey, respond to emergent vegetation only as an escape from tides, and not because of some associated plant factor, I experimentally established three refuge treatments (artificial refuge present, refuge control, and no refuge) in two marsh habitats: low-elevation meadows, where inundation is frequent and deep, and high-elevation meadows, where tides are infrequent and shallow. I created artificial vertical refuge by adding upright dead stems (50 cm in length) of the invasive reed *Phragmites australis* to rectangular experimental plots (1.5 by 5 m) of *Spartina* in a 10cm by 10 cm grid, for a total of ~800 stems per plot. Meadow grass reached approximately 20 cm in height, so this treatment added 30 cm of vertical refuge. I established a refuge control treatment by inserting the same number of short *Phragmites* stems into *Spartina* plots such that the top of the stems did not extend above the *Spartina* canopy. The third treatment was an un-manipulated, stem-free *Spartina* control. Triads of plots were established between May 17 and June 30, 2003. Treatments were randomly assigned to plots within each triad, and plots within a triad were one meter apart. In all, twelve triads were established, six in high-elevation and six in low-elevation meadows of *Spartina* (Fig. B, appendix 2.1).

I sampled arthropods from all plots on July 17, August 13, and September 8, 2003 using a D-vac suction sampler. All three samples were taken following at least 5 days of higher-than-average high tides. I used planned contrasts in repeated-measures ANOVA (Proc Mixed) to test the hypothesis that predator and prey densities in long-

stem plots were greater than densities in either of the other two treatments. A five-stem grass sample was taken from all plots on July 17 and September 8 to verify that any shading arising from the refuge treatment did not influence the height of *Spartina*. I pooled grass heights from the two samples and performed repeated-measures ANOVA (Proc Mixed) with treatment as the independent variable and sample location as the repeated factor.

*Predator and prey density in relation to refuge availability in the field*

To assess the effects of tides and vertical refuge on natural populations, I measured the density of *Prokelisia* planthoppers, *Pardosa*, and *Tytthus* under different levels of inundation along 18 three-point transects. The first sample location in each transect was located in tall creek-side *Spartina*, the second in the adjacent low-elevation meadow, and the third in a more distant high-elevation meadow (Fig. 2.1). I arbitrarily classified meadows less than 26 cm above the border with creek-side *Spartina* as low-elevation. Sample sites in low-elevation meadows were all within 5 meters of the border with creek-side *Spartina*. Because of differences in topography, high-elevation sample locations ranged from 11 to 32 meters from the border with creek-side *Spartina*. Transects were at least 30 meters from one another and were selected to provide wide variation in elevation and vertical refuge within each of the three habitats.

I determined the vertical refuge provided by the *Spartina* canopy at each sample location by measuring the elevation of the marsh surface with an auto level

(model NA30, Wild Heerbrugg, Gais, Switzerland) and adding to this elevation the height of the *Spartina* canopy. Thus, vertical refuge is an index of the amount of sanctuary provided by the *Spartina* canopy assuming equal tide height across all sites.

I sampled planthoppers and predators along all transects using a D-vac suction sampler at low tide on July 5, July 13, August 1, and August 10, 2002. One sample was taken at each sample location and consisted of nine 4-sec placements of the D-vac head ( $0.036\text{m}^2$ ) on the marsh surface; thus  $0.32\text{ m}^2$  was sampled at each site on each date. The first and third samples were taken when tides had been relatively low for several days, whereas the second and forth were taken following the highest tides of July and August (Fig. C, appendix 2.1).

Only data from locations consisting of pure *Spartina alterniflora* were used in analyses, because both *Tytthus* and *Prokelisia* planthoppers are restricted to this grass habitat. Eleven high-elevation sample locations did not meet this criterion, so there were a total of 7 sample locations in high-elevation meadows, as opposed to 18 in both low-elevation meadows and creek-side banks.

I assessed the relationship between vertical refuge, tide height and the density of *Pardosa*, *Tytthus*, and planthoppers using regression (SAS Proc Mixed with repeated measures). For each species, data were analyzed first with all dates and habitats pooled, followed by a separate analysis of each habitat. The predator/prey ratio (*Pardosa* + *Tytthus* density divided by planthopper density) was also analyzed in

each habitat. To achieve homogeneous variances and normality, densities of *Pardosa* and *Tytthus*, and predator-prey ratios were square-root transformed. Planthopper densities were log-transformed.

To test whether observed relations between predators and vertical refuge might actually be caused by correlations with covariates, I calculated Pearson partial correlations between predator densities and vertical refuge after controlling for elevation, planthopper density and the density of the other predator (SAS Proc Corr). To assess the impact of tide height on opportunities for intraguild predation, I calculated the Pearson correlation between *Pardosa* and *Tytthus* densities during the highest tides and during more modest tides (SAS Proc Corr) and calculated the significance of the change in correlation with a t-test on z-transformed correlations (Sokal and Rohlf 1995).

## Results

### *Pardosa's use of vertical refuge*

There was a significant effect of tidal inundation treatment on the number of *Pardosa* remaining on potted *Spartina* plants ( $F_{2, 17.7} = 47.19$ ,  $P < .0001$ ). Roughly equal numbers of *Pardosa* remained in the partial-inundation and no-inundation treatments, whereas virtually no *Pardosa* remained in the full-inundation treatment (Fig. 2.2). These results suggest that *Pardosa* emigrates extensively from fully-inundated plants that provide no vertical refuge from rising tides, and that emigration is much reduced when even partial vertical refuge exists.



### *Predator response to artificial vertical refuge*

In low-elevation meadows, predator densities were significantly greater in long-stem plots than in either type of control (*Pardosa* long vs. short stems  $t_{94}=2.27$ ,  $P=0.0126$ , *Pardosa* long vs. no stems  $t_{94}=2.90$ ,  $P=0.0023$ , *Tytthus* long vs. short stems  $t_{94}=1.76$ ,  $P=0.041$ , *Tytthus* long vs. no stems  $t_{94}=1.96$ ,  $P=0.027$ ) (Figs 3A, 3B). Planthopper density did not differ among treatments in low-elevation meadows (long vs. short stems  $t_{94}=0.49$ ,  $P=0.31$ , long vs. no stems  $t_{94}=-0.16$ ,  $P=0.56$ ) (Fig. 3C). In high-elevation meadows, densities did not differ among treatments for either predators or prey (*Pardosa* long vs. short stems  $t_{94}=-0.90$ ,  $P=0.81$ , *Pardosa* long vs. no stems  $t_{94}=-1.67$ ,  $P=0.95$ , *Tytthus* long vs. short stems  $t_{94}=0.66$ ,  $P=0.26$ , *Tytthus* long vs. no stems  $t_{94}=-0.20$ ,  $P=0.58$ , planthoppers long vs. short stems  $t_{94}=1.09$ ,  $P=0.14$ , planthoppers long vs. no stems  $t_{94}=0.18$ ,  $P=0.43$ ) (Figs 3D, 3E, 3F). There was no significant effect of the refuge treatment on the height of *Spartina* in plots ( $F_{2,32} = 0.35$ ,  $P = 0.71$ ) suggesting that any shading effects from *Phragmites* stems were minor.

### *Predator and prey density in relation to refuge availability in the field*

Vertical refuge was most abundant along the banks of tidal creeks, least abundant in low elevation meadows (Fig 2.4A). Grass in half the low-meadow sites was completely covered by the highest tides of July and August, whereas grass in the other two habitats was never completely covered. Tide water did reach at least ground level at all sites during the highest tides. Averaged across the four sample dates,

*Pardosa* density paralleled refuge abundance (Fig. 2.4B), whereas both *Tytthus* and planthopper density increased with decreasing elevation (Figs 2.4C, 2.4D).

When data from the three habitats were pooled, densities of predators *Pardosa* and *Tytthus*, but not planthopper herbivores, showed a significant positive correlation with availability of vertical refuge, regardless of tide height (*Pardosa*  $F_{1,166} = 11.46$ ,  $P = 0.0009$ , *Tytthus*  $F_{1,166} = 8.92$ ,  $P = 0.0032$ , planthopper  $F_{1,166} = 0.63$ ,  $P = 0.43$ ) (Fig. 2.5). For both *Pardosa* and *Tytthus*, the correlation strengthened during the highest monthly tides (refuge  $\times$  tide height for *Pardosa*  $F_{1,166} = 8.13$ ,  $P = 0.0049$ , for *Tytthus*  $F_{1,166} = 12.78$ ,  $P = 0.0005$ ) (Figs 2.5A, 2.5B). The non-significant planthopper correlation with vertical refuge did not change with tide height (refuge  $\times$  tide height  $F_{1,166} = 3.39$ ,  $P = 0.07$ ) (Fig. 2.5C)

When regressions were done separately within each of the three habitats, *Pardosa* density was positively correlated with vertical refuge only in low-elevation meadows ( $F_{1,66} = 22.94$ ,  $P < 0.0001$ ). *Tytthus* density was not correlated with refuge in any habitat, but was correlated with tide height in low-elevation meadows ( $F_{1,66} = 4.24$ ,  $P = 0.04$ ), with significantly lower densities during the highest tides (Fig 2.6). Planthopper density decreased significantly with increasing refuge in both low-elevation meadows ( $F_{1,67} = 5.76$ ,  $P = 0.019$ ) and creek-side vegetation ( $F_{1,67} = 11.29$ ,  $P = 0.0013$ ). The predator/planthopper ratio was positively correlated with vertical refuge in the same habitats (low meadow  $F_{1,67} = 34.07$ ,  $P < .0001$ , creek-side  $F_{1,67} = 9.44$ ,  $P = 0.0031$ ).

The correlation between *Pardosa* and *Tytthus* densities increased from  $\rho = -0.260$  ( $P = 0.016$ ) during lower-than-average tides to  $\rho = +0.184$  ( $P = 0.09$ ) during the highest tides, a significant increase ( $P = 0.0036$ ). Densities of both predators were significantly correlated with vertical refuge even after controlling for elevation, planthopper density and the density of the other predator marsh-wide (*Pardosa*  $\rho = 0.346$   $P < .0001$ , *Tytthus*  $\rho = 0.397$   $P < .0001$ ) and in low-elevation meadows (*Pardosa*  $\rho = 0.431$   $P = 0.0002$ , *Tytthus*  $\rho = 0.416$   $P = 0.0004$ ).

## Discussion

I have shown that in a terrestrial intertidal food web, predators moved to avoid the stress imposed by tides, while prey distribution was unaffected, as predicted by the Consumer Stress Model (CSM) (Menge and Sutherland 1987). But unlike the situation typically envisioned by CSM, these predators were not forced to completely abandon stressful areas, provided refuge was available in the form of vegetation above tide water. As a result, predator distribution was determined not by stress alone, as predicted by CSM, but by both stress and refuge availability. Predators were most abundant in the most stressful habitat, along tidal creeks (Figs 2.4B, 2.4C) because of ample refuge in that habitat (Fig. 2.4A). Notably, within each of the two habitats most affected by tides, increased refuge was correlated with a significant increase in the predator-to-prey ratio and a significant decrease in prey density. However, this pattern did not hold across habitats, partly because plant quality differs greatly across

habitats, increasing at lower elevations, promoting high prey density in the lowest-elevation habitat (Fig. 2.4D).

*Pardosa* wolf spiders remained in experimental mesocosms as long as some marsh grass remained above water, abandoning them only as grass approached total submersion (Fig. 2.2). This behavior led to higher densities of both major predators in experimental plots with artificially-enhanced vertical refuge (Fig. 2.3A, 2.3B) and to a positive correlation between predators and naturally-occurring refuge, a correlation that increased as tide height rose (Figs 2.5A, 2.5B). Both predators exhibited significant spatial correlations with vertical refuge even after I controlled for the potentially confounding factors of elevation, prey density, and density of the other predator. Planthopper herbivores, on the other hand, showed no response to either artificial refuge (Fig. 2.3C) or to naturally-occurring refuge (Fig. 2.5C), consistent with an assumption of the CSM that prey are less vulnerable to stress than their predators.

Predator affinity for refuge differed among habitats because the need for refuge differed with tidal intensity. Predators did not respond to either artificial or natural refuge in high-elevation meadows where tides were shallow and infrequent (Figs 2.3A, 2.3B), confirming that predators used refuge to escape tides and not because of some other refuge characteristic. Predators responded strongly to both artificial and natural refuge in low-elevation meadows, where tides were more frequent, and where refuge varied from absent to moderate. Somewhat surprisingly, I

did not detect a correlation between predator density and refuge availability within the intensely tidal creek-side habitat. Refuge is universally abundant in this habitat, possibly indicating that additional refuge above some adequate level has diminished effect on predator distribution. The definition of an “adequate level” of refuge changes with tide height, so refuge distribution might have a stronger effect during tides higher than those experienced in this survey.

Within each of the two habitats most affected by tides, increased refuge was correlated with a significant increase in the predator-to-prey ratio and a significant decrease in prey density. Mean *Pardosa* density in low-elevation meadows increased from 5 per m<sup>2</sup> at sites with the least refuge to 111 per m<sup>2</sup> at sites with the most refuge, a range that has been shown to significantly decrease planthopper densities (Denno et al. 2003). Interestingly, prey density decreased in high-refuge areas of the creek-side habitat, even though I was not able to detect a relationship between predator density and refuge in that habitat. Increased refuge therefore enabled increased predation in the two most stressful habitats.

The correlation between refuge and predation did not hold across habitats. The creek-side habitat, with its abundant refuge, supported higher herbivore densities and lower predator-to-prey ratios than other habitats (Fig. 2.4). High planthopper density along tidal creeks is made possible by the high nitrogen content in creek-side *Spartina* (Ornes and Kaplan 1989), but may also be enhanced by predator inefficiency caused by two factors. First, suppression of planthoppers is likely

weakened by increased intraguild predation of *Tytthus* by the high densities of *Pardosa* in that habitat (Denno et al. 2005). Shared use of vertical refuge during high tides increases opportunities for such predation. Second, the fact that predators must climb grass stems twice daily to avoid submersion limits their foraging time in this habitat and forces them to re-locate prey when tides recede. Uncertainty about predation level in this habitat is increased by the fact that neither predator use of vertical refuge nor planthopper adaptation to submersion is likely to be completely effective, so tides may cause mortality among both predators and prey. More study will be required to estimate the magnitude of that mortality and its relative importance to predators and their planthopper prey.

Differences in mobility led to responses on different spatial scales by the two predators. During the highest monthly tides, substantial numbers of flight-capable *Tytthus* left low-elevation meadows for the abundant refuge of the creek-side habitat (Fig. 2.6). *Pardosa*, less mobile than *Tytthus*, moved to better refuge but stayed within low meadows. The movement by *Tytthus* to the most stressful habitat during the highest tides again highlights the fact that predator distribution was determined by both tidal stress and refuge availability.

Tides introduce fine-scale variation in predation within both low-elevation meadows and creek banks because of variation in the availability of vertical refuge. Such variation can stabilize predator-prey interactions (Holt 2002). Stability can also be increased by predator movement between habitats when predators behave as ideal

consumers, leaving one habitat when it becomes more profitable to forage in another (McCann et al. 2005, Eveleigh et al. 2007, Rooney et al. 2008). However, the movements of *Tytthus* that I have observed between low meadows and creek banks are synchronized with tide height rather than with prey dynamics in either habitat. These movements are therefore just as likely to destabilize as to stabilize food webs.

This research documents a natural-system analog to the agricultural practice of increasing predation through enhanced predator refuge. Vertical refuge in the marsh allowed increased predation in the face of tidal disturbance that is much more frequent than disturbance from most farming practices. Importantly, increased predation in the marsh did not depend on predators and prey sharing the refuge, a mechanism that is important in some freshwater systems (Lancaster 1996, Felten et al. 2008). It is noteworthy that predation is enhanced in the marsh when predators are required to move relatively short distances to reach refuge. Poor predator performance farther from refuges is a continuing challenge for conservation biological control.

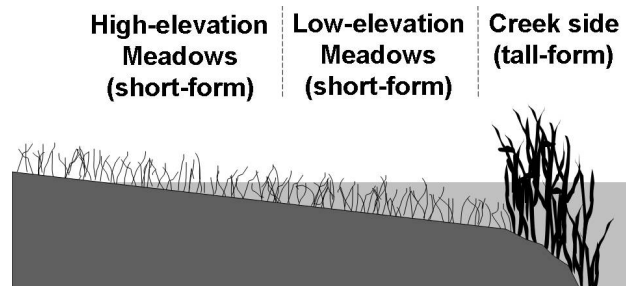
An implication of this research is that several kinds of anthropogenic change could have a marked effect on the marsh food web. Winds associated with storms can drive tides to levels much higher than the highest in this study. If the frequency and/or intensity of storms increases, as some climate-change models predict (Boer et al. 2001), and some empirical studies have observed (Woodworth and Blackman 2004),

more exaggerated predator redistributions will likely result, leading to greater variation in the intensity of predation pressure.

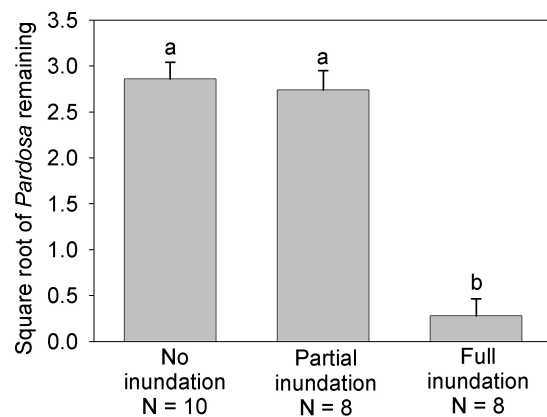
Many salt marshes have experienced increased nutrient input in recent years due to development (Bertness et al. 2002). If this input results in more robust plant growth, especially in low-elevation meadows, the increased vertical refuge could reduce predator migrations caused by tides. For example, the substantial shift of *Tythus* from low-elevation meadows to creek-side vegetation could be eliminated, decreasing predation on planthopper eggs along creek banks, where planthopper outbreaks are already most common.



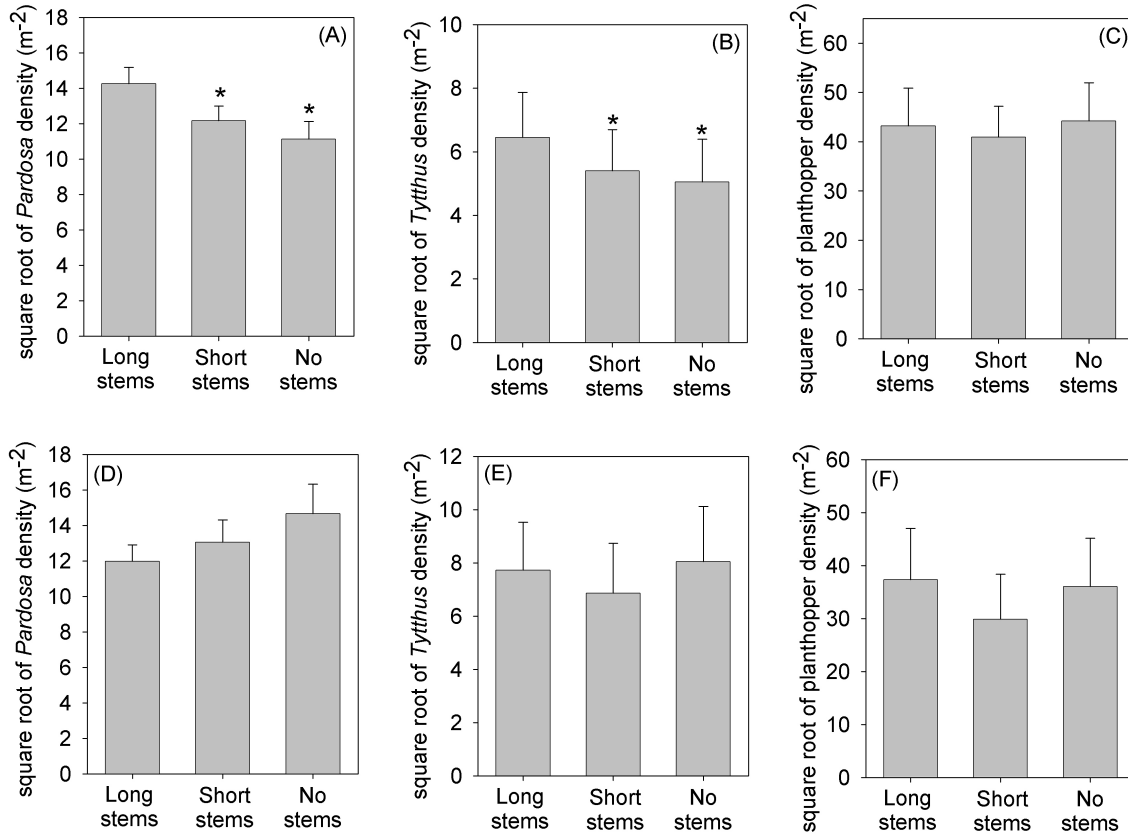
## Figures



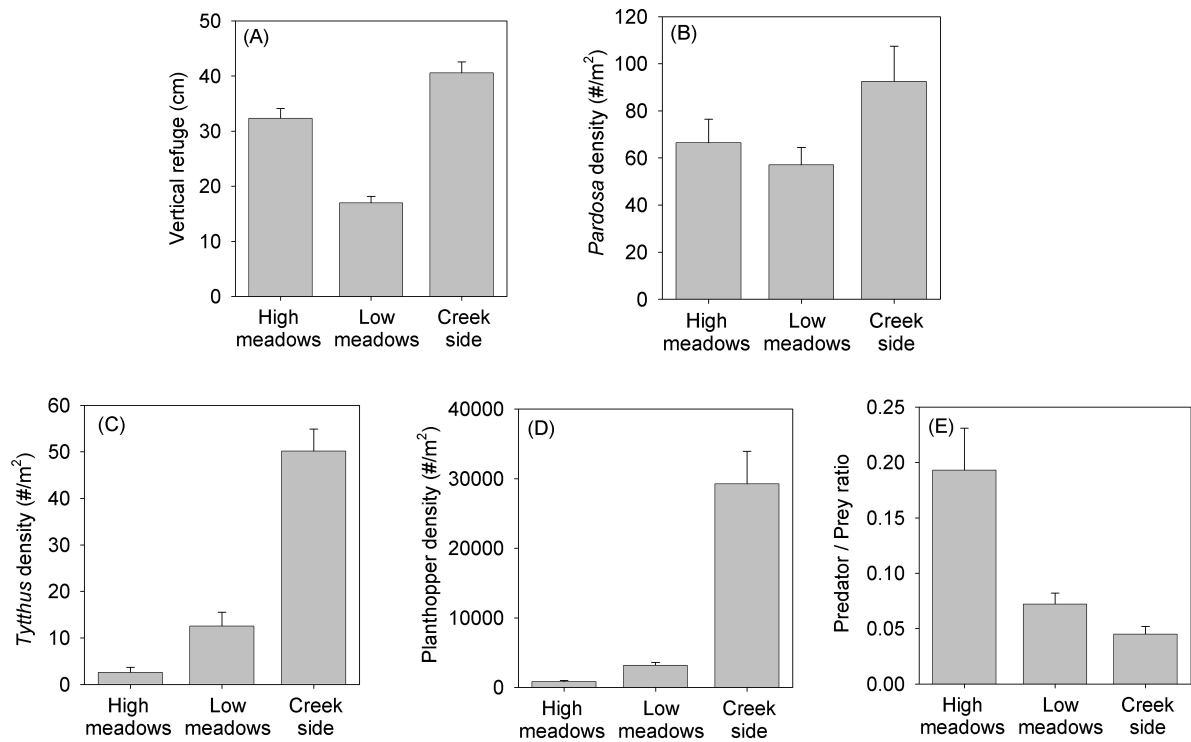
**Figure 2.1.** Three marsh habitats occupied by *Spartina alterniflora*. Creek-side vegetation is substantially taller than meadow grass, and as a result, more vegetation extends above tide water in the creek-side habitat than in the other two. This vertical refuge is least available in low-elevation meadows.



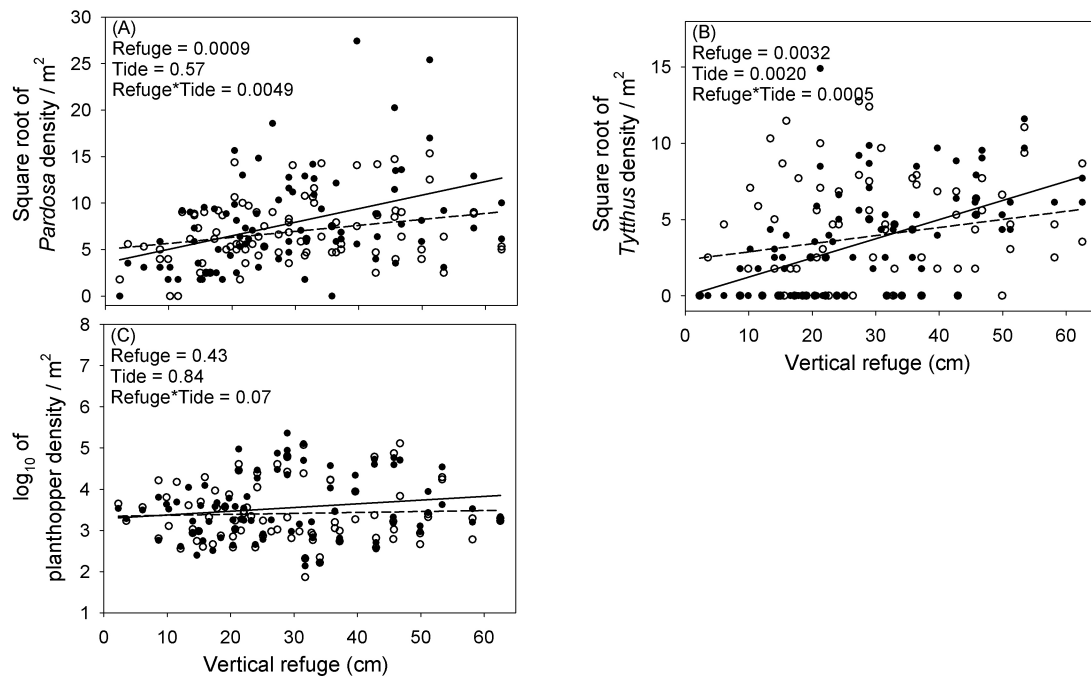
**Figure 2.2.** Square-root-transformed number  $\pm$  SEM of *Pardosa* remaining in each of the inundation treatments, out of the 15 originally stocked. Letters indicate significant differences.



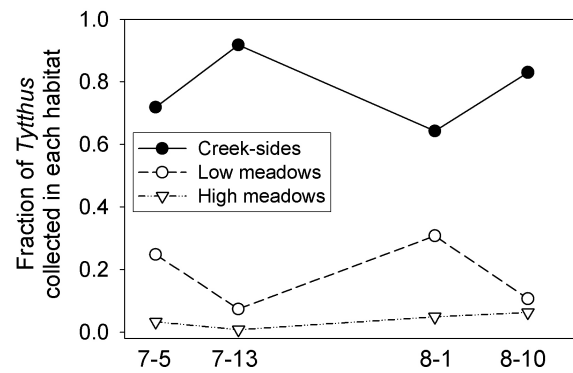
**Figure 2.3.** Mean density  $\pm$  SEM of *Pardosa* (A, D), *Tytthus* (B, E), and *Prokelisia* planthoppers (C, F) in low-elevation plots (A, B, C) and in high-elevation plots (D, E, F). An asterisk signifies that a mean density was significantly less than a long-stem density, determined by rejecting one of the one-sided *a priori* null hypotheses  $H_0$ : long-stem density  $\leq$  short-stem density or  $H_0$ : long-stem density  $\leq$  no-stem density ( $\alpha = 0.05$ ). “Long-stem” plots supplemented *Spartina* with 50 cm vertical stems of *Phragmites*, providing arthropods with the opportunity to climb above rising tides. Stems in “Short-stem” plots were 20 cm high, approximately the height of the *Spartina* canopy. Short-stem and no-stem plots provided no refuge from tides. Tides in high-elevation meadows are shallow and infrequent, making vertical refuge unnecessary.



**Figure 2.4.** Mean values  $\pm$  SEM for the three habitats, pooled across the four sample dates of the field survey, for vertical refuge (A), predatory *Pardosa* density (B), predatory *Tytthus* density (C), herbivorous planthopper density (D), and predator-to-prey ratio (E).



**Figure 2.5.** Response of *Pardosa* density (A), *Tytthus* density (B), and planthopper density (C) to availability of vertical refuge and to tide height. Tide height was treated as discrete, with two values, “modest” and “highest”. Open circles and dashed lines show data and regression solutions for the two samples collected during relatively modest high tides. Closed circles and solid lines show data and regression solutions for the two samples taken during the highest monthly tides. P values are displayed within the plots. Significant interactions mean that slopes differ with tide height.



**Figure 2.6.** Fractions of *Tyttthus* collected in each of the three habitats, corrected for the number of sample points in each habitat. The three fractions add to 1.0 on each date. Samples taken on July 13 and August 10 followed the highest tides of July and August, and the fraction of *Tyttthus* collected in low-elevation meadows fell by roughly two-thirds on those days, while the fraction collected in the creek-side habitat rose.

## **CHAPTER 3: Abiotic stress differentially impacts higher trophic levels despite a predator refuge**

### **Abstract**

Environmental stress decreases the importance of predation in many systems because predators are more vulnerable to stress than their prey. However, a predator refuge from stress could allow strong predation even in the most stressful habitats. Stress in the form of salt water tides can be deadly for terrestrial arthropods, but salt marsh spiders and insect predators find a refuge in vegetation extending above water. They frequently climb vegetation to avoid submersion, and show a preference for marsh areas with more of this vertical refuge, a preference not shared by their prey. Tidal stress is most acute at the lowest marsh elevations, along tidal creeks, but marsh grass is especially tall in this habitat, possibly allowing predation to remain strong. I tested the possibility that tall-grass refuges allow undiminished predation in creek-side habitats, as well as the assumption that marsh herbivores suffer little tidal mortality, by eliminating tides from experimental field mesocosms while allowing control mesocosms to experience normal tidal inundation. I found that abundances at all trophic levels were lower in tidal treatments, indicating substantial tide-related mortality even among herbivores. Notably, tide-related decreases were many times greater among predators than among prey, indicating that tides decrease predation levels, as predicted by consumer stress models. The predator refuge from tides provided by emergent vegetation thus proved to be incomplete, allowing significant tidal mortality and decreased predation even in a habitat where it is abundant.

## **Introduction**

The importance of predation is often negatively correlated with environmental stress (Connell 1975, Menge and Sutherland 1976), where stress refers to environmental factors that bring an organism near the edge of its ecological niche (Van Straalen 2003). One formulation of this pattern is the consumer stress model (CSM), which proposes that the importance of predation in organizing community structure declines as environments become more physically harsh because prey are, in general, more tolerant of stress than predators (Menge and Sutherland 1987, Menge and Olson 1990). This model was initially developed for desiccation stress in the rocky intertidal (Connell 1961), and is well-established there (Bertness 1981, Brown and Stickle 2002, Petes et al. 2008), but it has also been observed for other types of stress in other habitats, including hypoxic stress in subtidal areas (Altieri 2008), salinity stress in estuaries (Hemminga and van Soelen 1988), and altitude stress in mountains (Preszler and Boecklen 1996).

Naturally-occurring stress gradients have been useful in investigating the relationship between stress and predation (Bertness and Callaway 1994), but in terrestrial systems a gradient of stress on predators and herbivores is frequently accompanied by a gradient in plant-associated characteristics, such as nutritional quality for herbivores. Such gradients can obscure the stress-predation relationship (Hacker and Bertness 1995, Bowdish and Stiling 1998). One way to clarify the relationship is to experimentally manipulate the intensity of top-down and bottom-up factors at various locations along a stress gradient in the field (e.g., Moon and Stiling



2004, Albarracin and Stiling 2006, Fleeger et al. 2008). Another solution is to manipulate the intensity of stress while keeping bottom-up factors constant (e.g., Preisser and Strong 2004). This approach can be useful when it is difficult to manipulate predators without affecting prey. I took this approach in an investigation of tidal stress and its effects on predation in the terrestrial food web of an intertidal salt marsh on the Atlantic coast of North America.

Terrestrial inhabitants of salt marshes are stressed by submersion in saltwater because of the osmotic difference between hemolymph and saltwater (Boomsma and Isaaks 1982). Since the primary physiological adaptation to cope with osmotic stress is an impermeable integument (Boomsma and Isaaks 1982), arthropods are especially vulnerable during and shortly after hatching and molting (Pfeiffer and Wiegert 1981). For example, newly-hatched aphids were killed by a two-hour submergence (Foster and Treherne 1976), and larvae of a beetle survived submergence in saltwater considerably longer ten days after molting than they did six hours after (LeMasne 1938, as reported in Foster and Treherne 1976).

Consumer stress models therefore predict that predation will decline at lower marsh elevations where tidal-induced salinity stress is more frequent and long-lasting. Herbivores should therefore become more abundant at lower elevations, a gradient that has been observed in some salt marsh studies (Hacker and Bertness 1995, Bowdish and Stiling 1998, Denno et al. 2005), but not others (Foster 1984, Hemminga and van Soelen 1988, 1992). Elevational gradients in plant quality make

interpreting both kinds of result problematic. For example, a previous study found that the most abundant herbivore on the study marsh, a planthopper, does increase in density at lower elevations, but this increase is caused at least in part by a parallel increase in nutritional quality of marsh grass (Denno et al. 2005). The contribution of tidal stress to planthopper distribution therefore remains unclear.

Spiders are among the most important predators of marsh herbivores (Foster and Treherne 1976), and several lines of evidence show that they avoid saltwater submersion. Greenstone (1979) observed that many spider species prefer to float on the water surface rather than allow themselves to be submerged. In chapter two, I found that predators of planthoppers retreated to vegetation extending above water as a refuge from tides, but planthoppers exhibited no such tendency. This may indicate that planthoppers are less vulnerable to salinity stress than predators, as predicted by the CSM, but I was not able to verify that assumption. I was also unable to determine whether use of vertical refuge by predators completely negated any tidal impact on predation.

In the current two-year field study, I attempted to answer these questions by comparing predator and prey densities in tide-free grass patches (mesocosms) with densities in mesocosms subjected to normal tidal flooding. Tide-free mesocosms were created by allowing them to float. Mesocosms allowed unrestricted immigration and emigration by all predators and prey, and were located in the lowest marsh elevations, along tidal creeks. This habitat experiences deep tides twice-daily, but also supports

the tallest marsh grass, supplying ample refuge above tide water. This approach ensured that arthropods experienced the same abiotic factors, except tides, in all treatments. I measured grass carbon and nitrogen content to test my assumption of consistent nutritional quality across treatments.

With this experiment I aimed to increase our understanding of how tidal stress affects the level of predation in a terrestrial food web that consists of a top predator, intermediate predators, and herbivores. Understanding tidal effects is becoming more important since tide heights have been predicted to rise as a result of global climate change. Specifically, this experiment attempted to determine (1) whether tides have a negative impact on predators even in the presence of abundant vertical refuge, and (2) whether herbivores possess adaptations that make them invulnerable to tidal mortality. If tides decrease the importance of predation, I expected tidal treatments to support lower predator densities, lower predator-to-prey ratios, and higher herbivore densities than those in tide-free mesocosms because of increased predator mortality or decreased foraging success. On the other hand, if vertical refuge protects predators from tides and allows them to hunt effectively, predator-to-prey ratios and herbivore density would not be changed by tidal inundation.

## **Methods**

### *Study system and focal food web*

This experiment was conducted on an intertidal salt marsh in the Great Bay-Mullica River estuarine system in Tuckerton, Ocean County, New Jersey, USA.

Within the intertidal zone, this marsh is dominated by the perennial cordgrass

*Spartina alterniflora* (Redfield 1972, Denno et al. 1996), which occurs in two different growth forms. At the lowest elevations, along the banks of tidal creeks, where this experiment was conducted, tall-form *S. alterniflora* can reach heights of two meters (Redfield 1972, Bertness and Ellison 1987), but culm density is relatively low ( $\sim 250/\text{m}^2$ ) (Denno and Grissell 1979). In this habitat, tidal flooding occurs twice daily and plants incur inundation 55% of the time (Redfield 1972). In meadows at higher elevations, *S. alterniflora* reaches heights of only 10-30 cm and culms grow more densely ( $>3,000$  culms/ $\text{m}^2$ ) (Denno and Grissell 1979).

I focused on five species, the most abundant insect and spider species of the creek-side habitat. The planthopper *Prokelisia marginata* (Homoptera: Delphacidae), henceforth *Prokelisia*, is by far the most abundant herbivore on *S. alterniflora* throughout most of the Atlantic coast (Denno 1976, Vince and Valiela 1981). In New Jersey, *Prokelisia* are trivoltine (Denno 1977). *Prokelisia* eggs are deposited within *Spartina* leaf blades and hatch after two weeks. The second most abundant herbivore in tall-form *Spartina* on this marsh is the mirid bug *Trigonotylus uhleri* (Hemiptera: Miridae), henceforth *Trigonotylus*, which is bivoltine. The most important predator of *Prokelisia* eggs is another mirid bug, *Tytthus vagus* (Hemiptera: Miridae), henceforth *Tytthus*. Both nymphs and adults hunt *Prokelisia* eggs and adult *Tytthus* can kill up to 24 planthopper eggs per day (Döbel and Denno 1994). The spider *Grammonota trivitatta* (Araneae: Linyphiidae), henceforth *Grammonota*, is the most abundant web-building spider on the marsh (Döbel et al. 1990). *Grammonota* has been shown to have a mild effect on *Prokelisia* populations (Denno et al. 2004). Its effect on

*Trigonotylus* and *Tytthus* populations is unknown. The hunting spider *Pardosa littoralis* (Araneae: Lycosidae), henceforth *Pardosa*, is the top predator in this food web. It is the major predator of *Prokelisia* nymphs and adults on the marsh (Döbel et al. 1990). It is also capable of reducing densities of the more efficient planthopper predator *Tytthus* to such an extent that overall predation of *Prokelisia* declines (Finke and Denno 2003). To a lesser extent, *Pardosa* also preys on the web-builder *Grammonota* (Denno et al. 2004).

### *Experimental mesocosms*

Tall-form creek-side *Spartina alterniflora* was transplanted from marsh creek banks into 16 plastic storage tubs, each 95cm long, 48cm wide and 42cm deep (Rubbermaid 50 gal. storage tote, Newell Rubbermaid Inc. Atlanta, Georgia, USA). Tidal mesocosms (inundation treatment) were established by sinking 8 tubs to ground level in holes left in the creek bank by *Spartina* removal. Tide-free mesocosms (no inundation) were established by affixing empty one-gallon (3.79 liter) plastic jugs around the outer rim of the remaining 8 tubs to provide flotation. Floating mesocosms were also placed in holes left by *Spartina* removal, and were held in place by four vertical boards positioned at the corners of the tub and driven into the creek bank. Tubs could then slide up and down with the tide (Fig. 3.1). A third treatment consisted of unmanipulated open control plots on the creek bank the same size as tubs, marked on four corners with bamboo poles. Treatments alternated along a single tidal creek with at least one meter between them. The first and last treatments were both open plots, so there were nine open plots, eight tidal mesocosms and eight floating

mesocosms for a total of 25 experimental units. Installation was completed on the Tuckerton marsh on 9 May 2005.

To estimate densities, insects and spiders were sampled from all plots and mesocosms using a D-vac suction sampler (D-Vac Company, Ventura, California, USA) monthly from July to October of 2005 and from May to October of 2006, with one additional sample in September 2005 for a total of eleven sample dates. On all dates a separate sample was taken from each of the 25 experimental units during low tide, consisting of two non-overlapping ten-second placements of the D-vac head (21 cm diameter) over the *Spartina*. I chose two placements as a compromise that would allow me to estimate arthropod density while leaving the community relatively intact. Arthropods were preserved in alcohol, and density per square meter was calculated at each sample location for the five focal members of the marsh food web: *Prokelisia*, *Trigonotylus*, *Tytthus*, *Grammonota*, and *Pardosa*.

My experimental design assumed that grass nutritional quality would be constant across treatments, so I could ascribe changes in arthropod density to the presence or absence of tides. To test that assumption, I cut three randomly-chosen leaves from each mesocosm and open plot on 22 May 2006. Leaves were dried, ground in a Wiley mill, and analyzed for percent carbon and nitrogen using a CHN elemental analyzer.

### *Analysis*

To test for differences in arthropod density among treatments, I pooled data from all sample dates and performed repeated-measures analysis of variance separately for each of the five focal species using Proc Mixed (SAS 2002). The repeated factor was experimental unit. The first analysis used the three treatments as levels for the independent variable. A second analysis combined open plots with tidal mesocosms so the independent variable had only two levels, tide-free and tidal. To achieve normality and homogeneous variances, all densities were square-root transformed. After the square-root transformation, *Pardosa* variances still differed significantly among treatments, so separate variance estimates were made for each treatment.

To test whether tidal effect differed across trophic levels, I pooled data from all dates and all species and regressed log-transformed density against trophic level, treatment, and their interaction. Trophic level was a numeric variable with value 1 for herbivores, 2 for intermediate predators and 3 for the top predator. Experimental unit was a repeated factor. A significant interaction would mean that treatment effect changed with trophic level.

I defined a treatment response for each species on each sample date as the mean density for the species in floating mesocosms divided by mean density in tidal treatments. To interpret results, it was important to know whether treatment responses stabilized or continued to change over the course of the season. I therefore regressed

the log of the treatment response for each species against the day of the year when the sample was taken, expressed as an integer from 1 to 365.

To test whether predator-to-prey ratios differed between treatments, I calculated the ratio for each predator-prey combination for each experimental unit on each sample date for which both predators and prey were present. Ratios were log-transformed to achieve normality and homogeneous variances, and repeated-measures analysis of variance was performed using Proc Mixed with treatment as a two-level categorical independent variable. Experimental unit was the repeated measure.

I expected that juveniles might respond to treatments differently from adults, since they are often more vulnerable to salinity stress. Sufficient numbers of both juveniles and adults of *Prokelisia* and *Tytthus* were collected to test this hypothesis, and I calculated the nymph-to-adult ratio for each experimental unit on each sample date. Ratios were analyzed as described above for predator-to-prey ratios. To test whether tides affected the nymph-to-adult ratios of the two species differently, I included treatment, species (*Prokelisia* or *Tytthus*) and their interaction as independent variables in a repeated-measures analysis of variance.

To test whether plant quality varied among treatments, I performed analysis of variance on percent nitrogen and percent carbon from each experimental unit using Proc Anova (SAS 2002) with treatment as a three-level categorical independent variable.



## Results

For the most part, arthropod densities did not differ between tidal mesocosms and open plots, the two types of tidal treatment. The two exceptions were spiders *Pardosa* ( $T_{22}=3.34$ ,  $P=0.003$ ) and *Grammonota* ( $T_{22}=2.47$ ,  $P=0.022$ ) (Fig. 3.2). In both cases, mean density in tidal mesocosms was significantly lower than density in open plots, which was in turn significantly lower than density in tide-free mesocosms. In results that follow, I combine data from tidal mesocosms and open plots to calculate densities for tidal treatments, and contrast them with densities for the tide-free mesocosm treatment. This is justified even for the two cases in which densities differed between tidal treatments, because both tidal densities were significantly lower than tide-free densities. This results in a more conservative test than comparing the two types of mesocosm.

Densities of all five species in the food web were significantly lower in tidal treatments than in tide-free mesocosms (*Pardosa*  $F_{1,23}=209.35$ ,  $P<.0001$ , *Tytthus*  $F_{1,23}=61.38$ ,  $P<.0001$ , *Grammonota*  $F_{1,23}=38.19$ ,  $P<.0001$ , *Trigonotylus*  $F_{1,23}=14.26$ ,  $P=0.0010$ , *Prokelisia*  $F_{1,23}=18.70$ ,  $P=0.0003$ ) (Fig. 3.2). This treatment effect was consistent throughout the study. In eleven samples taken over two years, no species was more abundant in tidal treatments more than twice. (Appendix 3.1 gives results broken down by sample date.) Tides reduced densities of higher trophic levels more than those of lower trophic levels, as indicated by a significant treatment by trophic level interaction ( $F_{1,1263} = 48.53$ ,  $P < 0.0001$ ) (Fig. 3.3).

The *Pardosa* treatment response (tide-free density / tidal density) became progressively larger over the course of the season ( $F_{1,7}=34.51$ ,  $P=0.0006$ ) (Fig. 3.4). Responses of other species did not change consistently over time (*Tytthus*  $F_{1,7}=2.06$ ,  $P=0.19$ , *Grammonota*  $F_{1,9}=0.67$ ,  $P=0.43$ , *Prokelisia*  $F_{1,9}=0.05$ ,  $P=0.82$ , *Trigonotylus*  $F_{1,7}=0.02$ ,  $P=0.89$ ).

Nymphs of both *Prokelisia* and *Tytthus* exhibited greater treatment responses than their adults (Table 3.1). The ratio of nymphs to adults for both species was significantly higher in tide-free mesocosms than in tidal treatments (*Prokelisia*  $F_{1,23}=21.43$ ,  $P=0.0001$ , *Tytthus*  $F_{1,23}=12.53$ ,  $P=0.0018$ ) (Fig. 3.5). The mean nymph-to-adult ratio for *Prokelisia* was 45% higher in tide-free mesocosms than in tidal treatments, and the *Tytthus* mean was three times as high. Although tides affected the *Tytthus* ratio more than the *Prokelisia* ratio, the difference between the species was not significant (species by treatment interaction  $F_{1,212}=2.73$ ,  $P=0.10$ ).

Predator/prey ratios were significantly higher for predators *Pardosa* and *Tytthus* tide-free mesocosms than in tidal treatments (*Pardosa*/*Tytthus*  $F_{1,21}=5.95$ ,  $P=0.02$ , *Pardosa*/*Grammonota*  $F_{1,23}=28.79$ ,  $P<.0001$ , *Pardosa*/*Prokelisia*  $F_{1,23}=11.95$ ,  $P=0.002$ , *Pardosa*/*Trigonotylus*  $F_{1,23}=9.34$ ,  $P=0.006$ , *Tytthus*/*Prokelisia*  $F_{1,19}=13.39$ ,  $P=0.002$ ) (Table 3.2). Ratios did not differ significantly for *Grammonota* (*Grammonota*/*Prokelisia*  $F_{1,23}=0.34$ ,  $P=0.57$ , *Grammonota*/*Trigonotylus*  $F_{1,23}=1.89$ ,  $P=0.18$ )

Plant quality did not contribute to differences in arthropod density among treatments. Neither percent carbon ( $F_{2,22}=2.33$ ,  $P=0.12$ ), percent nitrogen ( $F_{2,22}=2.60$ ,  $P=0.10$ ) nor C:N ratio ( $F_{2,22}=1.72$ ,  $P=0.20$ ) showed a significant difference among treatments (Fig. 3.6).

## Discussion

I found that densities of all species were significantly lower in tidal treatments than in tide-free mesocosms (Fig. 3.2), with greater decreases among higher trophic levels (Fig. 3.3), resulting in significantly lower predator-to-prey ratios in tidal treatments (Table 3.2). Tides therefore had two effects in the creek-side habitat. First, they decreased the importance of predation, as predicted by consumer stress models. Notably, this weakened predation occurred in the presence of abundant vertical refuge for predators, implying that the refuge is far from complete. Second, tides decreased herbivore abundance, indicating direct tide-related mortality among herbivores was substantial enough to overcome the indirect tidal benefit of weakened predation. The high herbivore densities commonly observed along marsh creek banks would therefore be even higher if not for tidal mortality.

I combined the two tidal treatments, open plots and tidal mesocosms, in tests of tidal effects. Densities for spiders differed in the two tidal treatments, but both tidal densities were significantly lower than those in tide-free mesocosms (Fig. 3.2). Density differences between the tidal treatments may have been caused by sparser

grass in mesocosms, both tide-free and tidal (D. Lewis, personal observation), making the very high spider densities in tide-free mesocosms especially remarkable.

### *Tides decreased predation rates*

Previous studies show that the reductions in predator density associated with tides in this experiment are sufficient to substantially decrease predation and increase prey density. One study, which did not involve tides, found that a decrease in *Pardosa* density from 110/m<sup>2</sup> to 15/m<sup>2</sup>, smaller than the reduction in the current study, caused a 61% increase in adult planthopper density, a 178% increase in planthopper nymph density, and a rise in *Tytthus* density from 1/m<sup>2</sup> to 70/m<sup>2</sup> (Denno et al. 2002). A field study decreased *Tytthus* density from 320/m<sup>2</sup> to 100/m<sup>2</sup>, a bit more than the decrease in the current study, and planthopper density increased six-fold (Finke and Denno 2003). A third study reduced *Pardosa* density from 600/m<sup>2</sup> to 200/m<sup>2</sup>, and observed a 61% rise in *Grammonota* density (Denno et al. 2004). It is true that if lower *Pardosa* density results in higher density of the effective specialist predator *Tytthus*, total predation on planthoppers can increase (Finke and Denno 2003), but tides in this study reduced *Tytthus* to one-third of its tide-free density. The presence of tides therefore decreased the level of predation on both herbivores and intermediate predators. This confirmation of consumer stress models is one of relatively few in a terrestrial food web.

### *Tides increased herbivore mortality*

Tides reduced herbivore densities (Fig. 3.2), despite relaxed predation, through either increased mortality or decreased fecundity. Since grass quality, as measured by nitrogen and carbon content, did not differ among treatments (Fig. 3.6), and competition among herbivores was lower in tidal treatments, there was no reason for females to lay fewer eggs. Immature insects are known to be more vulnerable to salinity stress than adults (Pfeiffer and Wiegert 1981), so tides would be expected to reduce their densities more than adult densities, and this is what I observed.

*Prokelisia* nymph densities decreased 39% in tidal mesocosms versus 30% for adults (Table 3.1). In addition, there were significantly fewer nymphs per adult in tidal treatments (Fig. 3.5A). The nymph-to-adult ratio changes throughout the season as generations come and go, but on ten of the eleven sample dates the ratio was lower in tidal treatments. On average, there were 57% fewer nymphs per adult in tidal treatments than in tide-free mesocosms, implying higher nymphal mortality in the presence of tides.

Candidate mortality agents in tidal treatments include salt-water immersion and fish predation. This experiment could not distinguish between the two, but I note that fish predation would not explain higher mortality among nymphs. Adult *Prokelisia* are shorter than 3.5 mm, small enough to be consumed by very small fish, and so are just as vulnerable to predation as *Prokelisia* nymphs.

### *Tides negatively impacted predators*

Predators in tidal treatments experienced lower competition-related costs than those in tide-free mesocosms, implying higher costs due to other mechanisms. Competition-related costs were lower because of lower predator-to-prey ratios (Table 3.2). In addition, the top predator *Pardosa* likely experienced lower levels of cannibalism. Wolf spiders (Lycosidae) are among the most cannibalistic of spider families (Wise 2006) and cannibalism decreases with decreasing conspecific density (Wagner and Wise 1997, Buddle et al. 2003). A field study decreased *Pardosa* density from 63/m<sup>2</sup> to 16/m<sup>2</sup>, smaller than the decrease in the current study, and observed a 59% increase in *Pardosa* survival (Langellotto and Denno 2006). To offset lower costs from competition, tides must increase predator mortality, decrease fecundity, or decrease foraging efficiency. Further study will be required to determine the relative importance of those mechanisms, which can potentially reinforce one another. For example, if tides separate predators from prey, forcing them to relocate prey twice daily, hunting efficiency could suffer, affecting fecundity.

Like planthoppers, nymphs of the intermediate predator *Tytthus* were more negatively impacted by tides than adults. Nymph densities decreased 73% in tidal mesocosms versus 53% for adults (Table 3.1), and there was a 62% decline in the number of nymphs per adult (Fig. 3.5B). Tides could cause these adult-nymph differences through higher nymphal mortality as well as through decreased fecundity.

Immigration is a possibly complicating factor in these results. Since tide-free mesocosms constituted favorable habitats surrounded by flooded marsh, organisms at all trophic levels may have migrated to them. However, migration would be expected to continue only as long as floating mesocosms were more suitable than the surrounding marsh. Migration might therefore speed the attainment of altered equilibrium densities in floating mesocosms, but would not change the equilibrium densities themselves. Treatment responses for most species did not change consistently over time, indicating that equilibrium densities were reached relatively quickly. The exception was *Pardosa*, whose treatment response increased consistently over the course of both seasons, at least until September (Fig. 3.4). This may indicate that *Pardosa* immigration to the creek-side habitat is slowed by the need to migrate from their winter refuge, as suggested elsewhere (Döbel et al. 1990).

### *Implications*

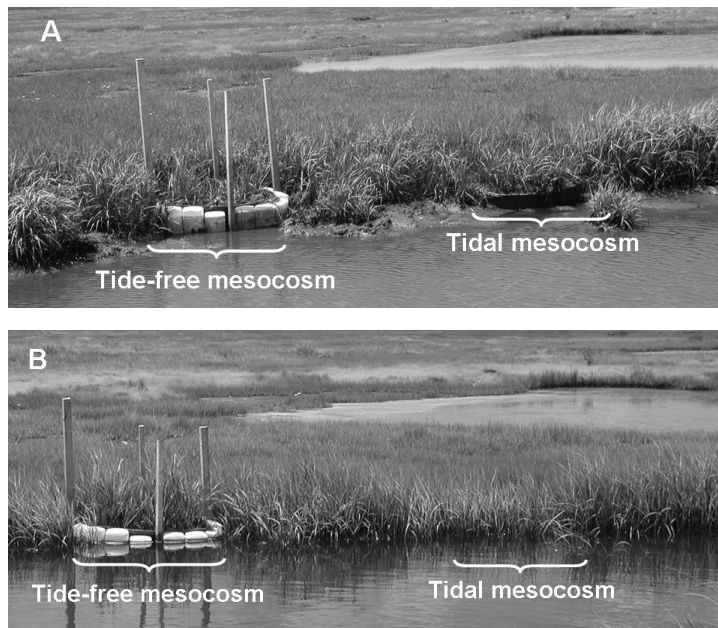
These results shed new light on earlier findings. In chapter two, I found that *Pardosa* and *Tytthus* aggregate in areas with abundant vegetation above tide water during especially high tides. During the highest tides of the month, substantial numbers of *Tytthus* migrate from low-elevation meadows, where vegetation can be totally submerged, to the ample vertical refuge of the creek-side habitat. Results from the current study show that emergent vegetation is an incomplete refuge where predators continue to suffer substantial impacts from tides. The fact that vertical refuge remains attractive to predators shows the importance of even a partial refuge.

In chapter two I also found that *Prokelisia* planthoppers, unlike predators, show no correlation with vertical refuge, suggesting that they were relatively invulnerable to tidal inundation. The current results show that planthoppers, especially nymphs, do suffer significant tide-related mortality. Their lack of response to vertical refuge may indicate that the dangers involved in moving to find refuge outweigh the benefits. Movement may increase chances of being dislodged from a grass leaf, and young nymphs have great difficulty in relocating a plant once they have been dislodged (Denno and Grissell 1979).

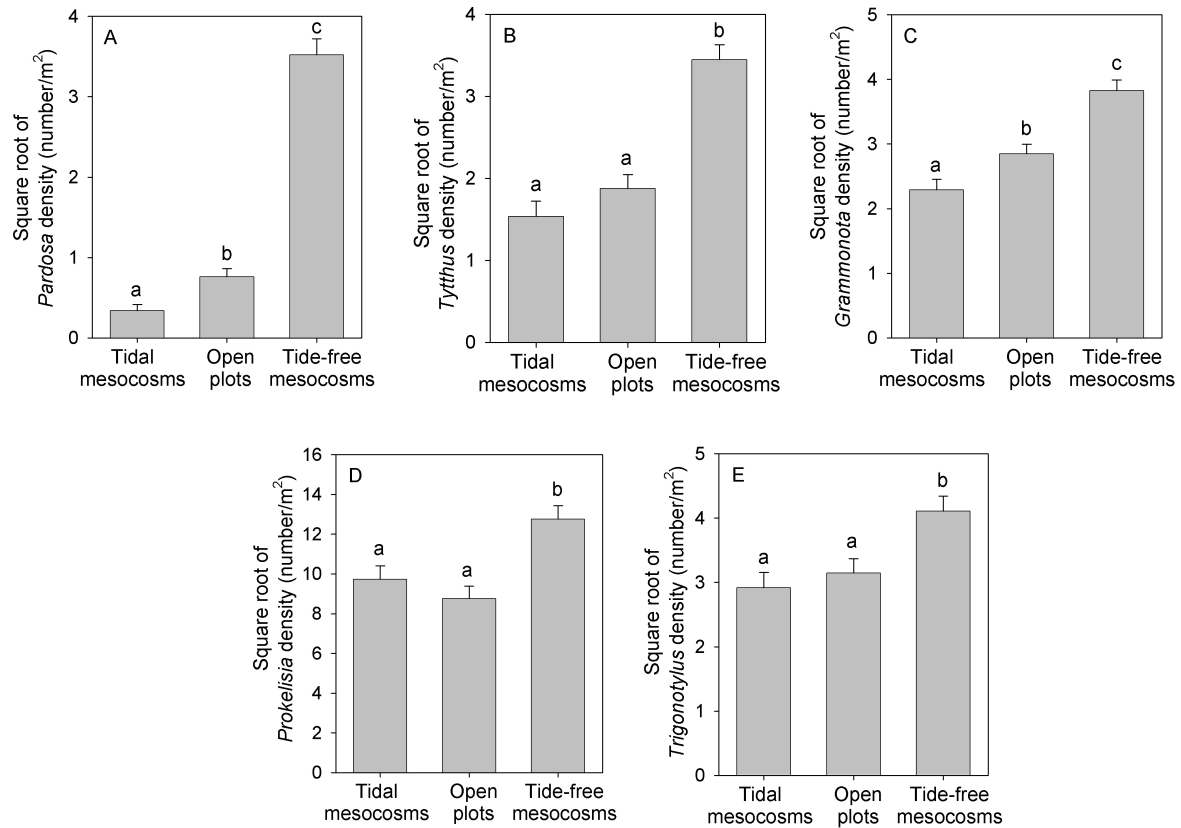
A more long-term implication of this research is that anthropogenic change could have a marked effect on the marsh food web. Winds associated with storms can substantially raise tide height. If the frequency and/or intensity of storms increases, as some climate-change models predict (Boer et al. 2001), and empirical studies have observed (Woodworth and Blackman 2004), my findings indicate that tidal mortality at all trophic levels will increase. Climate variability is also expected to increase, and variability alone can decrease natural enemy impact (Stireman et al. 2005). Thus, climate change has the potential to either increase or decrease marsh herbivore density, directly affecting *Spartina* biomass (Denno et al. 2002), and indirectly affecting *Spartina* mutualists, including mussels (Bertness 1984) and fiddler crabs (Bertness 1985).



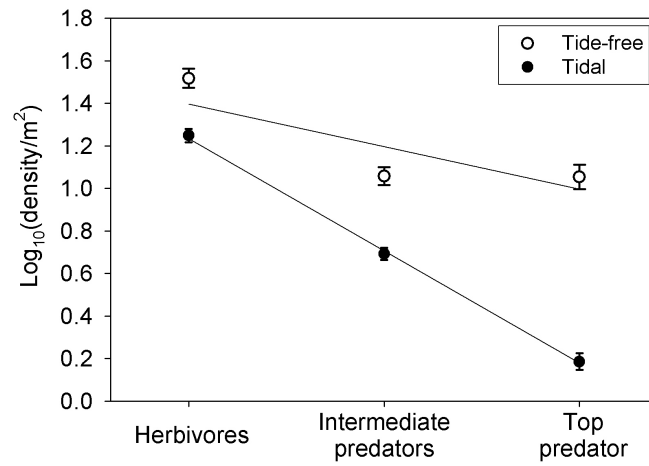
## Figures



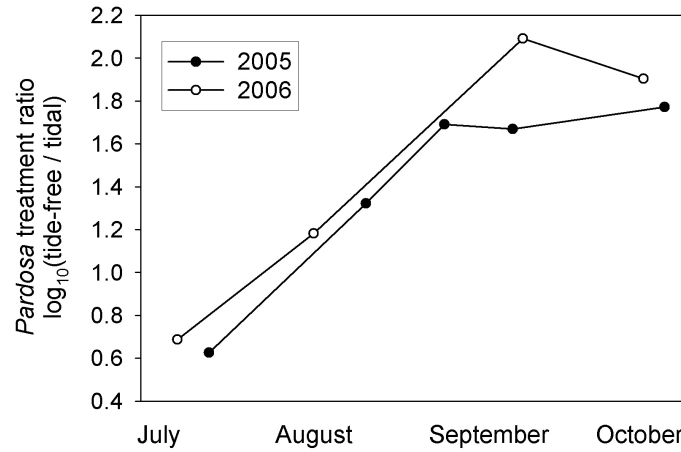
**Figure 3.1.** One tide-free mesocosm and one tidal mesocosm during a low tide (A) and a somewhat higher tide (B). White plastic bottles provide flotation for the tide-free mesocosm, and upright boards keep it in place while floating. Pictures were taken in June, when creek-side *Spartina* was approximately half the height it would attain by August.



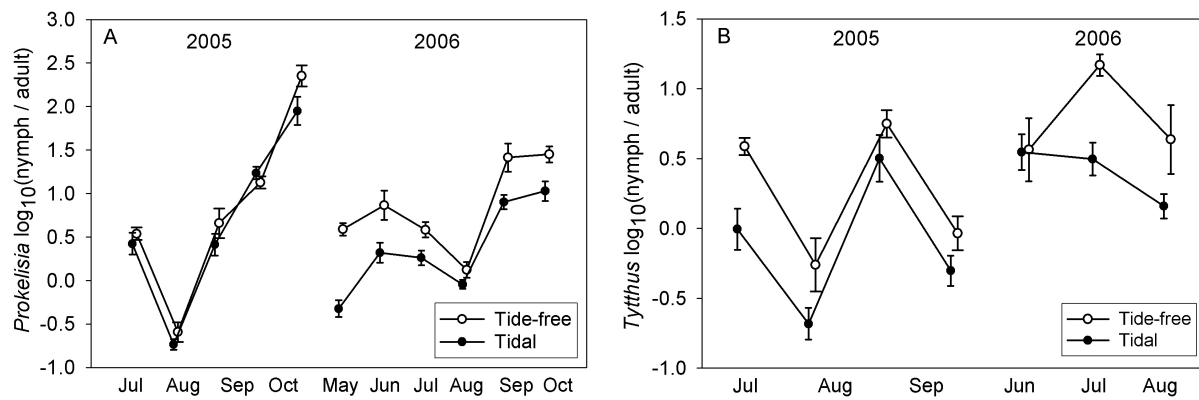
**Figure 3.2.** Effect of treatment on densities of (A) *Pardosa*, (B) *Tytthus*, (C) *Grammonota*, (D) *Prokelisia*, and (E) *Trigonotylus*. Densities were square-root transformed before analysis. Error bars display standard errors of the means. Treatments that do not share a letter are significantly different ( $\alpha = 0.05$ ).



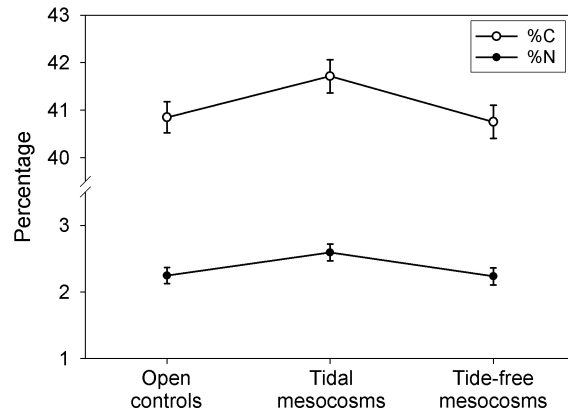
**Figure 3.3.** Mean ( $\pm$  standard error of the mean) of log-transformed densities of the three trophic levels in tidal and tide-free treatments. Slopes for the regression lines are significantly different (trophic level by treatment interaction  $F_{1,1263} = 48.53$ ,  $P < 0.0001$ ), showing that densities of higher trophic levels were reduced more by tidal inundation than those of herbivores.



**Figure 3.4.** *Pardosa* treatment ratios (mean density in tide-free mesocosms divided by mean density in tidal treatments) for all dates on which *Pardosa* were present in both treatments. *Pardosa* treatment ratios increased over the course of both seasons of the experiment. No other species ratio changed consistently with time.



**Figure 3.5.** Nymphs per adult for *Prokelisia* (A) and *Tytthus* (B) in tide-free and tidal treatments for all dates on which both nymphs and adults were present. Error bars show standard errors of the ratio means.



**Figure 3.6.** Percent nitrogen and carbon in *Spartina* cordgrass samples taken from the three treatments on 22 May 2006. Error bars show standard errors of mean percentages. Percentages did not differ significantly among treatments.

## Tables

Trophic position		Tide-free mean/m <sup>2</sup>	Tidal mean/m <sup>2</sup>	Treatment ratio	P
Intermediate predator	<i>Tytthus</i> nymphs	157.2	42.5	3.7	<0.0001
	<i>Tytthus</i> adults	66.5	31.0	2.1	0.0002
Herbivore	<i>Prokelisia</i> nymphs	2078.8	1260.0	1.6	0.0001
	<i>Prokelisia</i> adults	720.9	502.9	1.4	0.20

**Table 3.1.** Mean densities for adults and nymphs of *Tytthus* and *Prokelisia*, pooled over all sample dates, for tide-free and tidal treatments. Tidal treatment means combine data from open control plots and tidal mesocosms. Treatment ratios equal tide-free means divided by tidal means. P values are from repeated-measures F tests for equality of treatments.

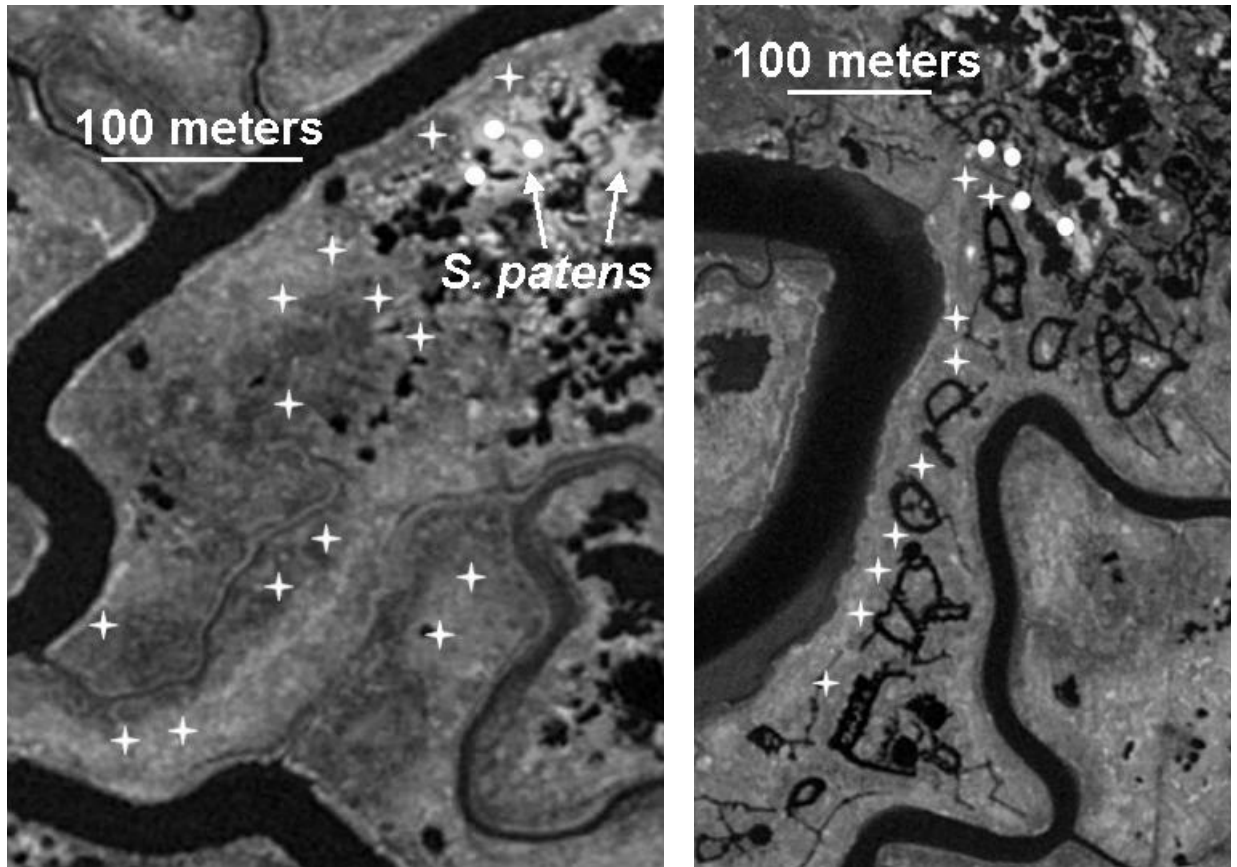
predator / prey	Tide-free ratio	Tidal ratio	Treatment effect	P
<i>Pardosa</i> / <i>Tytthus</i>	1.32	0.67	1.97	0.02
<i>Pardosa</i> / <i>Grammonota</i>	0.86	0.22	3.91	<.0001
<i>Pardosa</i> / <i>Prokelisia</i>	0.05	0.02	2.28	0.002
<i>Pardosa</i> / <i>Trigonotylus</i>	0.55	0.19	2.89	0.006
<i>Tytthus</i> / <i>Prokelisia</i>	3.23	1.27	2.54	0.002
<i>Grammonota</i> / <i>Prokelisia</i>	0.10	0.11	0.89	0.57
<i>Grammonota</i> / <i>Trigonotylus</i>	1.06	0.80	1.33	0.18

**Table 3.2.** Predator-to-prey ratios for all predator-prey combinations, averaged over all dates when both predators and prey were present. The “Treatment effect” column divides the ratio in tide-free mesocosms by the ratio in tidal treatments. P values are from repeated-measures F tests for equal ratios in tide-free and tidal treatments.



## Appendices

### Appendix 1.1



Aerial photographs of the two transects. The widest black lines are major tidal creeks. Light patches are *Spartina patens*, surrounding gray areas are *Spartina alterniflora*. White circles mark locations of *S. patens* sample sites, stars mark *S. alterniflora* sites.

## Appendix 1.2

Regression tables in the order they were mentioned in the results section of chapter 1

All tables give results from tests of fixed effects from regressions by SAS procedure “Mixed”. Repeated-measures regression was performed because the same locations were sampled on all dates.

Effect	Num DF	Den DF	F Value	Pr > F
Distance from <i>S. patens</i>	1	19	2.35	0.1415

Table 1. Test for a *Pardosa* density gradient on August 16, 2002, following a mild winter (Fig. 1A). Response variable was the square root of *Pardosa* density at a single sample location on a single sample date.

Effect	Num DF	Den DF	F Value	Pr > F
Distance from <i>S. patens</i>	1	21	23.61	<0.0001

Table 2. Test for a *Pardosa* density gradient on August 26, 2003, following a severe winter (Fig. 1B). Response variable was the square root of *Pardosa* density at a single sample location on a single sample date.

Effect	Num DF	Den DF	F Value	Pr > F
Distance from <i>S. patens</i>	1	460	21.88	<0.0001
Winter temperature	1	460	3.69	0.0554
Sample day	1	0	50.57	.
Elevation	1	0	5.71	.
Distance X temperature	1	460	6.49	0.0112

Table 3. Repeated-measures regression testing the effect of the previous winter’s mean temperature on the strength of the *Pardosa* gradient in *S. alterniflora* after the onset of *Pardosa* reproduction (Fig. 2A). Response variable was the square root of *Pardosa* density at a single sample location on a single sample date.

“Sample day” in this and following tables is a number from 1 to 365 giving the day of the year on which the sample was taken. “Elevation” is the elevation of the marsh surface at a sample location. Both sample day and elevation are random factors.

Effect	Num DF	Den DF	F Value	Pr > F
Transect	1	592	0.03	0.8590
Habitat	1	592	56.45	<0.0001
Sample day	1	0	26.90	.

Table 4. Repeated-measures regression testing for differences between the two transects. “Habitat” in this and following tables is a discrete variable with two possible values, *S. patens* and *S. alterniflora*.

Effect	Num DF	Den DF	F Value	Pr > F
Distance from <i>S. patens</i>	1	458	0.26	0.6113
Winter temperature	1	458	2.72	0.0997
Sample day	1	0	55.58	.
Elevation	1	0	0.00	.
Distance X temperature	1	458	0.14	0.7116

Table 5. Repeated-measures regression testing the effect of the previous winter’s mean temperature on the strength of any adult planthopper gradient in *S. alterniflora* during the summer (Fig. 2B). Response variable was log<sub>10</sub> of planthopper density at a single sample location on a single sample date. Both sample day and elevation are random factors.

Effect	Num DF	Den DF	F Value	Pr > F
Habitat	1	73	43.56	<0.0001

Table 6. Repeated-measures regression testing the effect of habitat on planthopper adult density during the summer, after the onset of *Pardosa* reproduction. Response variable was log<sub>10</sub> of adult planthopper density at a single sample location on a single sample date.

Effect	Num DF	Den DF	F Value	Pr > F
Habitat	1	73	11.15	0.0013

Table 7. Repeated-measures regression testing the effect of habitat on planthopper nymph density during the summer, after the onset of *Pardosa* reproduction. Response variable was log<sub>10</sub> of planthopper nymph density at a single sample location on a single sample date.

Effect	Num DF	Den DF	F Value	Pr > F
Habitat	1	53	26.15	<0.0001
Sample month	1	28	44.11	<0.0001
Habitat X month	1	28	10.22	0.0034

Table 8. Repeated-measures ANOVA comparing spring *Pardosa* size in the two habitats in March and June, before the onset of *Pardosa* reproduction (Fig. 3). All *Pardosa* collected at all sites in March and June were measured except that when more than 50 *Pardosa* were collected at one sample location, 50 random *Pardosa* were measured. Response variable was the square root of the mean size of all *Pardosa* collected at a site. Explanatory variables “Habitat” and “Sample month” were discrete, with two levels each.

Effect	Num DF	Den DF	F Value	Pr > F
Habitat	1	35	25.27	< 0.0001

Table 9. Repeated-measures regression comparing the size of *Pardosa* juveniles in the two habitats, after the onset of *Pardosa* reproduction. The same response variable was used as in table 8.

Effect	Num DF	Den DF	F Value	Pr > F
Habitat	1	35	0.27	0.6068
Sample day	1	351	850.05	<0.0001
Habitat X day	1	351	0.71	0.4008

Table 10. Repeated-measures regression testing whether the change in *Pardosa* juvenile size over the summer was the same in the two habitats. The same response variable was used as in table 8.

Effect	Num DF	Den DF	F Value	Pr > F
Habitat	1	68	93.89	<0.0001
Winter temperature	1	218	16.64	<0.0001
Habitat X temperature	1	218	4.56	0.0339

Table 11. Repeated-measures regression testing whether mean winter temperature affected spring *Pardosa* density and whether the effect was the same in the two habitats (Fig. 4A). Response variable was the square root of *Pardosa* density at a single sample location on a single sample date.

Effect	Num DF	Den DF	F Value	Pr > F
Habitat	1	68	7.77	0.0069
Winter temperature	1	203	0.24	0.6223
Habitat X temperature	1	203	0	0.9725

Table 12. Repeated-measures regression testing whether mean winter temperature affected spring density of planthopper nymphs and whether the effect was the same in the two habitats (Fig. 4B).

### Appendix 1.3

Test for spatial autocorrelation among sample sites on *Spartina alterniflora* transects

Two transects consisting of sample sites in *Spartina alterniflora* at increasing distances from the nearest *Spartina patens* were used to test for the existence of a gradient in *Pardosa* density with increasing distance from *S. patens*. This appendix describes a test for spatial autocorrelation in *Pardosa* density among transect sites.

General approach:

1. *Pardosa* density was regressed against distance from *S. patens* separately for each sample date.
2. Residuals from those regressions were used to create an empirical variogram.
3. Three theoretical variograms were fit to the empirical data: Spherical, Linear, and a horizontal line. The horizontal line modelled the case in which autocorrelation range is smaller than the shortest inter-site distance.
4. The most appropriate theoretical variogram was chosen based on its sum of squared errors, corrected for the number of parameters fitted, using AIC<sub>C</sub>. The range of that variogram gives the minimum inter-site distance that can be considered independent.

Sampling methods

- One transect consisted of nine sample sites along a relatively straight line. The other transect consisted of 14 sites that fanned out from *S. patens*. (See appendix 1.1 for aerial photographs.)
- In two cases, sample sites were slightly more than 15 meters apart. All other sites were at least 24 meters apart.
- Both transects were sampled 21 times over five years. The same sites were sampled on all occasions.

Regression methods

- *Pardosa* densities were square-root transformed to achieve normality and homogeneity of variance.
- Separate regressions were done for each of the 21 sample days. The only independent variable was a site's distance from *S. patens*. The dependent variable was the square root of *Pardosa* density at the site.

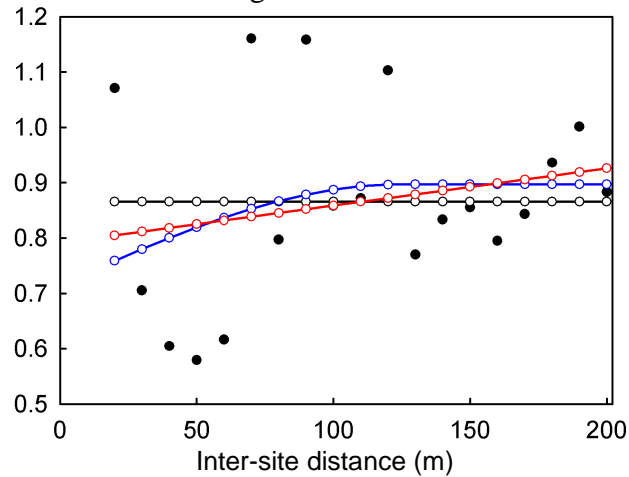
Empirical variogram methods

- Inter-site distances were measured directly for sample sites closer than approximately 50 meters apart. Distances for sites farther apart were calculated using site latitude-longitude, correcting longitude distances for site latitude.
- Regression residuals were standardized among days by dividing all residuals for a given day by the standard deviation of residuals for that day.
- Inter-site correlations were calculated separately for each of the 21 days and then pooled.

- SAS Proc Variogram was used to calculate pooled empirical variograms using both 10 and 20 meter lags.

Theoretical variograms were fit to the empirical data using SAS Proc Model.

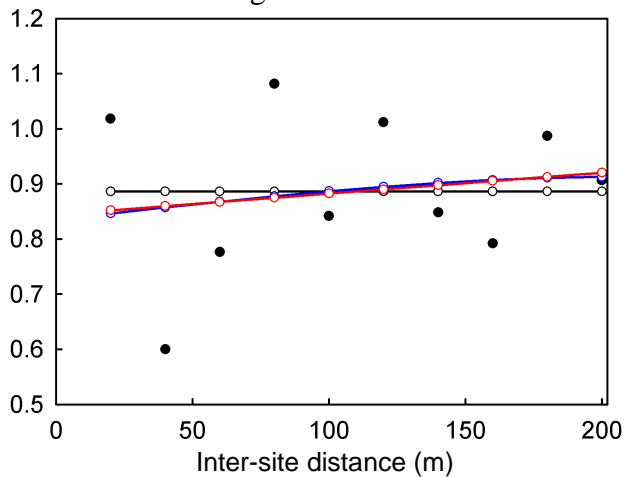
Results for 10-meter lag classes:



Black dots = empirical variogram values  
 Blue line = fitted spherical variogram.  
 Red line = fitted linear variogram.  
 Black line = fitted horizontal line.

Model	SSE	# data points	# parameters	AIC	AIC <sub>C</sub>	Δ AIC <sub>C</sub>
Spherical	0.5174	19	3	-62.46	-60.86	4.07
Linear	0.5280	19	3	-62.08	-60.47	4.46
Horizontal	0.5538	19	1	-65.17	-64.94	

Results for 20-meter lag classes:



Black dots = empirical variogram values  
 Blue line = fitted spherical variogram.  
 Red line = fitted linear variogram.  
 Black line = fitted horizontal line.

Model	SSE	# data points	# parameters	AIC	AIC <sub>C</sub>	Δ AIC <sub>C</sub>
Spherical	0.1834	10	3	-33.99	-29.99	7.24
Linear	0.1863	10	3	-33.83	-29.83	7.39
Horizontal	0.1883	10	1	-37.72	-37.22	

Formulas used:

$AIC = N \ln(SSE/N) + 2K$ , where  $N$  = number of data points,  $K$  = number of parameters.

$$AIC_C = AIC + (2K(K + 1)) / (N - K - 1)$$

The “horizontal” model is the most parsimonious, so autocorrelation of *Pardosa* density is at a scale smaller than 15 meters, the minimum distance between sample sites. All sample sites can therefore be considered independent in regressions.



## Appendix 1.4

Numbered sections below provide details of calculations used to establish the following conclusions:

1. *Pardosa* density increased faster in *S. alterniflora* than in *S. patens* during the summer months.
2. Reproduction was higher in *S. patens* than in *S. alterniflora* in May, June and July. In August there was no significant difference between the two habitats.
3. *Pardosa* size decreased with increasing density before the onset of reproduction.
4. Winter temperature was not correlated with the size discrepancy between habitats.
5. There was a *Pardosa* size gradient in *S. alterniflora* during the summer.

Regression tables below give results from tests of fixed effects by SAS procedure “Mixed”. Repeated-measures regression was performed because the same locations were sampled on all dates.

1. *Pardosa* density increased faster in *S. alterniflora* than in *S. patens* during the summer months.

Data from the two *patens*-to-*alterniflora* transects on the following dates were used: 25 June 2003, 26 August 2003, 29 May 2004, 25 August 2004, 31 July 2005, 4 September 2005, 17 July 2006 and 4 August 2006.

Regression model: square root(*Pardosa* density) = Habitat Time Habitat\*Time  
*Pardosa* densities were square-root transformed to achieve homogeneity of variance and normality.

Habitat was a discrete variable with values “*S. patens*” and “*S. alterniflora*”  
Time was also a discrete variable, “early” for the May, June and July samples, “late” for the August and September samples.

	Num	Dem		
Effect	DF	DF	F Value	Pr > F
Habitat	1	217	24.69	<.0001
Time	1	217	10.95	0.0011
Habitat*Time	1	217	4.41	0.369

Estimate	square root( <i>Pardosa</i> density)	<i>Pardosa</i> density
<i>S. patens</i> early	10.2731	105.5
<i>S. patens</i> late	11.0003	121.0
<i>S. alterniflora</i> early	4.8218	23.2
<i>S. alterniflora</i> late	8.0252	64.4

So during the course of the summer, *Pardosa* density increased 15.5 per m<sup>2</sup> in *S. patens*, and 41.2 per m<sup>2</sup> in *S. alterniflora*, on average.

2. Reproduction was higher in *S. patens* than in *S. alterniflora* in May, June and July. In August there was no significant difference between the two habitats.

I used density of *Pardosa* with carapace width less than 0.62 mm at each site as a measure of local reproduction level. There is variation in size at moult, but *Pardosa* this small are typically in the first instar and are riding on the mother's abdomen. They become separated from the mother during vacuum sampling. The distribution of those densities was not normal even with a log transformation, so a non-parametric two-sided Wilcoxon test was performed on densities in the two habitats.

Separate tests were performed for each sample date, with the following results:

Date	mean density		P
	<i>S. patens</i>	<i>S. alterniflora</i>	
25 June 2003	8.09	0.35	0.08089
2 July 2003	75.21	2.85	<.0001
6 July 2003	89.41	1.75	<.0001
19 July 2003	14.06	3.78	0.0171
26 August 2003	21.72	11.19	0.3745
29 May 2004	4.92	5.18	0.7763
13 June 2004	129.56	28.92	0.0008
24 June 2004	82.55	9.74	0.0003
16 July 2004	51.00	14.22	0.0005
25 August 2004	0.93	0.28	0.6378
17 July 2006	54.45	13.63	0.0293
4 August 2006	21.47	23.9	0.1404

Mean hatchling density was significantly higher in *S. patens* than in *S. alterniflora* in all samples except for samples in August of all years and on 29 May 2004. The difference was not significant in any of those exceptions.

3. *Pardosa* size decreased with increasing density before the onset of reproduction.

All data collected in May and June were used. Sample dates were 24 May 2001, 31 May 2001, 5 June 2001, 10 June 2003, 1 June 2005, 5 June 2005, and 2 June 2006.

Carapace width was measured on a total of 120 *Pardosa* in *S. patens*, 67 in *S. alterniflora*.

Regression model:  $\text{Size} = \text{Habitat} + \text{Density} + \text{Habitat} * \text{Density}$

Experimental units were sample dates, so size and density are means for a habitat on a single date.

Effect	Num DF	Dem DF	F Value	Pr > F
Habitat	1	9	34.36	0.0002
Density	1	9	8.06	0.0195
Habitat*Density	1	9	4.72	0.0580

Parameter estimates:

In *S. patens*:  $\text{Size} = 1.8772 - 0.00574 * \text{Density}$

In *S. alterniflora*:  $\text{Size} = 2.2838 - 0.04312 * \text{Density}$

Size decreased at higher densities, the opposite of what would be expected if size was being significantly affected by cannibalism.

4. Winter temperature was not correlated with the size discrepancy between habitats.

To look for an effect before the onset of reproduction, data from the two *patens*-to-*alterniflora* transects on the following dates were used: 16 March 2003, 28 March 2003, 10 June 2003, 19 March 2005, 1 June 2005, 16 March 2006, 27 March 2006, and 2 June 2006.

Carapace width was measured on a total of 147 *Pardosa* in *S. patens*, 57 in *S. alterniflora*.

Regression model:  $\text{Size} = \text{Temperature} + \text{Habitat} + \text{Temperature} * \text{Habitat}$

Temperature was the mean temperature of the preceding winter.

Habitat was a discrete variable with values “*S. patens*” and “*S. alterniflora*”

Time during the spring was treated as a random factor.

Experimental units were sample sites, so size is the mean of all *Pardosa* measured at a sample site on a single date.

Effect	Num DF	Dem DF	F Value	Pr > F
Temperature	1	62	0.37	0.5454
Habitat	1	62	7.86	0.0068
Temperature*Habitat	1	62	0.24	0.6232

The non-significant effect of the temperature by habitat interaction means that the difference in size between the two habitats was not affected by temperature.

To look for an effect among juveniles after the onset of reproduction, the following dates were used: 25 June 2003, 26 August 2003, 29 May 2004, 25 August 2004, 31 July 2005, 4 September 2005, 17 July 2006 and 4 August 2006. Carapace width was measured on a total of 5,248 *Pardosa* in *S. patens*, 3,610 in *S. alterniflora*.

The regression model used was identical to the model used for pre-reproduction data.

Effect	Num DF	Dem DF	F Value	Pr > F
Temperature	1	385	1.85	0.1742
Habitat	1	385	38.32	<.0001
Temperature*Habitat	1	385	0.43	0.5111

The non-significant effect of the temperature by habitat interaction means that the difference in size between the two habitats was not affected by temperature.

5. There was a *Pardosa* size gradient in *S. alterniflora* during the summer.

The same data was used as in section 4, above, for juveniles, except that only data from *S. alterniflora* were used.

Regression model: Size = Distance

“Distance” is the distance of a sample site from *S. patens*.

Time during the summer was treated as a random factor.

Experimental units were again sample sites, so size is the mean of all *Pardosa* measured at a sample site on a single date.

Effect	Num DF	Dem DF	F Value	Pr > F
Distance	1	214	6.38	0.0122

The distance parameter was positive, so *Pardosa* size does increase as distance from *S. patens* increases.

## Appendix 2.1

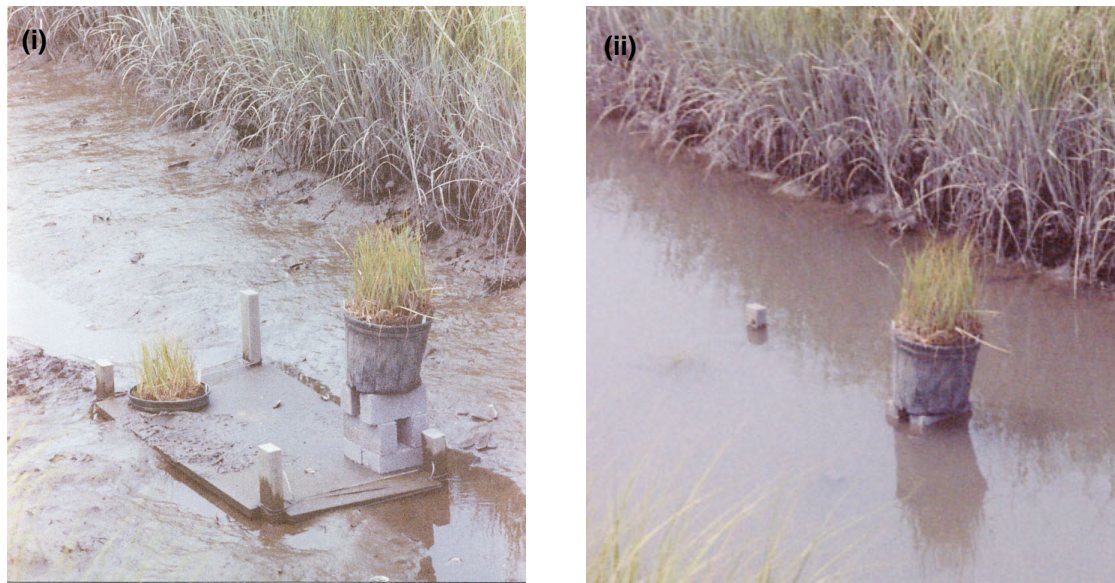


Figure A. I stocked potted *Spartina* with 15 *Pardosa* and placed them at different elevations on platforms in a tidal creek during low tide (i), where they remained until the tide peaked (ii). The pot on the left experienced total submersion, the pot on the right, no submersion. Only two treatments were implemented per platform, and the half-submersion treatment was not represented on this platform. Immediately after high tide, we removed pots from the creek and counted remaining *Pardosa*.

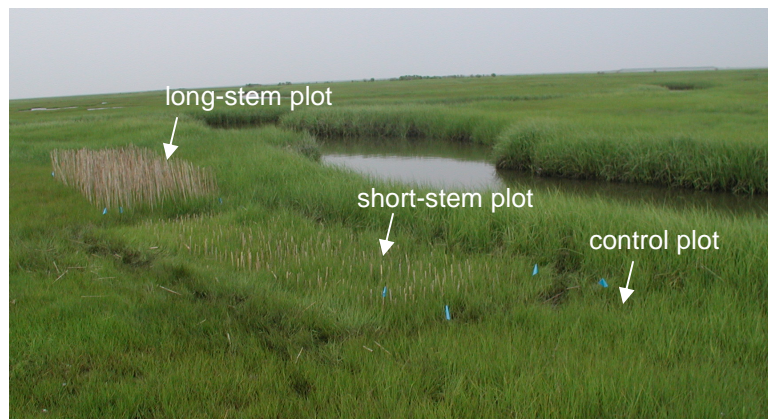


Figure B. One block, containing plots for each of the three treatments: (1) artificial refuge present, with 50 cm-long dead stems of the reed *Phragmites*, (2) refuge control, consisting of 20 cm-long stems, the same height as surrounding *Spartina*, and (3) un-manipulated control plots. The block pictured is one of six in low-elevation meadows, where tidal inundation is more frequent than in high-elevation meadows, where six additional blocks were placed.

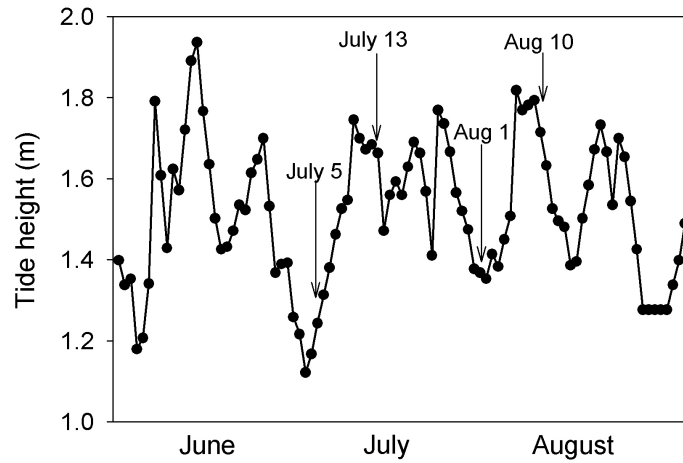


Figure C. The height of the highest tide at Atlantic City on each day during the summer of 2002. Dates of the four transect samples are shown. Samples were collected at low tide, but the first and third samples were taken when tides had been relatively low for several days, whereas the second and fourth were taken following the highest tides of July and August. Atlantic City is approximately 22 Km from the Tuckerton marsh. (Source: NOAA)

### Appendix 3.1

Densities, in number per square meter, and treatment ratios for each sample date for all members of the focal food web. The “Tide-free density” column contains the mean for the eight floating mesocosms. The “Tidal density” column contains the mean for the eight tidal mesocosms and the nine open plots. The “Treatment ratio” column contains the ratio of floating to tidal density. “Overall” rows pool all sample dates.

#### *Pardosa*

	Tide-free density	Tidal density	Treatment ratio
23-Jul-05	154.93	36.62	4.23
22-Aug-05	295.78	14.09	21.00
06-Sep-05	86.27	1.76	49.00
19-Sep-05	77.47	1.66	46.75
18-Oct-05	317.78	5.39	59.01
10-May-06	1.76	0.00	infinity
02-Jun-06	5.28	0.00	infinity
17-Jul-06	136.82	28.17	4.86
12-Aug-06	554.58	36.45	15.21
21-Sep-06	204.23	1.66	123.25
14-Oct-06	70.42	0.88	80.00
Overall	174.66	11.18	15.62

#### *Tytthus*

	Tide-free density	Tidal density	Treatment ratio
23-Jul-05	213.28	61.03	3.50
22-Aug-05	260.56	116.20	2.24
06-Sep-05	422.54	112.68	3.75
19-Sep-05	568.66	202.99	2.80
18-Oct-05	21.13	0.00	infinity
10-May-06	140.85	44.73	3.15
02-Jun-06	109.16	130.90	0.83
17-Jul-06	408.45	108.28	3.77
12-Aug-06	205.99	21.54	9.57
21-Sep-06	109.16	14.92	7.32
14-Oct-06	22.89	0.00	infinity
Overall	223.71	73.44	3.05

#### *Grammonota*

	Tide-free density	Tidal density	Treatment ratio
23-Jul-05	331.99	181.23	1.83
22-Aug-05	408.45	180.47	2.26
06-Sep-05	367.96	103.00	3.57
19-Sep-05	246.48	78.70	3.13
18-Oct-05	132.93	79.54	1.67
10-May-06	61.62	62.97	0.98
02-Jun-06	123.24	77.06	1.60
17-Jul-06	613.68	176.94	3.47
12-Aug-06	470.07	254.35	1.85
21-Sep-06	107.39	72.90	1.47
14-Oct-06	49.30	35.62	1.38
Overall	259.99	117.16	2.22

#### *Trigonotylus*

	Tide-free density	Tidal density	Treatment ratio
23-Jul-05	575.45	403.76	1.43
22-Aug-05	279.93	176.93	1.58
06-Sep-05	630.28	125.89	5.01
19-Sep-05	237.68	167.35	1.42
18-Oct-05	0.00	0.00	
10-May-06	82.75	33.97	2.44
02-Jun-06	535.21	304.89	1.76
17-Jul-06	291.75	191.03	1.53
12-Aug-06	149.65	154.10	0.97
21-Sep-06	49.30	30.65	1.61
14-Oct-06	0.00	0.83	0.00
Overall	253.36	141.31	1.79

***Prokelisia***

	Tide-free density	Tidal density	Treatment ratio
23-Jul-05	2472.83	2993.42	0.83
22-Aug-05	5989.43	3978.00	1.51
06-Sep-05	5264.08	3117.08	1.69
19-Sep-05	5482.39	5595.69	0.98
18-Oct-05	3348.59	1098.18	3.05
10-May-06	213.03	82.85	2.57
02-Jun-06	408.45	120.13	3.40
17-Jul-06	1414.49	806.34	1.75
12-Aug-06	1730.63	746.48	2.32
21-Sep-06	2401.41	715.00	3.36
14-Oct-06	1857.39	436.62	4.25
Overall	2799.70	1762.85	1.59

***Tytthus* nymphs**

	Tide-free density	Tidal density	Treatment ratio
23-Jul-05	158.95	37.56	4.23
22-Aug-05	89.79	11.44	7.85
06-Sep-05	353.87	96.83	3.66
19-Sep-05	276.41	67.11	4.12
18-Oct-05	12.32	0.00	infinity
10-May-06	140.85	44.74	3.15
02-Jun-06	89.79	101.08	0.89
17-Jul-06	360.16	91.55	3.93
12-Aug-06	158.45	6.63	23.91
21-Sep-06	105.63	14.09	7.50
14-Oct-06	8.80	0.00	infinity
Overall	157.22	42.49	3.70

***Tytthus* adults**

	Tide-free density	Tidal density	Treatment ratio
23-Jul-05	52.31	23.47	2.23
22-Aug-05	167.25	104.75	1.60
06-Sep-05	63.38	15.85	4.00
19-Sep-05	279.93	135.87	2.06
18-Oct-05	8.80	0.00	infinity
10-May-06	0.00	0.00	0.00
02-Jun-06	19.37	29.83	0.65
17-Jul-06	26.16	16.73	1.56
12-Aug-06	15.85	14.91	1.06
21-Sep-06	3.52	0.83	4.25
14-Oct-06	14.09	0.00	infinity
Overall	66.49	30.95	2.15

***Prokelisia* nymphs**

	Tide-free density	Tidal density	Treatment ratio
23-Jul-05	1919.52	2421.60	0.79
22-Aug-05	1154.93	624.12	1.85
06-Sep-05	4424.29	2459.51	1.80
19-Sep-05	5082.74	5303.23	0.96
18-Oct-05	3334.51	1093.21	3.05
10-May-06	176.06	27.34	6.44
02-Jun-06	371.48	83.68	4.44
17-Jul-06	1128.77	568.66	1.99
12-Aug-06	1045.77	358.74	2.92
21-Sep-06	2302.82	637.95	3.61
14-Oct-06	1666.67	392.61	4.25
Overall	2078.77	1259.98	1.65

***Prokelisia* adults**

	Tide-free density	Tidal density	Treatment ratio
23-Jul-05	553.32	571.83	0.97
22-Aug-05	4834.51	3353.87	1.44
06-Sep-05	839.79	657.57	1.28
19-Sep-05	399.65	292.46	1.37
18-Oct-05	14.09	4.97	2.83
10-May-06	36.97	55.51	0.67
02-Jun-06	36.97	36.45	1.01
17-Jul-06	285.71	237.68	1.20
12-Aug-06	684.85	387.74	1.77
21-Sep-06	98.59	77.05	1.28
14-Oct-06	62.60	27.29	2.29
Overall	720.93	502.86	1.43



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