

Claudio Gratton · Robert F. Denno

## Seasonal shift from bottom-up to top-down impact in phytophagous insect populations

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**Abstract** Although many studies now examine how multiple factors influence the dynamics of herbivore populations, few studies explicitly attempt to document where and when each is important and how they vary and interact. In fact, how temporal variation in top-down (natural enemies) and bottom-up (host plant resources) factors affect herbivore dynamics has been suggested as a particularly important yet poorly understood feature of terrestrial food webs. In this study we examined how temporal changes in predator density (wolf spiders, sheet-web builders, and mirid egg predators) and host-plant resources (plant quality and structural complexity) influence the population dynamics of the dominant phytophagous insects on Atlantic-coast salt marshes, namely *Prokelisia* planthoppers (Homoptera: Delphacidae). We designed a factorial experiment in meadows of *Spartina alterniflora* to mimic natural variation in vegetation quality and structure by establishing two levels of plant nutrition (leaf nitrogen content) by fertilization, and two levels of habitat complexity by adding leaf litter (thatch). We then assessed seasonal changes in the strength of bottom-up (plant quality) and top-down (predator) impacts on planthopper populations. Planthopper populations responded positively to increased plant quality treatments in late summer. Despite the greater number of planthopper adults colonizing fertilized *Spartina* plots compared to unfertilized controls, the offspring of these colonists were much less abundant at the end of the season in fertilized plots, particularly those with thatch. The initial colonization effect was later erased because arthropod predators selectively accumulated in fertilized plots where they inflicted significant mortality on all

stages of planthoppers. Predators rapidly colonized fertilized plots and reached high densities well in advance of planthopper colonization, a response we attribute to their rapid aggregation in complex-structured habitats with readily available alternative prey. Our results suggest that plant resources not only mediate the strength of predator impacts on herbivore populations, but they also promote the coupling of predator and prey populations and thus influence when enemy impacts are realized.

**Keywords** Alternate prey · Habitat complexity · Multichannel omnivory · Predator-prey · Temporal variation

### Introduction

It is now generally accepted that bottom-up and top-down forces act in concert to influence populations of most phytophagous insects (Hartvigsen et al. 1995; Hunter et al. 1997). Moreover, researchers now readily acknowledge that interactions between plants and natural enemies are commonplace (Forkner and Hunter 2000; Denno et al. 2002). Thus, host plants can impact herbivores directly by influencing their performance and survival, and indirectly by mediating the effects of natural enemies (Lawton and McNeill 1979; Price et al. 1980). For instance, predator-prey and parasite-host interactions can be modified by host plants such that enemy effects on herbivore populations are either enhanced (Kareiva 1987; Dicke and Sabelis 1988; Kareiva and Sahakian 1990; Turlings et al. 1990, 1998; Takabayashi et al. 1998; English-Loeb et al. 1999) or diminished (Campbell and Duffey 1979; Treacy et al. 1986; Kauffman and Kennedy 1989; Espelie et al. 1991; Bottrell et al. 1998).

Despite the recognized importance of such interactions, we know little about how the direct and interactive effects of host plants and natural enemies on herbivore dynamics vary either temporally throughout the year or spatially across habitats (but see Polis et al. 1998; Polis 1999; Denno et al. 2002). Recent studies suggest that the

C. Gratton (✉)

Department of Entomology, University of Wisconsin - Madison,  
237 Russell Labs, 1630 Linden Drive, Madison, WI 53706, USA  
e-mail: cgratton@wisc.edu  
Tel.: +1-608-2653762  
Fax: +1-608-2623322

R. F. Denno

Department of Entomology, University of Maryland,  
4144 Plant Science Building, College Park, MD 20742, USA

relative importance top-down and bottom-up effects in natural communities can vary both within a season as well as among years (Walker and Jones 2001). For example, Kato (1994) found that the first generation of a leaf-mining agromyzid fly in Japan was resource limited, whereas the second generation was not, but rather was attacked intensively by a complex of parasitoids. Walker and Jones (2001) showed that, even for the same species, the relative importance of natural enemies and host plants change from year to year. Notwithstanding a growing body of empirical studies examining temporal variation in top-down and bottom-up effects on terrestrial communities (Power et al. 1996; Polis et al. 1998; Ernest et al. 2000; Ostfeld and Keesing 2000), and an increasing recognition of its importance to food web dynamics (Hunter and Price 1992; Holt 2000), little is known of the processes that influence this variation.

In this experimental study we examined how bottom-up factors (plant nutrition and vegetation structure) in a *Spartina* salt marsh influenced temporal changes in the abundance of arthropod predators (spiders and mirid bugs) in open field plots and what impact this might have on herbivore populations (*Prokelisia* planthoppers) as the season progresses. Although previous studies of *Spartina*-planthopper-natural enemy interactions found substantial spatial variation in the influence of bottom-up factors on both herbivores and their natural enemies (Denno et al. 2002) no attempts were made to measure how these factors change over the course of the season to influence herbivore populations. These earlier studies showed that planthopper populations would be greatest in patches of high plant quality (leaf nitrogen content) that promote rapid population growth and enhanced survival. Planthoppers are known for their sensitivity to variation in host-plant quality and respond rapidly by selectively colonizing (Cook and Denno 1994) and developing faster on nitrogen-rich plants (Denno et al. 1986; Olmstead et al. 1997). In contrast, we anticipated that planthopper populations would be suppressed in areas where predator density is high, such as in habitats rich in leaf litter (Döbel and Denno 1994; Denno et al. 2002). Spiders and other invertebrate predators often accumulate at high densities in complex-structured vegetation independent of prey availability (Bultman and Uetz 1982; Döbel et al. 1990; Reichert and Bishop 1990; Döbel and Denno 1994; Landis et al. 2000), a response that has been attributed to a more favorable microclimate or reduced cannibalism and intraguild predation (Hallander 1970; Langellotto 2002). In this study we focused on temporal variation of the effects of natural enemies and host plants on herbivore populations as they changed over the course of the growing season. This emphasis was based on the observation that natural enemies generally build up as the season progresses on the marsh (Döbel and Denno 1994). In this context, we suspected that enemy impacts on herbivores might increase temporally as well. We hypothesized that early-season accumulation of arthropod predators in response to bottom-up factors would result in the enhanced late-season suppression of herbivore popu-

lations (e.g., Settle et al. 1996). We anticipated that enhanced vegetation structure and increases in alternative prey might promote the accumulation and retention of predators earlier in the season (Vince et al. 1981; Döbel and Denno 1994; Settle et al. 1996). Thus, understanding how bottom-up factors advance or delay the temporal onset of top-down impacts is an under-explored aspect of the interactive effects of plant resources and natural enemies on herbivore dynamics (Polis et al. 1998).

## Materials and methods

### Natural history and study site

Our experiment was conducted on an expansive salt marsh near Tuckerton, New Jersey (39° 30.8'N, 74° 19.0'W) dominated by the cordgrass *Spartina alterniflora* (Lois.) (see Denno et al. 2002 for detailed description of study system). The most abundant herbivores on *Spartina* are the specialist planthoppers *Prokelisia dolus* Wilson and *Prokelisia marginata* (Van Duzee). Both planthoppers are phloem feeders, trivoltine, and have similar phenology, generation time ( $\approx 40$  days), life-time fecundity, and growth rate (Denno 1994).

The most common natural enemies of planthoppers include the generalist lycosid spiders *Pardosa littoralis* Banks (50–100 individuals/m<sup>2</sup>) and the linyphiid *Grammonota trivitatta* Banks (300–600 individuals/m<sup>2</sup>). The major natural enemy of *Prokelisia* eggs is the mirid bug *Tytthus vagus* Knight (200–400 individuals/m<sup>2</sup>) (Finke and Denno 2002). Parasitoids of planthoppers such as strepsipterans and dryinids are uncommon at our sites (<5% parasitism, Denno 1983). Salt marsh spiders are broad generalists and are known to feed on a variety of prey items associated with *Spartina* habitats (Marples 1966; Lasalle and Delacruz 1985), including the phytophagous mirid *Trigonotylus uhleri* Reuter as well as small flies such as chloropids and ephydriids (Döbel and Denno 1994). Moreover, *Pardosa* is an intraguild predator that readily consumes other spiders such as *Grammonota* (C. Gratton and R.F. Denno, unpublished data) and *Tytthus* (Finke and Denno 2002). In addition, these predators are known to accumulate in complex-structured habitats rich in *Spartina* leaf litter and to respond numerically to increases in prey density (Döbel and Denno 1994).

### Host plant/habitat manipulations

Our objective was to examine temporal changes in the impact of natural enemies on the population dynamics of *Prokelisia* planthoppers under conditions of variable vegetation nutrition and structure that occur naturally on the high marsh in Atlantic-coastal salt marshes. To achieve this we manipulated bottom-up effects and measured changes over time in herbivores and their natural enemies. We established combinations of plant nutrition and habitat structure by crossing two plant-quality treatments (fertilized and unfertilized) with two thatch treatments (thatch addition and no thatch addition) in a factorial design. Each treatment was replicated twice within 5 complete blocks, for a total of 40 treatment plots. Within a block, the 8 treatment plots (1.22×1.22 m,  $\approx 1.5$  m<sup>2</sup> area) were spaced 1.5 m from each other in a 2×4 array. Treatments were assigned randomly within blocks and block areas were selected haphazardly in our study site, with blocks separated by 3–40 m.

The high plant-nutrition treatment was established by repeated fertilizer additions (44.5 g/m<sup>2</sup> ammonium nitrate and 13.8 g/m<sup>2</sup> of acid phosphate), whereas the low plant quality treatment went unfertilized. Fertilization occurred biweekly from 21 May to 9 July 1998 during the peak growth period of *Spartina*. This level of fertilization resulted in plants of high biomass and nitrogen content comparable to those found around pot-holes and on mud flat

vegetation whereas unfertilized plots were of low quality and similar to short-form *Spartina* growing in high-marsh meadows (Denno et al. 1980; Vince et al. 1981).

Thatch-enhanced plots were achieved by first raking all plots of any existing leaf litter, followed by the re-application of thatch to half of the plots. Thatch-addition plots received two applications of approximately 117 g/m<sup>2</sup> and 559 g/m<sup>2</sup> (dry weight) of dead *Spartina* on 21 May and 21 July 1998, respectively, to achieve a level of thatch that is about twice the ambient average but falls within the naturally occurring range (Döbel and Denno 1994). Thatch was obtained by raking neighboring *Spartina* meadows, and then it was gently inserted at ground level within the matrix of living *Spartina* plants. By the end of the experiment (1 October 1998) the amount of thatch remaining in thatched plots was 381±40 g/m<sup>2</sup> (mean±SEM, n=20), an amount that is equivalent to early-season levels of ambient thatch. Non-thatched plots (≈0 g/m<sup>2</sup>) were representative of mud flat vegetation where thatch is typically scarce (<100 g/m<sup>2</sup>, Denno et al. 2002).

To achieve comparable starting conditions for planthoppers and predators, all plots were defaunated twice by exhaustive D-vac suctioning 2 weeks prior to the start of the arthropod sampling. A sample was taken just before the last defaunation on 8 July to verify the effectiveness of mid-season defaunations.

#### Arthropod and plant sampling

Population densities of planthoppers (*Prokelisia*), predators (lycosid spiders, *Tytthus*, and other spiders that were mostly linyphiids), and alternative prey (phytophagous mirids and flies) in each treatment plot were estimated using a D-vac suction sampler with a 0.093-m<sup>2</sup> sampling head. Samples consisted of two non-overlapping 8-s placements of the D-vac sampling head over the *Spartina* vegetation (except for the 1 October sample that consisted of five 8-s placements). Sampling began on 28 July 1998, 2 weeks after the last defaunation, and continued approximately every 2 weeks until 1 October to correspond to the last generation of *Prokelisia* planthoppers. Arthropod densities are reported as number/m<sup>2</sup>. Alternate prey were censused once just prior to *Prokelisia* adult colonization (12 August 1998).

The structure and nitrogen content of *Spartina* was determined once at the end of the season (1 October) in each plot by clipping all vegetation within a 0.047-m<sup>2</sup> quadrat with electric lawn shears. For each sample we determined plant biomass (live and standing dead), culm density, and the thatch biomass. Samples were oven dried at 80°C for 48 h before being weighed. Subsequently, all live plant biomass was ground to a powder in a Wiley mill, passed through a 1-mm screen and analyzed for percent nitrogen by the University of Maryland NRSLA Soils Testing Laboratory (College Park, Md.) using a CHN automated analyzer. *Spartina* biomass and nitrogen content do not change appreciably during August and September (Denno and Grissell 1979; Vince et al. 1981), and a late-season

plant sample therefore represented the condition of plants colonized and fed upon by planthoppers during middle and late summer.

#### Statistical analysis

We examined the effect of the treatment combinations on the population density of herbivores and predators using repeated-measures MANOVA (von Ende 1993). The model design included a block effect and was fully factorial (2 fertilization × 2 thatch treatments). Block by treatment interactions were not significant and thus were not included in the final model. The dependent variables measured over time were the density of herbivores (*Prokelisia* adults combined, *P. marginata* adults, *P. dolus* adults, and *Prokelisia* nymphs combined) and predators (lycosid spiders, other spiders, and *Tytthus*). Wilk's  $\Lambda$  test statistic was used to assess treatment effects for MANOVA. In addition, treatment effects on planthopper load (number of nymphs per g live *Spartina* biomass) were assessed on the last sample date (1 October) by ANOVA. Treatment effects on *Spartina* characteristics (percent nitrogen, live biomass, dead biomass, and number of culms) were also examined by ANOVA. In addition, a MANOVA was used to examine the effects of treatments on all plant characteristics considered simultaneously. Treatment effects on the pooled density of non-*Prokelisia* arthropods (alternative prey for spiders such as phytophagous mirids and flies) were assessed using ANOVA on data collected once (12 August) just prior to peak adult *Prokelisia* colonization. Correlations were used to examine the relationship between mid-season predator density (average of 25 August and 8 September) and the load of *Prokelisia* nymphs (1 October). For all analyses, normality assumptions were checked and log  $x+1$  transformations were used when necessary to normalize variances across treatments, but means (±SEM) are reported untransformed. Analyses were performed using JMP 4.0 (SAS Institute 2000).

## Results

### Treatment effects on plant nitrogen and structure

Fertilization of *Spartina* resulted in large and significant increases in plant biomass and nitrogen content (Table 1, MANOVA, significant Fertilizer effect). *Spartina* in fertilized plots was significantly more nutritious (2.12±0.05% N) than that in unfertilized plots (1.54±0.04% N) (Table 1). Moreover, fertilization resulted in significantly greater live biomass and dead biomass and nitrogen content (%) than that growing in unfertilized plots (Table 1). At the end of the growing season, the live

**Table 1** ANOVA results for the effects of block (5 marsh areas), fertilizer (added or not), thatch (added or not), and their interaction on the nitrogen content (% dry live weight), biomass (live and dead g dry weight), and number of culms per m<sup>2</sup> of *Spartina alterniflora* measured in experimental plots on 1 October 1998 on a marsh near

Tuckerton, New Jersey. A MANOVA was performed as well to assess the effect of the treatments on all plant characteristics simultaneously. Bolded *P*-values highlight significant treatment effects ( $P<0.05$ )

Source	<i>df</i> <sup>a</sup>	Percent nitrogen		Live wt. (g / m <sup>2</sup> )		Dead wt. (g / m <sup>2</sup> )		Culms / m <sup>2</sup>		MANOVA		
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>df</i> <sup>a</sup>	<i>F</i> <sup>b</sup>	<i>P</i>
Block	4, 32	3.60	<b>0.016</b>	0.87	0.490	0.21	0.214	18.91	<b>&lt;0.0001</b>	16, 89	5.19	<b>&lt;0.0001</b>
Fertilizer (F)	1, 32	122.26	<b>&lt;0.0001</b>	250.48	<b>&lt;0.0001</b>	28.13	<b>&lt;0.0001</b>	0.03	0.857	4, 29	145.48	<b>&lt;0.0001</b>
Thatch (T)	1, 32	4.39	<b>0.044</b>	0.03	<b>0.030</b>	0.39	0.534	8.99	<b>0.005</b>	4, 29	8.90	<b>&lt;0.0001</b>
F × T	1, 32	2.00	0.167	0.95	0.947	0.08	0.783	0.76	0.390	4, 29	1.00	0.422
<i>R</i> <sup>2</sup>		0.82		0.89		0.52		0.73				

<sup>a</sup> Numerator, denominator degrees of freedom

<sup>b</sup> Test using Wilk's  $\Lambda$  statistic

biomass of *Spartina* in fertilized plots more than doubled ( $544 \pm 12 \text{ g/m}^2$ ) compared to that in unfertilized plots ( $187 \pm 20 \text{ g/m}^2$ ). The biomass of standing dead *Spartina* was also much greater in fertilized ( $495 \pm 25 \text{ g/m}^2$ ) compared to non-fertilized plots ( $348 \pm 13 \text{ g/m}^2$ ), and was likely due to an increase in the sloughing off of larger and more abundant leaves. Fertilization did not alter culm density (average  $2,721 \pm 91 \text{ culms/m}^2$ ).

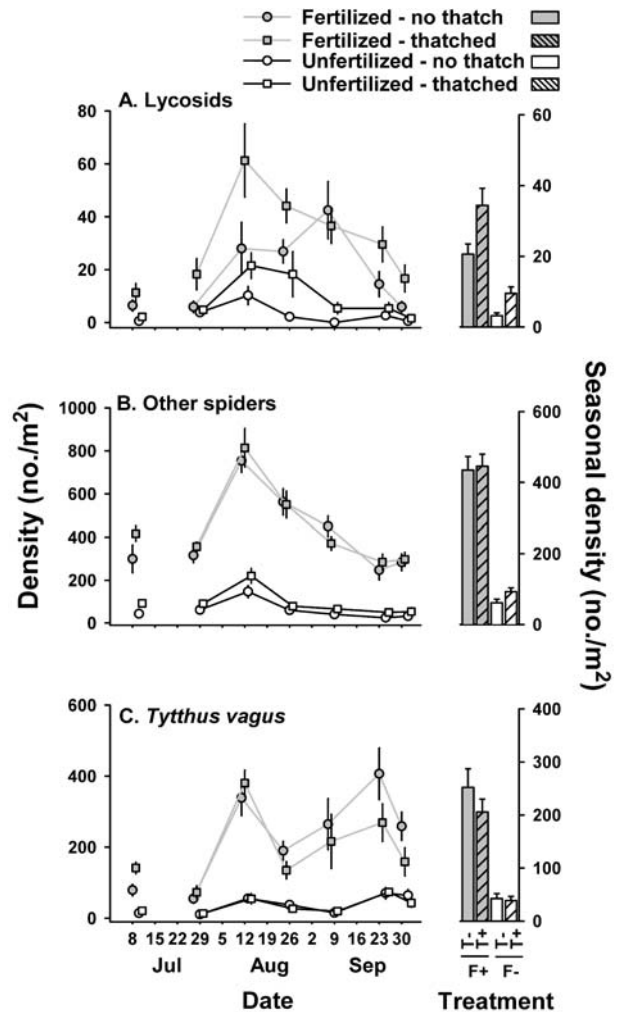
In contrast to the strong impact of fertilization, thatch addition had only a minor but statistically significant effect on the nitrogen content and structure of *Spartina* (Table 1). Plants in the thatch-addition plots contained slightly less nitrogen (1.77%) compared to those in the non-thatched plots (1.89%), but thatch addition explained only 2.5% of the variation in nitrogen content compared to the fertilizer effect (70%). Most notably, the density of living culms was 11% lower in thatched plots ( $2,564 \pm 113 \text{ culms/m}^2$ ) compared to those where thatch was withheld ( $2,879 \pm 137 \text{ culms/m}^2$ ). However, the biomass of live *Spartina* was slightly higher in thatched plots ( $391 \pm 45 \text{ g/m}^2$ ) compared to plots not receiving thatch ( $340 \pm 43 \text{ g/m}^2$ ) (Table 1).

#### Seasonal dynamics of predators and responses to bottom-up treatments

The abundance of all predators was significantly higher in fertilized plots. For example, lycosid spider densities in fertilized plots were on average 440% higher than densities in unfertilized plots (Fig. 1A). Fertilized plots also carried significantly higher densities of other non-lycosid spiders (Fig. 1B) and *Tytthus* (Fig. 1C) compared to unfertilized plots (Table 2). Thatch-addition plots also supported higher densities of lycosids (Fig. 1A) and other spiders (Fig. 1B; Table 1, significant Thatch effect) than did non-thatched plots. All predator densities changed over the course of the season (Fig. 1A–C; Table 2, significant Time effects). Significant Time  $\times$  Fertilizer interactions (Table 2) indicate that changes in predator density over time differed between the two fertilizer treatments. For example, predator populations remained at consistently low levels in unfertilized plots, whereas predator densities in fertilized plots increased rapidly from initially low levels, peaked in early August or September, and then declined (Fig. 1A–C). Notably, predator densities increased in plots at a time when *Prokelisia* were rare in *Spartina* (early August).

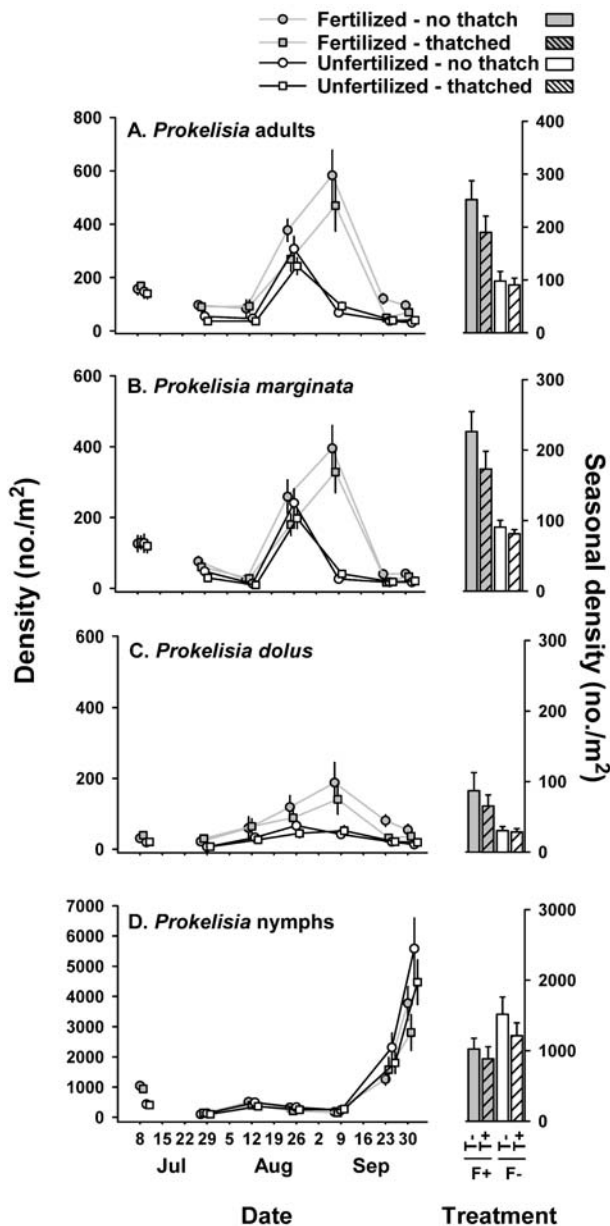
#### Seasonal dynamics of planthoppers and responses to bottom-up treatments

Planthopper phenology was similar among all treatment plots. Following the final defaunation (9 July), populations of *Prokelisia* adults remained similarly low through early August in all treatment plots ( $<200 \text{ individuals/m}^2$ , Fig. 2A). During mid-August, planthopper adults began colonizing plots and reached peak densities in either late



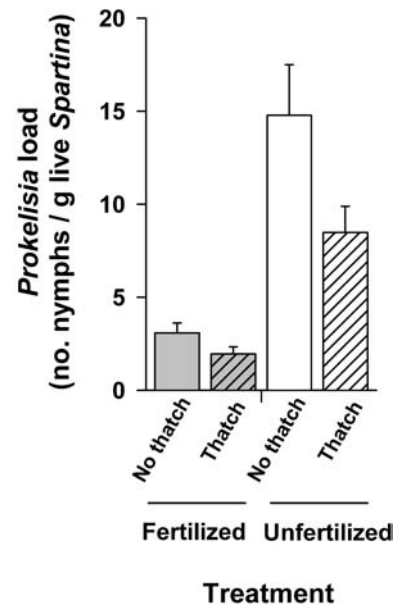
**Fig. 1A–C** Mean density of predators ( $\pm$ SEM) over the season in fertilized (shaded symbols) and unfertilized (open symbols) plots, and thatched (squares) and non-thatched (circles) plots of *Spartina alterniflora*. Mean seasonal density ( $\pm$ SEM) of predators in the different treatment combinations is also shown in the right panel. Shaded and open bars are fertilized plots (F+) and unfertilized plots (F-), and hatched and unhatched bars are thatched (T+) and non-thatched plots (T-), respectively. Predators are **A** lycosid spiders, primarily *Pardosa littoralis*, **B** other spiders, mostly *Grammonota trivittata*, and **C** *Tytthus vagus* (adults and nymphs pooled)

August or early September (Fig. 2A–C). Plot colonization coincided with the annual fall migration of *P. marginata* from low-marsh to high-marsh habitats (Denno et al. 1996). Most adults of *P. marginata* collected during the August–September peak were flight-capable macropterous forms ( $85.0 \pm 1.8\%$  of adults) (Fig. 2B). By contrast, few adults of *P. dolus* were macropterous ( $8.9 \pm 1.8\%$  of adults), and in general were less common ( $93 \pm 15 \text{ adults/m}^2$ ,  $n=40$  during peak density; Fig. 2C) than *P. marginata* ( $209 \pm 19 \text{ adults/m}^2$ ; Fig. 2B). Eggs deposited by colonizing adults began to hatch in mid-September and populations of nymphs subsequently increased in abundance until peak density was reached in early October (Fig. 2D).



**Fig. 2A–D** Mean density of planthoppers ( $\pm$ SEM) over the season in fertilized (shaded symbols) and unfertilized (open symbols) plots, and thatched (squares) and non-thatched (circles) plots of *Spartina alterniflora*. Mean seasonal density ( $\pm$ SEM) of planthoppers in the different treatment combinations is shown in the right panel. Shaded and open bars are fertilized plots (F+) and unfertilized plots (F-), and hatched and unhatched bars are thatched (T+) and non-thatched plots (T-), respectively. Planthoppers are **A** total *Prokelisia* adults, **B** adults of *P. marginata* and **C** *P. dolus*, and **D** *Prokelisia* nymphs

Despite similarities in planthopper phenology among treatment plots, there was a strong effect of plant quality on the density of *Prokelisia* adults, whereby planthoppers selectively colonized fertilized plots (Table 3, Time  $\times$  Fertilizer effect; Fig. 2A). Peak densities of *P. marginata* and *P. dolus* were 11 times and 3.5 times greater in fertilized than in non-fertilized plots, respectively



**Fig. 3** Mean *Prokelisia* nymphal load (number of nymphs per g dry live mass of *Spartina*,  $\pm$  SEM) on 1 October 1998 in fertilized plots and unfertilized plots of *Spartina*, (shaded and open bars, respectively), and in thatched and non-thatched plots (hatched and unhatched bars, respectively)

(Fig. 2B, C; Table 3). This pattern remained even when adult densities were expressed as a load (no. individuals/g live *Spartina* biomass), thereby accounting for differences in plant biomass among treatments. For instance, peak planthopper load (pooled *Prokelisia* adults from 8 September) was significantly higher on fertilized plants ( $0.995 \pm 0.132$  individuals/g *Spartina*) compared to non-fertilized ones ( $0.457 \pm 0.065$  individuals/g live *Spartina*) ( $F_{1,32}=28.3$ ,  $P<0.0001$ ). There was no significant effect of thatch addition on adult planthopper density (Table 3).

In contrast to the elevated densities of adults in fertilized plots during September, nymphal densities realized at the end of the season in October (the offspring of August–September colonists) were significantly higher in unfertilized plots (Fig. 2D, Table 3). Expressing *Prokelisia* nymph density as a load (number/g live *Spartina*) did not change this pattern (Fig. 3). In addition, nymphal loads also tended to be lower in plots supplemented with thatch (Fig. 3, Table 3 significant Thatch effect), although the effect of thatch addition on *Prokelisia* nymph density was not significant when analyzed using repeated measures MANOVA (Fig. 2D, Table 3,  $P=0.25$ ).

In general, there was an inverse power relationship between *Prokelisia* nymphal load at the end of the season and the mid-season density of predators in experimental plots. Plots with the highest predator densities during the period of peak planthopper colonization in August and September (Fig. 1A–C) had the lowest nymphal load at the end of the season (log-log transformed: lycosids,  $r=-0.76$ ,  $P<0.001$ ; *Tytthus*,  $r=-0.72$ ,  $P<0.001$ ; other spiders  $r=-0.79$ ,  $P<0.001$ ). However, it was not possible

**Table 2** Repeated-measures MANOVA results for the effects of block (5 marsh areas), fertilizer (added or not), thatch (added or not), and their interaction on the density (no. individuals/m<sup>2</sup>, log x+1 transformed) of lycosid spiders, other spiders (non-lycosid),

and *Tytthus vagus* in experimental plots of *Spartina alterniflora* on a marsh near Tuckerton, New Jersey. Bolded *P*-values highlight significant treatment effects ( $P < 0.05$ )

Source	<i>df</i> <sup>a</sup>	Lycosids		Other spiders		<i>Tytthus vagus</i>	
		<i>F</i> <sup>b</sup>	<i>P</i>	<i>F</i> <sup>b</sup>	<i>P</i>	<i>F</i> <sup>b</sup>	<i>P</i>
Between subjects							
Block	4,32	1.73	0.17	1.56	0.21	2.26	0.08
Fertilizer (F)	1,32	94.50	<b>&lt;0.0001</b>	206.25	<b>&lt;0.0001</b>	169.64	<b>&lt;0.0001</b>
Thatch (T)	1,32	25.88	<b>&lt;0.0001</b>	4.92	<b>0.03</b>	1.26	0.27
F × T	1,32	0.01	0.97	2.94	0.10	0.06	0.80
Within subjects							
Time (Ti)	5,28	38.55	<b>&lt;0.0001</b>	99.55	<b>&lt;0.0001</b>	66.94	<b>&lt;0.0001</b>
Ti × Block	20,92	1.69	<b>0.05</b>	2.40	<b>&lt;0.01</b>	2.37	<b>&lt;0.01</b>
Ti × F	5,28	5.04	<b>&lt;0.01</b>	8.31	<b>&lt;0.0001</b>	5.22	<b>&lt;0.01</b>
Ti × T	5,28	0.52	0.76	1.64	0.18	1.21	0.33
Ti × F × T	5,28	2.25	0.08	0.08	0.25	1.76	0.15

<sup>a</sup> Numerator, denominator degrees of freedom

<sup>b</sup> Test using Wilk's  $\Lambda$  statistic

**Table 3** Repeated-measures MANOVA results for the effects of block (5 marsh areas), fertilizer (added or not), thatch (added or not), and their interaction on the density (no. individuals/m<sup>2</sup>, log x+1 transformed) of *Prokelisia* planthopper adults (pooled total, *P. marginata*, and *P. dolus*) and nymphs in experimental plots of

*Spartina alterniflora* on a marsh near Tuckerton, New Jersey. Effect of the same treatment combinations on nymphal load (no. of individuals/ g dry weight *Spartina*) was analyzed by ANOVA from data collected on 1 October 1998. Bolded *P*-values highlight significant treatment effects ( $P < 0.05$ )

Source	<i>df</i> <sup>a</sup>	Adults						Nymphs			
		Total <i>Prokelisia</i>		<i>P. marginata</i>		<i>P. dolus</i>		Density		Load <sup>c</sup>	
		<i>F</i> <sup>b</sup>	<i>P</i>	<i>F</i> <sup>b</sup>	<i>P</i>	<i>F</i> <sup>b</sup>	<i>P</i>	<i>F</i> <sup>b</sup>	<i>P</i>	<i>F</i> <sup>d</sup>	<i>P</i>
Between subjects											
Block	4,32	7.92	<b>&lt;0.0001</b>	3.27	<b>0.02</b>	18.95	<b>&lt;0.0001</b>	6.47	<b>&lt;0.001</b>	3.79	<b>0.01</b>
Fertilizer (F)	1,32	83.78	<b>&lt;0.0001</b>	78.82	<b>&lt;0.0001</b>	46.97	<b>&lt;0.0001</b>	6.05	<b>0.02</b>	94.20	<b>&lt;0.0001</b>
Thatch (T)	1,32	1.70	0.20	3.14	0.09	0.01	0.94	1.40	0.25	9.31	<b>&lt;0.01</b>
F × T	1,32	2.74	0.11	1.84	0.18	0.12	0.72	0.07	0.79	2.30	0.59
Within subjects											
Time (Ti)	5,28	163.61	<b>&lt;0.0001</b>	159.47	<b>&lt;0.0001</b>	97.09	<b>&lt;0.0001</b>	223.18	<b>&lt;0.0001</b>		
Ti × Block	20,92	3.40	<b>&lt;0.0001</b>	3.55	<b>&lt;0.001</b>	2.52	<b>&lt;0.01</b>	1.70	<b>0.05</b>		
Ti × F	5,28	16.28	<b>&lt;0.0001</b>	21.57	<b>&lt;0.0001</b>	3.08	<b>0.02</b>	1.22	0.33		
Ti × T	5,28	2.62	<b>0.05</b>	1.59	0.20	2.88	<b>0.03</b>	1.39	0.26		
Ti × F × T	5,28	2.83	<b>0.03</b>	1.88	0.13	5.16	<b>&lt;0.01</b>	2.08	0.10		

<sup>a</sup> Numerator, denominator degrees of freedom

<sup>b</sup> Test using Wilk's  $\Lambda$  statistic

<sup>c</sup> No. individuals/g dry weight live *Spartina*, log x+1 transformed

<sup>d</sup> Univariate ANOVA

to attribute this pattern to any one particular predator taxon due to the high correlations among predator densities ( $r > 0.70$ ) across all plots and treatments. The negative associations between predator densities and final nymphal load were driven in large part by differences between fertilized and non-fertilized plots and to a lesser extent by the thatching treatment (Table 2).

#### Alternate prey

Fertilization of *Spartina* also brought about changes in other arthropods that served as potential prey for spiders. Small flies (chloropids, ephydriids, and dolichopodids)

comprised 68% of all other insects (non-*Prokelisia*) collected at or near peak predator density (12 August). These small flies (<3 mm) were nearly twice as abundant in fertilized plots ( $413 \pm 38$  flies/m<sup>2</sup>) compared to unfertilized plots ( $234 \pm 31$  flies/m<sup>2</sup>,  $F_{1, 32} = 35.37$ ,  $P < 0.0001$ ). The second most common insect collected was *T. uhleri*, an herbivorous mirid that accounted for 9% of non-*Prokelisia* insects in samples. *T. uhleri* was also much more common in fertilized plots ( $70 \pm 16$  mirids/m<sup>2</sup>) compared to unfertilized plots ( $14 \pm 5$  mirids/m<sup>2</sup>,  $F_{1, 32} = 20.20$ ,  $P < 0.0001$ ). Although *T. uhleri* was not as abundant as the small flies, it is significantly larger (10–12 mm) and represented more biomass than flies.

## Discussion

Populations of *Prokelisia* planthoppers experienced a temporal change from bottom-up promoted increases during summer to strong top-down suppression later in the season in fertilized plots of *Spartina*. Despite the greater number of planthopper adults (mostly macropterous *P. marginata*) colonizing nitrogen-enriched *Spartina* plots in late summer (Fig. 2A–C), and their increased potential for rapid development there (Denno et al. 1986; Olmstead et al. 1997), the offspring of these colonists were far less abundant in fertilized plots at the end of the season, particularly in those containing thatch (Fig. 2D, Table 2). The selective accumulation of spiders and other invertebrate predators in fertilized and thatched plots in mid-summer (Fig. 1), in advance of planthopper colonization (Fig. 2), resulted in enhanced mortality on all developmental stages of planthoppers and lower populations of nymphs later in the season. The ultimate effect was lower planthopper abundance on fertilized *Spartina* compared to that in unfertilized controls. Thus, the direct and positive effects of enhanced plant nutrition on planthopper populations were later erased by both direct (habitat complexity) and indirect effects (alternate prey) of the same bottom-up factors that intensified predator impacts toward the end in the season.

### Bottom-up basis for temporal variation in top-down effects

Several factors likely promoted planthopper suppression by predators in fertilized meadow vegetation. Direct effects of bottom-up factors on natural enemies can have immediate consequences on predator abundance. For example, vegetation structure or habitat complexity has been shown to promote increases in the abundance of a variety of invertebrate predator taxa (Reichert and Bishop 1990; Döbel and Denno 1994; Halaj et al. 2000; Landis et al. 2000). Vegetation structure was explicitly manipulated by the addition of thatch to experimental plots, a treatment that resulted in increased wolf-spider abundance (Fig. 1A). It is also likely that the near two-fold increase in total *Spartina* biomass (live and standing dead) in fertilized plots also enhanced habitat complexity and promoted predator aggregation and retention in these plots independent of planthopper availability. This increase in total biomass likely overshadowed the effect of manually added thatch that was decreasing in biomass over the course of the summer as it decomposed at the marsh surface. Thus by directly influencing predator aggregation and retention into a particular habitat (i.e., fertilized habitat), bottom-up effects can increase predator abundance even in the absence of prey.

A complimentary factor that may have encouraged the rapid build-up of predators in fertilized *Spartina* was the increase in alternate prey for generalist predators (“multi-channel omnivores” sensu Polis and Strong 1996; Polis 1999). Our fertilized plots were rich in a variety of non-

planthopper arthropods including small flies and herbivorous mirids (*Trigonotylus uhleri*) that likely served as alternate prey for lycosid spiders during the early part of the season when planthoppers were scarce. Theoretical models suggest that food webs can be stabilized by such subsidies (Huxel and McCann 1998) and empirical studies support the notion that allochthonous prey can intensify top-down effects (Scheu 2001). For example, Settle et al. (1996) found that in tropical rice an abundance of detritivores and planktivores early in the season promoted the build-up of invertebrate predators when rice herbivores were uncommon. Later in the season these predators acted in concert to suppress populations of rice herbivores, including planthoppers. Consistent with this finding, our results further suggest that bottom-up effects (e.g., enhanced vegetation structure and alternate prey) set the stage for enhanced natural enemy impacts on herbivores later in the season.

Ostfeld and Keesing (2000) emphasize that understanding the differences between in-situ population responses of predators (and the factors that influence them) versus predator movement into areas that have high concentrations of resources will prove critical to understanding temporal changes in the strength of top-down and bottom-up effects in communities. They suggest that the speed at which natural enemies respond to a bottom-up factor, and therefore the temporal sequence of top-down and bottom-up effects on herbivore populations, is a function of the life history, population growth and dispersal rates of the natural enemies. If predators respond to bottom-up effects via a numerical response to prey availability, there may be a substantial lag between bottom-up on herbivores and eventual top-down impacts on herbivore populations. For example, several fertilization studies found that bottom-up effects initially promoted herbivore population growth before natural enemy impacts were ultimately realized (Vince et al. 1981; Boyer and Zedler 1996; Forkner and Hunter 2000). Since, in these studies, predators primarily responded to changes in prey density, there was an initial period of rapid herbivore population growth followed by eventual suppression resulting from the delayed numerical response of predators. Polis et al. (1998) documented a 1-year lag between prey (spider) increases and eventual predator (pompilid wasp) suppression. In contrast, our study found no appreciable lag in predator effect on herbivore populations since predator abundance was already high in fertilized plots due to an aggregative response rather than a numerical response. Therefore, the temporal sequence of bottom-up and top-down effects on arthropod populations will depend on how organisms at the consumer and predator trophic level differentially respond to bottom-up variation and on environmental factors that modify that response.

This study emphasizes that when predators are free to move and respond to local increases in vegetation complexity and alternative prey, they can be effective at suppressing *Spartina* herbivores, albeit later in the season. In contrast, previous experiments in the same *Spartina*

system found that planthopper populations often escape natural-enemy controls when the dispersal ability of spider predators is limited and their aggregative response hampered (Döbel and Denno 1994; Denno et al. 2002). In a series of lab and field experiments spider abundance was experimentally manipulated and natural spider colonization of prey-rich/complex vegetation habitats was either completely blocked due to the presence of cages (in a mesocosm experiment) or severely curtailed by the presence of water (surrounding *Spartina* islets). In those experiments, planthopper populations were ultimately highest on fertilized treatments and lowest on unfertilized controls (Denno et al. 2002), a situation that paralleled the natural spatial variation in top-down and bottom-up effects on the marsh. Hence, when the bottom-up effects on the temporal development of natural enemies (via dispersal) are taken into account, different outcomes on the dynamics of prey are observed. Thus, elucidating those bottom-up related factors that mediate predator dispersal and aggregation is essential to unraveling the temporal and spatial dynamics of predator-prey interactions (Polis et al. 1998; Nakano et al. 1999) and could also be exploited in developing conservation biological control strategies for pest management (Settle et al. 1996; Landis et al. 2000).

#### Spatial and temporal variation of natural enemy and host plant impacts on the salt marsh

In the *Spartina* marsh system, the relative strength of bottom-up and top-down forces on planthopper populations change both temporally and spatially. In general, on the high marsh top-down forces increase in relative strength throughout the season as predator populations grow from low overwintering densities (Denno 1983; Döbel et al. 1990). In the context of predator-planthopper interactions in the field, it is important to note that nitrogen-rich *Spartina*, of the sort we artificially produced via fertilization, occurs on the high marsh only in certain habitats and is restricted primarily to pothole-edge habitats (Denno et al. 1996). In these habitats, predators should aggregate and have a greater late-season impact on planthopper populations than in adjacent high marsh meadows. *Spartina* growing in the expansive meadows at this time is generally nitrogen-poor (Denno 1983) with relatively low invertebrate predator abundance and was mimicked by our unfertilized treatment. Thus, the enhanced late-season impact of predators that occurred in our fertilized plots is unlikely to arise in all marsh habitats. However, thatchy enclaves of high-quality *Spartina* may act as predator sources and their size and proximity to other habitats may influence the spatial dynamics of predator impacts across habitats on the marsh.

In summary, local increases in generalist predators and the timing of their impact on planthopper prey in the marsh system were mediated largely by bottom-up related factors. Results from this experiment, studies we have

done in the past (Denno and Peterson 2000; Denno et al. 2002), and the work of others on phytophagous insects (Polis et al. 1998; Forkner and Hunter 2000), support the view that the strength of top-down and bottom-up forces change both temporally within habitats and spatially across them. Moreover, interactions between host plants and natural enemies are commonplace and plants often mediate predator impacts (Oksanen et al. 1981; Hunter and Price 1992; Power 1992). In this study, plant-factors not only influenced the strength of predator impacts on planthopper populations, but also dictated when such impacts were realized.

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