THE EFFECT OF FOOD WEB STRUCTURE ON THE POPULATION DYNAMICS OF PITCHER PLANT MICROFAUNA

by

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To my parents

Mark and Mary Ellen

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ABSTRACT

My objective was to quantify how local and regional dynamics affect the population dynamics of pitcher plant microfauna. I studied a) factors affecting arthropod community assembly, b) how top-down and bottom-up factors affected the local population dynamics of microfauna, c) the effects of community structure and growth rates on population synchrony of one microfaunal taxon. I showed that the assembly of the arthropod community was an important determinant of local and regional dynamics of the aquatic microfauna.

I found that both fine- and meso-scale factors affected the assembly of the arthropod community. All three taxa responded to the fine-scale factors, leaf length, and capture rate, but the strength of the responses frequently depended on plant density – a meso-scale factor. Midges, but not mosquitoes or mites, responded directly to plant density.

The abundance and dynamics of the microfauna community is potentially affected by both pitcher plant arthropods and the resources captured by the leaf. Ecological theory suggests that top-down and bottom-up effects can be stabilizing or destabilizing, depending on community structure. Predation tended to decrease and destabilize microfaunal populations, leading to higher temporal variability and lower persistence times. Bottom-up effects varied with taxon and depended on the manner in which resource availability was increased. Top-down effects tended to be destabilizing, but the influence of bottom-up factors on stability depended on patterns of midge abundance.

Community structure and growth rates can affect population synchrony, which, in turn affects regional persistence. Recent modelling studies predict that high population growth rates will decrease population synchrony by reducing the synchronizing effect of dispersal. I found that growth rates, and high mosquito and midge densities did lower population synchrony. Synchrony had no effect on local stability, but there was some evidence that greater synchrony decreased regional stability.

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CHAPTER 1

Introduction

An ecological community is the result of local and regional processes. Demographic processes such as birth, growth and death, and many types of interactions with the environment (physical and biotic) occur at the local scale. Interactions with the physical or chemical environment may include responses to temperature or pH, whereas biotic interactions include competition, facilitation and the avoidance of predators. Reproduction and the dispersal of offspring often require movement beyond this scale and therefore are examples of regional processes.

There has been some debate over whether communities are structured primarily by local or regional process (Ricklefs 1987, Ricklefs and Schluter 1993, Caley and Schluter 1997, Huston 1999, Srivastava 1999, Hubbell 2001). Huston (1999) contends that local processes along environmental gradients are sufficient to explain regional patterns in communities. Others argue that regional processes are more relevant to broad patterns in community structure (Ricklefs 1987, Mauer 1999, Hubbell 2001). Common sense, or maybe just a moderate view, suggests that both local and regional processes affect community structure and that this relationship will vary across communities. This view is both compelling and insightful because it focuses on the impact of local and regional processes across temporal and spatial scales (O'Neill et al. 1989, Levin 1992, Shurin and Srivastava in press). For example, patterns in intertidal communities are caused by a combination of factors affecting dispersal, recruitment and survival (Menge et al. 1997, Menge 2000).

Disentangling the effects of local and regional process on population or community dynamics can be difficult. Ecologists have used several methods. For example Simberloff and Wilson (1969) defaunated oceanic islands and observed the process of decolonisation. Quinn and Robinson (1987) and McNaughton et al. (1998) compared grassland communities where predators were excluded with natural areas. Others manipulated immigration or emigration by adding or removing individuals (Fahrig and Merriam 1985, Shurin 2001, Miller et al. 2002). Each of these methods gives some understanding of how local and regional processes affect communities.

Another approach is to study communities living in ephemeral or new habitat. As new habitat develops, the ecologist has the opportunity to study the process of community assembly. During community assembly local and regional processes interact to influence local dynamics (Belyea and Lancaster 1999, Weiher and Keddy 1999). For example, both local and regional processes can determine the rate of colonization. Habitat isolation affects the arrival of organisms to a habitat but establishment may depend on the abundance of resources and the presence of competitors. The success of further colonists can depend on the order in which species arrive. Early arrivers may inhibit the colonization of some species and facilitate others. Throughout community formation, both local and regional processes will shape community composition as some species increase in numbers and others go extinct. Local dynamics will in turn affect regional dynamics as individuals disperse to new habitat.

I have chosen to study how local and regional process affect small aquatic communities living in pitcher plants. The northern pitcher plant (*Sarracenia purpurea*) grows in bogs and develops 3 to 9 pitcher-shaped leaves each year that fill with rain (Fish and Hall 1978, Juniper et al. 1989). Insects and other organisms fall in and drown providing resources for the community and the plant. Four arthropods live only in the leaves of *S. purpurea*: a mosquito *Wyeomyia smithii*, a midge *Metriocnemus knabi*, a sarcophagid fly *Blaesoxipha fletcheri*, and an aquatic mite *Sarraceniopus gibsoni*. Mosquitoes prey on bacteria and protists in the water column, the sarcophagid fly feeds on floating insects and rotifers, while midges and mites feed on decaying material at the bottom of the leaf. All this feeding has an effect on the microfaunal community (Addicott 1974, Heard 1994, Cochran-Stafira and Von Ende 1998, Bledzki and Ellison 1998, Kneitel and Miller 2002, Miller et al. 2002). Addicott (1974) identified a diverse microfaunal community with over 40 taxa of protists and rotifers living in pitcher plants in southern Michigan. The three most common microfauna in this study, other than bacteria, were a small flagellate *Bodo sp.*, a ciliate *Cyclidium sp.*, and a bdelloid rotifer *Habrotrocha rosa*. This aquatic community assembles in new leaves each year because old leaves typically do not retain water for more than 13 months.

In this thesis I present three field experiments that aim to explain how local and regional processed affect the population dynamics of pitcher plant microfauna. I start by studying the process of arthropod community assembly within pitcher plant leaves. Since it is known that pitcher plant arthropods affect the microfaunal community, factors affecting arthropod assembly will indirectly influence microfaunal population dynamics. In the first chapter I attempt to extend the current understanding of pitcher plant colonization by arthropods to a slightly broader spatial scale. Other studies have shown that leaf size affects colonization rates. I determine if the density of surrounding pitcher plants is also an important component of local community assembly. My objective was to determine if colonization rate was affected by a meso-scale factor (plant density).

Throughout the process of community assembly local interactions affect community composition. For example, Miller et al. (2002) found that predator and resource levels affected the establishment of several protists. After establishment, local interactions continue to affect community structure. A food web summarizes many of these interactions including competition, predation and omnivory (McCann and Hastings 1997). All populations are a part of a greater food web, and the dynamics of any focal population will depend on resources, predation and food web structure. Ecologists have long struggled with explaining how food webs affect the stability of populations and communities, a topic that is related to the question, 'How do species persist?' (Rosenzweig 1971, May 1974, Pimm 1991, Abrams and Roth 1994). In the second chapter, I study how food web structure affects the population stability of three aquatic microfauna: *Bodo sp.*, *Cyclidium*, and *H. rosa*. I manipulated predator and resource levels, and monitored the population dynamics of these protists within pitcher plant leaves during July and August. I could then test for the effects of community structure (level of predators, resources and the feeding activity of midges) on two measures of population stability, temporal variability and persistence.

A less studied area is how local processes affect regional dynamics. One important way that a local process could affect regional dynamics is by influencing population synchrony. Several models show that the regional stability (persistence) of a population decreases as the synchrony in local populations increases (Harrison and Quinn 1989, Gilpin and Hanski 1991, Heino et al. 1997). This occurs because the probability of all populations decreasing to low size at the same time increases. Two models have shown that synchrony can depend on the strength of density regulation (Lande et al. 1999, Kendall et al 2000), which in the logistic model is proportional to the maximum rate of increase (Beddington and May 1977, Lande et al. 1999). In the last chapter I test this prediction using populations of *Bodo sp.* living in pitcher plants. I estimated the maximum rate of increase from the time series at six study sites, and then determined if populations at sites with higher rates of increase tended to have less synchronous dynamics.

CHAPTER 2

Colonisation of pitcher plant leaves at several spatial scales

INTRODUCTION

Colonization is a fundamental process influencing species diversity and community structure (Hanski and Gilpin, 1997), though its importance relative to processes occurring within the community varies, depending on population structure, movement rates, and the rate of habitat turnover. Colonization is likely to be particularly important in temporary habitats, where communities must re-assemble frequently (Southwood, 1962; Roff, 1990; Denno et al., 1996). The arthropod communities within the leaves of the pitcher plant *Sarracenia purpurea* L. are temporary assemblages, re-assembling each year through colonization (individual leaves last 1 to 1½ years). Mosquitoes *Wyeomyia smithii* Coquillett, midges *Metriocnemus knabi* Coquillett, and sarcophagid flies *Blaesoxipha fletcheri* Aldrich colonies through oviposition by flying adult females. Midge larvae also crawl from leaf to leaf (Wiens, 1972; Paterson and Cameron, 1982). Mites *Sarraceniopus gibsoni* Nesbitt crawl between leaves, and may move much longer distances by phoresy (O'Connor, 1994). Abundance patterns of mosquitoes, midges, and sarcophagid flies in pitcher plant leaves are thus determined by colonization, modified by any mortality of the developing eggs and larvae, while mite numbers are also a function of within-leaf reproduction.

Oviposition decisions of pitcher-plant mosquitoes and midges may occur at several spatial scales. Fine-scale factors, including leaf size, presence/abundance of captured insects, conspecifics, or other taxa, influence oviposition by mosquitoes (Mogi and Mokry, 1980; Paterson and Cameron, 1982; Bradshaw, 1983; Istock et al., 1983; Heard, 1994c). Less is known about factors influencing the colonization patterns of midges, mites, and sarcophagid flies, though midges also appear to respond to leaf size (Paterson and Cameron, 1982; Nastase et al., 1995).

In the work reported here, the responses of pitcher plant arthropods to meso-scale (plant density) and fine-scale (leaf size, capture rate) factors, and the effect of interactions between spatial scales on colonization, were examined. Communities were allowed to assemble in the newly opening leaves of 40 1-m^2 quadrats, from which overwintering pitcher plant arthropods had been removed. Quadrats were nested within different areas (80 x 100 m zones) of a coastal bog, and were selected to encompass a large range of plant densities. It was found that the arthropods' response could be related to factors at fine and meso spatial scales, and that the response at the fine scale depended on a meso-scale pattern (plant density).

METHODS

The effects of meso- and fine-scale factors on colonization were evaluated using a stratified random design, in a coastal bog in eastern Canada (44°29'N, 63°32'W) in 1998. In spring, a transect parallel to the coast was divided into four zones (~ 80 x 100 m), with eight to 12 1-m^2 quadrats in each zone, for a total of 40 quadrats (Fig. 2.1). In each zone, points were selected randomly and the density of pitcher plants was measured. As density categories were filled, additional points were selected until all categories were filled. The abundance of pitcher plant arthropods prior to the manipulation was determined from samples of one leaf (the first or second leaf produced in the previous year) taken from each of a maximum of four plants per quadrat between 5 and 17 June. The rest of the overwintering community was then removed from all plants in the quadrat. The objective was to eliminate the possibility that emerging adults would simply move to the nearest pitcher and oviposit. Leaves were slit open, the contents were drained, and the inside of each leaf was rinsed with insecticidal soap. New leaves began to open in mid June and were colonized during the summer. Autumn samples, taken between 7 and 14 October, consisted of the first leaf produced during that year from up to five plants per quadrat, for a total of 146 leaves.

Arthropod abundance, leaf length, and the number of insect head capsules were determined in the laboratory. Leaves were measured (base of the petiole to tip of the leaf), and leaf contents were rinsed into a tray, filtered through an 85 mm Nitex mesh, and examined at 25x magnification. Complete counts were made for mosquitoes, midges, and head capsules, but mites were subsampled prior to counting due to high numbers. The circular Nitex mesh was divided into eight equal sections, and the mites in two opposite sections, along with those attached to the filtering apparatus, were counted. There was a tight relationship between subsampled and complete counts (linear regression, $y = 2.63x + 2.80$, $R^2 = 0.91$, $n = 75$). *Blaesoxipha fletcheri* larvae were not present in the leaves at the time of collection.

Colonization of leaves by crawling midge larvae was documented in 2000. On 13 July, the first leaf of the season was collected from each of 20 plants (two leaves from 10 random locations). On 3 August, the second leaf of the season was collected from 20 additional plants. The leaves in these two samples were open for a maximum of 26 and 24 days respectively, based on field opening dates. At 26° C and with 'sufficient food', development from egg to fourth instar takes 21-25 days (Wiens, 1972). Average temperatures at the site were much lower (16° C), so it was assumed that any fourth instar larvae present must have crawled from another leaf.

Statistical analyses

Correlations among oviposition cues and arthropod taxa were examined at a fine (leaf) and meso (quadrat) scale for each year.

Colonization patterns were modelled as a function of zone, pitcher plant density, leaf length, and the number of insect head capsules (an estimate of resource level). The order was chosen to correspond to the probable behaviour of a flying female insect looking for oviposition sites. Flying females within a zone were assumed to make meso-scale (evaluation of plant density) followed by fine-scale (evaluation of leaf size then leaf contents) oviposition decisions. Because quadrats were nested within zone, abundance was analysed using a generalized linear mixed model, assuming a Poisson distribution of errors, with quadrat within zone specified as a random effect. One quadrat was excluded from the analysis [plant density > four standard deviations from the mean (60 plants per m^2)]. Second-order polynomials for pitcher plant density, leaf length, and the number of insect head capsules were tested, and dropped because in all cases they were not significant. Abundance estimates of the other arthropod community members within a leaf were included in the model, as were two-way interactions with plant density, leaf length, and the number of head capsules. *F*-tests were calculated for fixed effects using the Wald statistic (Little et al., 1996). Variation in the denominator degrees of freedom are due to adjustments made by SAS for matrices not being full rank. As a consequence of the controlled entry of variables into the models of arthropod incidence and abundance, reported F-tests are order dependent. These analyses were conducted in SAS using GLIMMIX version 8 (SAS Institute Inc., 2000)

RESULTS

Correlations among oviposition cues and among arthropod taxa

Correlations among the ovipositional cues, local plant density, leaf length, and resource availability, and the three arthropod taxa, were conducted:

(1) To determine whether, by choosing to oviposit in areas with high plant densities or in longer leaves, arthropods were indirectly selecting habitats with higher capture rates. It was found that plant density was not correlated with resources in the spring ($r = -0.05$, $P = 0.57$, $n = 121$) or autumn ($r = -0.12$, $P = 0.14$, $n = 146$). Leaf length, however, was a good indicator of resource availability; longer leaves captured more insects in both spring and autumn ($r = 0.35$ and 0.41, both $P < 0.001$, $n = 121$ and 146).

(2) To determine whether local plant density was correlated with leaf length, producing a possibly spurious relationship between plant density and oviposition. Leaf length was not related to plant density in spring ($r = 0.10$, $P = 0.27$, $n = 121$) or autumn ($r = 0.06$, $P = 0.44$, $n = 146$).

(3) To determine whether species associations (at leaf and quadrat scales) were consistent from spring to autumn. Mosquitoes and midges were correlated positively at the leaf scale in both spring ($P < 0.01$) and autumn ($P < 0.05$), but at the quadrat scale only in spring ($P = 0.01$). Midges and mites were correlated at both spatial scales, but only in the autumn ($P < 0.001$). Correlations between mosquitoes and mites were present only for leaves in the autumn ($P = 0.001$);

(4) To determine whether quadrats had similar arthropod abundance, leaf lengths, and resources in spring and autumn. Only mosquitoes showed a positive correlation between years ($r = 0.60$, $P < 0.001$, $n = 40$). The same quadrats tended to have longer leaves in both seasons ($r = 0.71$, $P < 0.001$, $n = 40$) but capture rates were uncorrelated ($r = 0.19$, $P = 0.25$, $n = 40$).

Factors influencing arthropod abundances

Mean abundances (+ SE) of pitcher plant arthropods for the spring (overwintering) and autumn were 1.3 + 0.3 and 1.5 + 0.3 mosquitoes, 13.7 + 1.2 and 8.8

+ 1.4 midges, 36.7 + 6.1 and 57.5 + 9.5 mites. Despite the positive associations among taxa, responses to oviposition cues were quite different for the three arthropods (Tables 2.1 and 2.2).

Overwintering leaves

The abundance of overwintering mosquitoes was affected most strongly by plant density and leaf length (Table 2.1). Abundances also varied with zone (lowest in zone 2) (Figs 2.1 and 2.2), and increased with plant density and leaf length (Table 2.1). Although the coefficients for plant density and leaf length are negative in Table 2.1, both relationships were positive after accounting for interactions. Mosquitoes were associated negatively with resource levels, but only for shorter leaves and lower plant densities (interaction terms). Mosquito abundances were not related to midge or mite abundances after other effects were removed. Overwintering midge abundances increased strongly with leaf length (Table 2.1). There were no direct effects of zone or plant density (Fig. 2.2), and the positive effects of resources were only seen at lower plant densities (interaction term). Midges were also more abundant in pitchers where mites were abundant. Overwintering mites showed the weakest relationships to all cues (Table 2.1). The principal effect, higher abundances in longer leaves, was limited to high plant densities (interaction). Mites were also more abundant where midges were abundant.

In summary, leaf length was an important factor explaining the variation among leaves in the overwintering abundance of mosquitoes, midges, and mites. Plant density modified the response to leaf length and/or resource level for all three taxa.

Autumn leaves

Mosquito abundance increased with both leaf length and resources in the autumn but did not vary significantly with zone or plant density (Table 2.2, Fig. 2.2). The positive effect of resources decreased with plant density, however (interaction). As in the spring, midges were more abundant in longer leaves but autumn abundances also increased with resources and plant density (Table 2.2, Fig. 2.2). Midge numbers did not vary among zones. The positive effect of leaf length was strongest at low plant densities and low resource levels (interaction terms). Midge abundances increased with mite numbers. Most of the variation in autumn numbers of mites was related to leaf length and resource level; mite numbers were highest in longer leaves with more head capsules (Table 2.2).

Higher plant densities increased the positive response of mites to resource availability. Mite numbers increased with midge and mosquito abundances.

Table 2.1. Effects of oviposition cues on the abundance of arthropods inhabiting pitcher plant leaves in the spring sample (overwintering generation, $n = 117$). Arthropod abundance was analysed using a generalized linear mixed model. Models assumed a Poisson distribution of errors, and specified quadrat within zone as a random effect. Variables were entered into the model in the order presented; consequently the reported F-tests are order dependent. F-tests were calculated using the Wald statistic. *N.d.f.* = numerator degrees of freedom. *D.d.f.* = denominator degrees of freedom.

Species	Variable	Coefficients	*N.d.f.*	*D.d.f.*	F value	$P > F$
Mosquitoes	Quadrat (zone) = 0.47, overdispersion parameter = 1.95					
	Zone		3	34	3.31	0.03
	Plant density	-0.029	1	71	12.18	0.001
	Leaf length	-0.004	1	71	17.39	0.001
	Head capsules	-0.128	1	71	2.96	0.09
	Midge	0.028	1	71	2.27	0.14
	Mite	-0.0006	1	71	0.05	0.82
	Plant density x leaf length	0.0004	1	71	0.52	0.47
	Plant density x head capsules	0.004	1	71	4.82	0.03
	Leaf length x head capsules	0.0006	1	71	4.92	0.03

Table 2.1. Continued.

Species	Variable	Coefficients	*N.d.f.*	*D.d.f.*	*F* value	*P* > *F*
Midges	Quadrat (zone) = 0.21, overdispersion parameter = 7.32					
	Zone		3	34	1.16	0.34
	Plant density	0.049	1	71	1.29	0.26
	Leaf length	0.014	1	71	24.20	0.001
	Head capsules	0.055	1	71	1.47	0.23
	Mosquito	0.023	1	71	0.19	0.66
	Mite	0.002	1	71	4.13	0.04
	Plant density x leaf length	0.00004	1	71	0.01	0.93
	Plant density x head capsules	-0.002	1	71	5.54	0.02
	Leaf length x head capsules	-0.0002	1	71	2.82	0.10

Table 2.1. Continued.

Species	Variable	Coefficients	*N.d.f.*	*D.d.f.*	*F* value	*P* > *F*
Mites	Quadrat (zone) = 0.24, overdispersion parameter = 63.82					
	Zone		3	35	1.20	0.32
	Plant density	-0.20	1	70	0.30	0.58
	Leaf length	-0.008	1	70	3.32	0.07
	Head capsules	0.022	1	70	3.43	0.07
	Midge	0.021	1	70	3.86	0.05
	Mosquito	-0.034	1	70	0.02	0.88
	Plant density x leaf length	0.002	1	70	8.57	0.005
	Plant density x head capsules	0.0003	1	70	0.06	0.81
	Leaf length x head capsules	-0.00008	1	70	0.19	0.66

Table 2.2. Effects of oviposition cues on the abundance of arthropods inhabiting pitcher plant leaves in the autumn (n = 141). Arthropod abundance was analysed using a generalized linear mixed model. Models assumed a Poisson distribution of errors, and specified quadrat within zone as a random effect. Variables were entered into the model in the order presented; consequently the reported F-tests are order dependent. F-tests were calculated using the Wald statistic. *N.d.f.* = numerator degrees of freedom. *D.d.f.* = denominator degrees of freedom.

Species	Variable	Coefficients	*N.d.f.*	*D.d.f.*	*F* value	*P* > *F*
Mosquitoes	Quadrat (zone) = 2.26, overdispersion parameter = 1.76					
	Zone		3	35	2.47	0.08
	Plant density	0.148	1	94	0.00	0.96
	Leaf length	0.023	1	94	26.16	0.001
	Head capsules	0.110	1	94	30.51	0.001
	Midge	0.010	1	94	0.62	0.43
	Mite	0.0008	1	94	0.43	0.51
	Plant density x leaf length	-0.00003	1	94	0.42	0.52
	Plant density x head capsules	-0.004	1	94	5.30	0.02
	Leaf length x head capsules	-0.0002	1	94	0.22	0.64

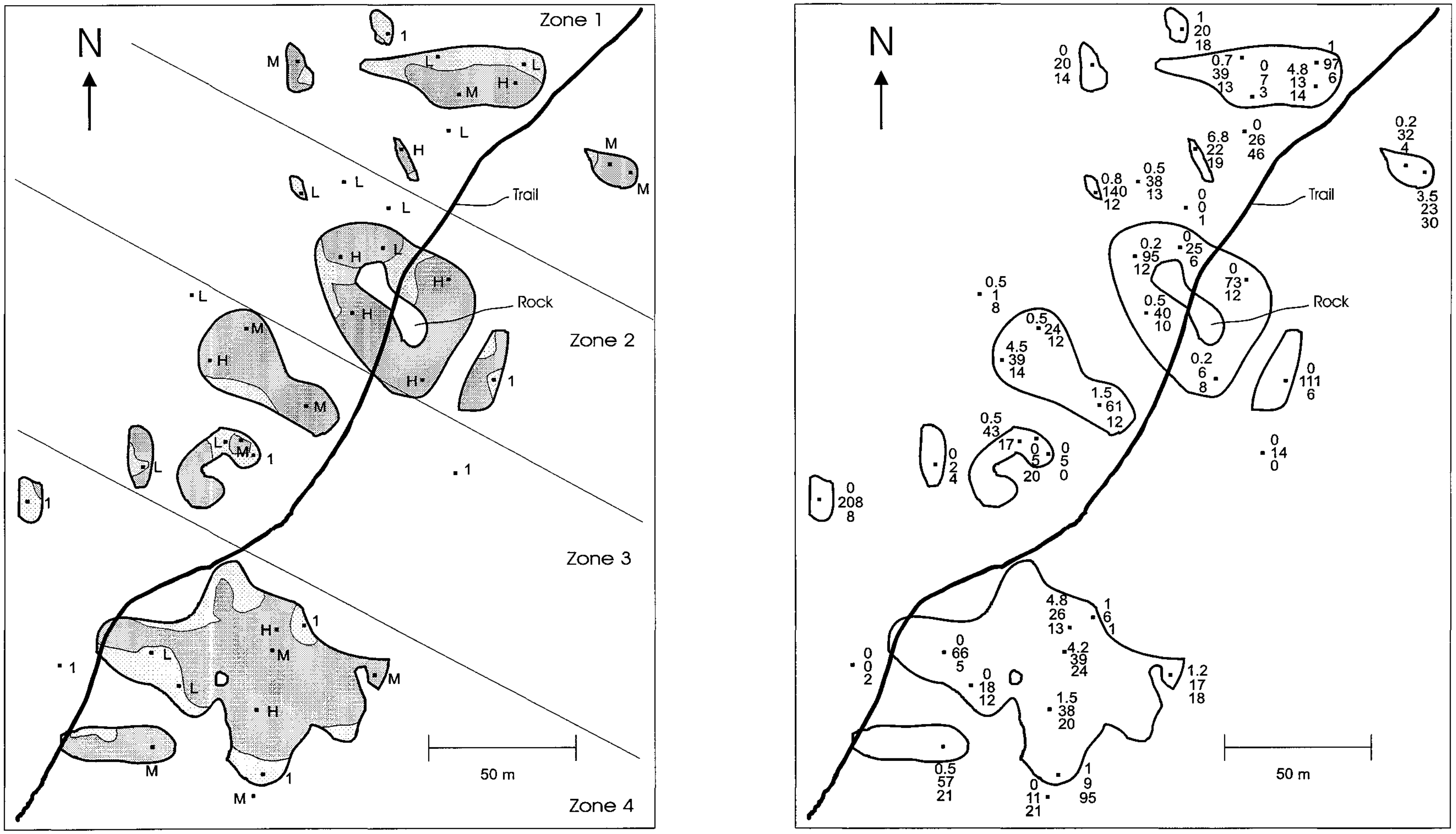
Table 2.2. Continued.

Species	Variable	Coefficients	*N.d.f.*	*D.d.f.*	*F* value	*P* > *F*
Midges	Quadrat (zone) = 0.92, overdispersion parameter = 4.08					
	Zone		3	34	0.28	0.84
	Plant density	0.177	1	95	4.65	0.03
	Leaf length	0.031	1	95	46.79	0.001
	Head capsules	0.113	1	95	34.24	0.001
	Mosquito	0.048	1	95	0.86	0.35
	Mite	0.002	1	95	19.15	0.001
	Plant density x leaf length	-0.001	1	95	15.55	0.001
	Plant density x head capsules	-0.001	1	95	3.19	0.08
	Leaf length x head capsules	-0.0006	1	95	8.39	0.005

Table 2.2. Continued.

Species	Variable	Coefficients	*N.d.f.*	*D.d.f.*	*F* value	*P* > *F*
Mites	Quadrat (zone) = 0.47, overdispersion parameter = 59.93					
	Zone		3	34	0.23	0.87
	Plant density	-0.035	1	95	1.65	0.20
	Leaf length	0.025	1	95	37.51	0.001
	Head capsules	0.085	1	95	28.68	0.001
	Midge	0.018	1	95	7.05	0.009
	Mosquito	0.078	1	95	3.83	0.05
	Plant density x leaf length	-0.0002	1	95	0.49	0.49
	Plant density x head capsules	0.003	1	95	4.27	0.04
	Leaf length x head capsules	-0.0008	1	95	7.92	0.006

Figure 2.1. Map of study site, located at Duncan's Cove, Nova Scotia, Canada, showing location of experimental quadrats and zones. Patches containing quadrats were mapped. Patch edges were defined by the absence of pitcher plants for a minimum of 3 m. Shading indicates larger regions of low (< 6 plants per m^2 ▒) and high (≥ 6 plants per m^2 ▓) plant densities. (a) Pitcher plant densities are shown as one plant (1), two to six plants (L), seven to 12 plants (M), and > 12 plants per m^2 (H). (b) Mean abundances of mosquitoes, midges, and mites (labelled from top to bottom next to quadrat) in pitcher plant leaves prior to manipulation (spring sample).


(a) Leaf density

(b) Spring arthropod abundance

Figure 2.1

Figure 2.2. The effects of zone and plant density on the abundance of mosquitoes, midges, and mites in pitcher plant leaves in the spring (no shading) and autumn (▨). Mean ± 1 SE. Pitcher plant density categories are one plant (One), two to six plants (Low), seven to 12 plants (Medium), and > 12 plants per m^2 (High).

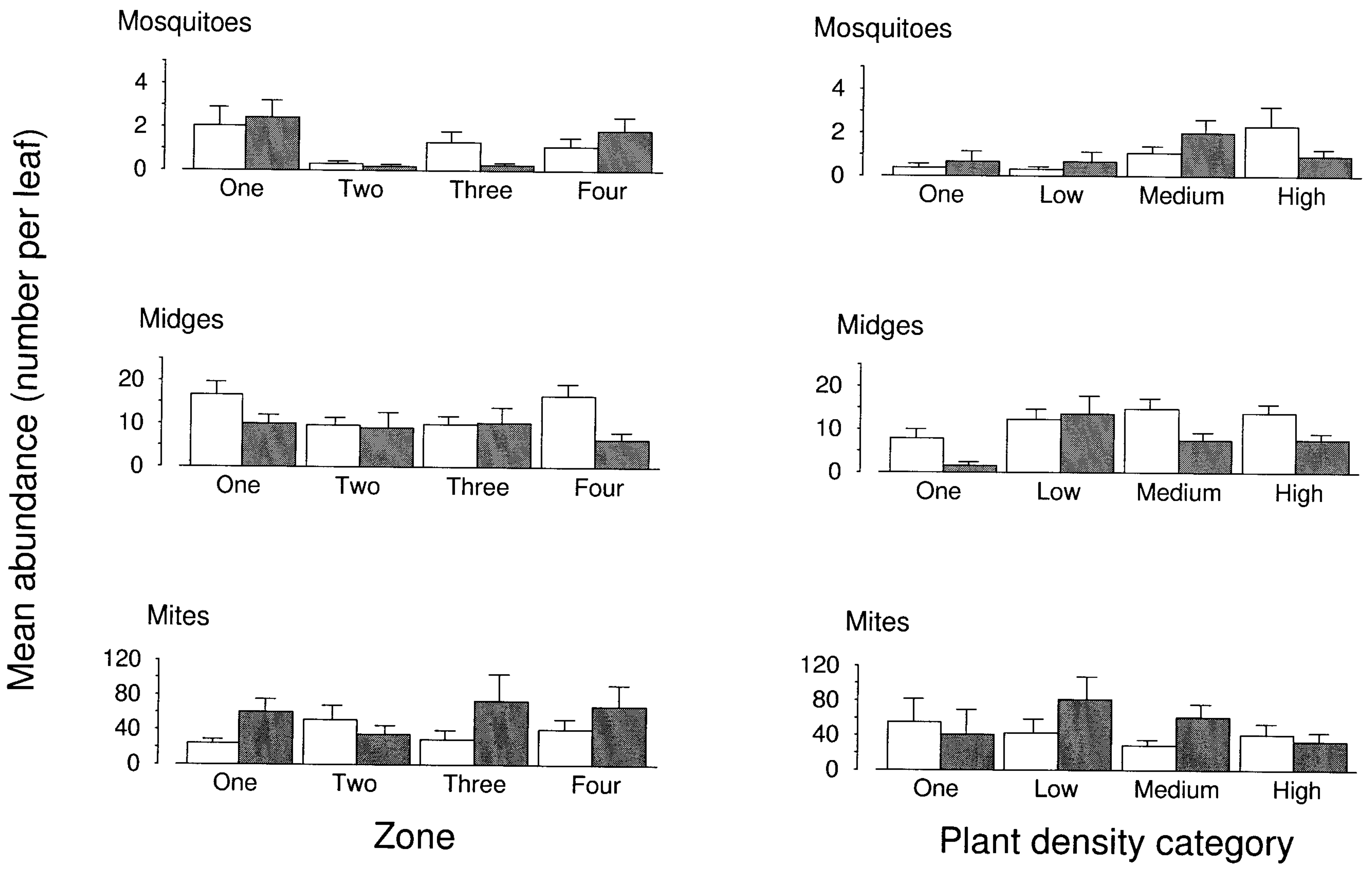

Mean abundance (number per leaf)
Mosquitoes
4
2
0
One
Two
Three
Four
Midges
20
10
0
One
Two
Three
Four
Mites
120
80
40
0
One
Two
Three
Four
Zone
Mosquitoes
4
2
0
One
Low
Medium
High
Midges
20
10
0
One
Low
Medium
High
Mites
120
80
40
0
One
Low
Medium
High
Plant density category

Figure 2.2

In summary, mosquitoes had a weaker association with meso-scale factors (plant density and zone) and a stronger association with resource availability in the autumn than in the spring. The relationship with resource availability was modified by plant density in both seasons (strongest at low densities). Autumn midge numbers but not spring midge numbers were related to plant density. Leaf length remained an important factor but response to resource availability was stronger in the autumn.

Colonization by midge larvae

Midge larvae also colonized leaves by crawling. Fourth-instar larvae were found in the first leaf (4/20 plants) and in the second leaf (2/20 plants) (two larvae per leaf in one case, otherwise one per leaf). Given that the leaves collected were < 26 days old and that the average temperature at this time in the study region is approximately16° C, these midges could not have developed within these leaves and must have arrived by crawling.

DISCUSSION

The key finding of this study is that meso-scale factors, density of plants, and zone within bog can influence habitat selection by pitcher plant arthropods at finer scales. Selection is probably influenced first by broad spatial features, e.g. proximity to forest edges (Miner and Taylor, 2002), and meso-scale factors, e.g. variation in plant density and in physical features such as granite outcroppings and shrubs that probably influence flight patterns. High rocks or bushes that serve as foci for mating, and nectar-producing plants that serve as food sources for feeding adults, influence oviposition patterns for other mosquito species (Nielsen and Nielsen, 1953; Smith and Gadawski, 1994; Renshaw et al., 1995; Service, 1997). Ultimate oviposition decisions clearly depend on fine-scale factors (leaf length and capture rate) (Mogi and Mokry, 1980; Naeem, 1988; Heard, 1994c; Nastase et al., 1995; this study). The abundance of pitcher plant arthropods also varies among bogs (Heard, 1994a; Harvey and Miller, 1996; Miner and Taylor, 2002), but these patterns are more likely the result of differential reproduction/survival than choices made by individual females.

Patterns in the two successive communities examined (the spring overwintering and the autumn assemblages) were the product of colonization, modified by egg and/or larval mortality. The two communities differ in two respects, over-winter mortality influenced spring patterns, and the local (1 m^2) pool of colonists was eliminated for the autumn sample. Summer mortality of mosquitoes and midges was probably low, as seen in other studies (Judd, 1959; Paterson and Cameron, 1982; Heard, 1994b). Over-winter mortality probably depends on snow cover, but was estimated at 3 to 5% in a neighbouring province (Paterson, 1971). Quadrats were cleared of overwintering individuals, so that patterns of assembly would be influenced less by what had previously been occupying the pitchers of the target plants.

Effects of fine- and meso-scale factors

Arthropods responded to both fine-scale factors; all taxa were more abundant in longer leaves and, in addition, numbers increased with resources in the autumn sample. It has been suggested that larger leaves are selected because they tend to capture more insects (Wolf, 1981; Naeem, 1988; Cresswell, 1993; Heard, 1998). Independent effects of resource availability have not been detected previously (Nastase et al., 1995; Naeem, 1988), perhaps because the effect depends on plant density (see below). Stronger and more consistent responses were seen in the autumn, suggesting that oviposition decisions rather than subsequent mortality produced the patterns. In the spring, abundances were unrelated to resources, suggesting higher over-winter mortality in leaves with high resource levels or, alternatively, that the number of insect head capsules present in the spring is a less reliable indicator of resource levels (Heard, 1998).

The responses by mosquitoes and midges to leaf length and resource level were modified by plant density in both the spring and autumn samples; the response to fine-scale factors depended on the meso-scale context. Weaker responses at high plant densities indicate less selectivity where there are many plants close together.

Mosquito abundance varied with plant density and zone within the bog in the spring but not in the autumn. Spring patterns include the effects of overwintering mortality, which may be higher in more exposed areas or where plant densities are low. Lower mortality in areas of high plant density might also explain the lack of selectivity with respect to fine-scale factors in these areas. Differences in patterns could simply reflect year-to-year variation, but the strong tendency for mosquitoes to choose the same quadrats in both samples makes this seem less likely. In contrast, autumn abundances of midges were higher where pitcher plant densities were high, suggesting an ovipositional response. The relationship was not present in spring, suggesting either a variable response to plant density (perhaps over-ridden in some years by other oviposition cues) or density-dependent mortality during the winter that removes the relationship with plant density.

Species interactions

Species interactions may affect community structure, even in temporary habitats where colonization patterns dominate, by influencing oviposition decisions, growth, and survivorship. Pitcher plant arthropods were not manipulated in this study, but the patterns observed are largely in concordance with those reported in other studies. Densities of mosquitoes and midges were correlated positively, as others have found (Bradshaw, 1983; Heard, 1994b, Miner and Taylor, 2002), but were uncorrelated after the effects of common oviposition cues were removed. The stronger midge-mosquito association in the spring suggests that midges might enhance the overwintering survivorship of mosquitoes.

There was a strong, positive association between midges and mites even after the effects of plant density, leaf length, and capture rate were removed. Two plausible explanations are phoresy and facilitation. Mites have not been observed moving with adult midges (O'Connor, 1994), but larval midges crawling between leaves have not been examined, and are a possible avenue for phoresy. Mites could also benefit from the shredding activity of midges in the same way that mosquitoes do, although work with mites and midges in the California pitcher plant suggests competitive interactions at high densities (Naeem, 1988).

Conclusion

Mechanisms occurring at several spatial scales interact over time to influence arthropod community assembly in pitcher plants. As leaves open in June, mosquitoes emerge and choose oviposition sites based on leaf length and resource level, with selectivity highest in areas with few pitcher plants. Late-instar midges crawl from old, decaying leaves to newly opened leaves at this time, perhaps bringing mites with them. During the summer, leaves capture insects and later (July and August) adult female midges tend to oviposit where plant densities are high, and in large leaves with high resource levels. Again, selectivity at fine spatial scales is highest where pitcher plants are sparse. Autumn and winter mortality produces a positive relationship between mosquitoes and meso-scale factors (plant density and zone) but removes the relationship between midge and plant density. In sum, in temporary habitats, habitat selection in response to cues at several spatial scales produces an assembly of species; species interactions and subsequent mortality then modify community structure, with midges playing a central role in pitcher plants.

CHAPTER 3

Stability of pitcher-plant microfaunal populations depends on food web structure

INTRODUCTION

The relative importance of top-down vs. bottom-up effects and the related question of the prevalence of trophic cascades is a topic of some debate (Power 1992, Strong 1992, Schmitz et al. 2000). An early mathematical model predicted that increasing the carrying capacity of the basal species in a 2-species system would be destabilizing, leading to the extinction of one or both species (the paradox of enrichment; Rosenzweig 1971). Similar results have been obtained with three trophic levels; the top predator level can be destabilized by increasing the carrying capacity of the basal species (Abrams and Roth 1994). Recently it has been shown that this result can be reversed if increases to the basal trophic level are modelled as an influx of an allochthonous resource (Huxel and McCann 1998), though the particulars of the predictions depend on consumer preferences. Thus, current models suggest that bottom-up effects can have positive or negative effects on stability, and that resource heterogeneity influences the outcome.

The consequences of top-down effects for stability and trophic cascades in food web models also depend on how predation is represented. Early predator-prey models suggested that predation could be stabilizing if functional responses were accelerating, if predators aggregated their efforts in space, or if they switch to feed on relatively more abundant prey (Murdoch and Oaten 1975, Hassell 1978). Generalist predation can be stabilizing (Murdoch and Oaten 1975, Holt and Lawton 1994) or destabilizing (Murdoch and Bence 1987) depending on feeding preference and generation time. Omnivory was first found to be destabilizing (May 1974, Pimm and Lawton 1978), but moderate levels can be stabilizing if predators are not too efficient at consuming the basal species (McCann and Hastings 1997). The effects of top-predators can cascade down through food chains (Hairston et al. 1960, Oksanen et al. 1981), though the strength of the cascade depends on resource heterogeneity and edibility, as well as prey preference (Leibold 1989, Huxel and McCann 1998, McCann et al. 1998a).

Empirical tests in aquatic systems have shown that many communities do not conform to the predictions of the paradox of enrichment. For example, increased exposure to light (higher carrying capacity) did not destabilize a stream community (Nisbet et al. 1997), and addition of nutrients does not appear to destabilize phytoplankton – *Daphnia* interactions in natural or semi-natural situations (McAllister et al. 1972, Watson et al. 1992, McCauley et al. 1999). Generalist aquatic predators are often destabilizing, causing local extinctions (Murdoch and Bence 1987). Trophic cascades are common in aquatic systems (Carpenter and Kitchell 1993, Cottingham and Schindler 2000), though exceptions exist (Brett and Goldman 1996).

Pitcher plant (*Sarracenia purpurea*) leaves contain small aquatic communities. The top trophic level consists of omnivorous mosquito larvae, which feed on microfauna (rotifers and protists) as well as on bacteria. The microfauna feed on the bacteria (basal species). The supply of bacteria is affected by resources (insects captured by the plant), and decomposition rates (influenced by the abundance of shredding midges) (Bradshaw and Holzapfel 1986, Naeem 1988, Heard 1994). Variation in colonization produces variation in community composition, which could lead to variation in the impacts of top-down factors and bottom-up factors. Previous studies have shown significant, though sometimes contradictory top-down and bottom-up effects on abundance and species diversity (Addicott 1974, Cochran-Stafira and Von Ende 1998, Kneitel and Miller 2002). In this study I manipulated resources and predators in a system open to colonization, and examined how top-down and bottom-up factors influenced microfaunal and bacterial stability. Specifically, I wanted to determine if the microfaunal populations were stabilized or destabilized by (1) enrichment (increased resources) or (2) an omnivorous predator.

METHODS

I manipulated resource level and mosquito density in the newly-opened leaves of 60 pitcher plants a coastal bog in eastern Canada (44°29'N, 63°32'W), and monitored, *in situ*, the densities of three microfaunal taxa over a period of two months. At the end of the season I collected the leaves and counted the arthropods present. I then tested for the effects of resources and predators on microfaunal abundance and stability (persistence and temporal variability).

Experimental manipulations

In the spring of 1999 (17 – 18 May), I marked 120 plants along two transects in the study area. Each transect was divided into three zones (approx. 80 m x 80 m), and 20 locations were randomly selected in each zone. Study leaves were the first 10 leaves to open within each zone.

My experiment consisted of two crossed factors, resource addition (3 levels) and predator addition (3 levels). I randomly assigned the ten leaves in each zone to one of the nine treatment categories, with the unmanipulated category replicated twice ($n = 60$). I manipulated resources by adding 0, 1 or 2, dead harvester ants (*Pogonomyrmex*, Wards biology) bi-weekly through the experiment. Ants were microwaved for 2 minutes to reduce the addition of bacteria to manipulated leaves. On 9 and 11 August (after the peak period of mosquito oviposition), I collected larvae for the mosquito manipulations. I combined the larvae from 100 leaves and gently transferred them through 3 baths of deionised water to reduce the associated transfer of protozoa. I then placed groups of 5 larvae in vials, along with 2 ml of water from the last bath. On 12 August I added 5 or 10 larvae to the appropriate leaves, and 2 ml of bath water without mosquitoes to control leaves.

Assessing abundance

I monitored microfaunal abundances by collecting water samples from each leaf twice a week from 2 June until 2 Sept. For each leaf, I first measured water level by inserting a 10 mm wide wooden stick, and then used a micropipetter to remove 3 water samples (170 μL) from mid-way between the water surface and the bottom, touching the edge of the leaf with the tip. Pipette tips were changed between samples. An effort was made to avoid stirring or disturbing the contents of the leaf while taking samples. I returned any captured mosquitoes and midges to the leaf and replaced the liquid removed with distilled water. Samples were preserved with 10 μL $HgCl_2$, and refrigerated until analysed. If water depth was less than 20 mm, I attempted to reduce the potential impact of my sampling on microfaunal abundances by taking fewer samples: depth < 5 mm: no sample, 5 – 10 mm: 1 sample, 11 – 20 mm: 2 samples.

I counted the three dominant taxa in the microfaunal assemblage, *Bodo sp.*, a small flagellate (8 – 10 μm), *Cyclidium sp.,* a ciliate (25 – 30 μm), and *Habrotrocha rosa*, a bdelloid rotifer (usually > 150 μm). These taxa have been the focus of other studies (Cochran-Stafira and Von Ende 1998, Bledzki and Ellison 1998, Kneitel and Miller 2002). *'Bodo'* was probably several species of heterotrophic flagellates, but the consistency of temporal counts suggests that the taxon was dominated by one to a few species.

Densities were frequently low, and I therefore concentrated samples (170 μL liquid from the leaf plus 10 μL $HgCl_2$ preservative) prior to counting. I centrifuged each sample lightly (500 g for 10 minutes), and then removed the top 145 μL (80%). I re-suspended the remaining 35 μL, and loaded a hemocytometer with two 10 μL drops. For each drop, I scanned 0.016 μL (4 small squares) at 400× for *Bodo*, and 0.9 μL (9 large squares) at 100× for *Cyclidium* and *H. rosa*.

I examined the effectiveness of my centrifuging technique using a lab culture of *Clamydomonas reinhardtii*, testing a range of densities comparable to those observed in the field (10^2 - 10^5 / mL). I compared density estimates from pre- and post-centrifugation, using ten 500 μL samples from the stock culture and from each of four dilutions (1:5, 1:10, 1:25, 1:100). Samples were processed and counted as above, except that I removed a larger proportion of the water (90 vs. 80%). On average, centrifuged samples produced density estimates that were 15% lower than uncentrifuged samples (log values). Centrifuging reduced the variation among replicate samples (at densities of 500 / mL, CV's were 0.3 and 1.0 for centrifuged and uncentrifuged samples respectively). Detection limits were well below 100/mL; at this density only one out of 10 samples had zero individuals.

I estimated microfaunal abundance (no. per leaf) by multiplying the densities (obtained from the counts above) by the volume of water in the leaf. Water volume was estimated for each leaf using a regression model that I obtained by adding known volumes of water (*vol*) at 5mL increments to a set of 50 leaves. I measured water depth (*h*), leaf length from petiole to the tip of the hood (*L*), and diameter at the widest point (*d*), often just below the pitcher lip. My best predictive model did not include leaf length, but included a quadratic term for water depth:

$$vol = 0.2619\,h + 0.004252\,h^2 + 0.1511\,d - 6.28 \quad (r^2 = 0.89)$$

This model slightly underestimated water volume (1.8 mL for 2 mL) and (32.8 mL for 35mL).

I began recording bacterial densities on 12 Aug, when I manipulated mosquitoes. I did rough counts at 400× in the samples scanned for *Bodo*, and then used five density categories: none, low, medium, high, and extremely high (0, 1-5, 6-99, 100-500, >500 cells per 0.004 μL).

I collected all 60 leaves at the end of the experiment. After leaf measurements (length, maximum diameter), I (1) rinsed contents into a tray, (2) dissected the leaf with two longitudinal cuts and rinsed again, and (3) filtered contents through an 85μm Nitex mesh. I examined the contents retained on the mesh at 25× power, counting mosquitoes, midges, mites, and head capsules of other arthropods. Sarcophagid larvae (*B. fletcheri*) were not present at this time, but I noted their presence in four pitchers during the course of the experiment.

Statistical analysis

I tested the effects of resource level and predator abundance on mean abundance, persistence and temporal variability of the three microfaunal taxa. I had 60 time series for each taxon, consisting of 20 sampling dates over a period of 64 days. For estimates of mean abundance and temporal variability, I divided the time series into two parts, pre- and post-mosquito manipulation. For each taxon in each leaf, I then calculated mean abundance and the coefficient of variation (CV) over 40 (pre) and 22 (post) days. I defined population persistence as the maximum time period (in days) over which consecutive non-zero counts were obtained (using the entire time series). I recorded a failure to persist after three consecutive zero counts (10 to 11 days), indicating either extinction or densities consistently below my detection level. my detection limits were 343 individuals per mL for *Bodo*, and 3.3 per mL for *Cyclidium* and *H. rosa*.

To test for effects on population dynamics (abundance, CV, persistence), I modelled the variation in these variables as a function of (1) variation in the covariates (a) mosquito colonization, (b) midge colonization and (c) insect capture rate, (2) resource and predator treatments, and (3) abundance of other microfaunal taxa. Covariates not a part of my experimental design were entered first (spatial effects (zone) and effects of colonization (mosquito, midge and capture rate covariates)). The idea was to remove the effects of other possibly confounding or correlated factors prior to testing for the effects of the experimental manipulations. I then entered treatment effects, and finally, abundances of other microfauna. Zone was dropped if it did not explain a significant proportion of the variation ($\alpha = 0.10$). I tested other possible orders, but order of entry made little quantitative difference, and no difference to any conclusions drawn.

Covariates were estimated as follows: Colonization by mosquitoes was the deviation from expected mosquito densities based on manipulations. In a few cases there were fewer mosquitoes than expected, due presumably to mortality. I classified leaves as those with (i) mortality (fewer mosquitoes than expected), (ii) little colonization or mortality (0 to 2 'extra' mosquitoes or (iii) significant colonization (3 or more 'extra' mosquitoes). Natural capture rates were calculated as the difference between the observed and expected number of head capsules. Midge colonization was simply the number of larvae found at the end of the experiment. Midge colonization and natural capture rates were entered as continuous variables.

Mean abundance and persistence followed an extra-Poisson distribution with many small values and a few large values. I therefore used a log-transformation, substituting 1/6 of the lowest non-zero value for zeroes in the analysis of abundance. Estimates of temporal variability (CV) tended to follow a Gaussian distribution; I used the raw estimates and assumed a Gaussian error distribution for these analyses. *F*-tests on deviances, scaled by their degrees of freedom, were used to assess the significance of explanatory variables (Venables and Ripley 1999).

Two leaves with aberrant mosquito densities were excluded from all analyses (a leaf with 0 mosquitoes should have had 10, and one with 15 should have had 0). One model (*H. rosa* CV post-manipulation) was sensitive to the inclusion of a leaf with uncommonly high midge densities (88 when next highest was 65); it was therefore excluded from this analysis. Diameter was not obtained for three leaves, and thus these were excluded from analyses of abundance and variability. Occupied leaves were used for analyses of CV and persistence. Interactions were not entered into analyses of CV for *Cyclidium* and *H. rosa* because of low sample size.

RESULTS

The microflagellate, *Bodo*, was both the most abundant and the most widely distributed of the three microfaunal taxa, occurring in all of the leaves examined. The ciliate, *Cyclidium*, and the rotifer, *H. rosa*, were found in 45% and 73% of the leaves respectively (Table 3.1). *Bodo* populations were also the most persistent and least variable over time (Table 3.1). Leaves included in this study were from 87 to 189 mm in length (mean ± std) 129 mm ± 19 from petiole to tip) and from 18 to 40 mm in diameter (mean 27 mm ± 5). An average of 24 ± 17 midges (range 0 to 88), and 113 ± 80 mites (range 14 to 450) were present at the end of the experiment.

Effects on abundance

Abundance of *Cyclidium* increased with resources (ant treatment), and was negatively related to *Bodo* abundance (Table 3.2). Abundance of *H. rosa* was lower in leaves with colonizing mosquitoes, before and after mosquitoes were manipulated (Table 3.2, Figs 3.1 and 3.2). In addition, *H. rosa* abundances were positively associated with *Bodo* numbers in the pre-manipulation period. *Bodo* abundances were influenced by predators and by colonizing midges (Table 3.2). In the pre-manipulation period, *Bodo* abundances were lower where mosquitoes tended to colonize and higher where midge abundances were high (Fig 3.1). There was also a tendency for a negative association with *Cyclidium* ($P = 0.06$). Post-manipulation, *Bodo* abundances were lower in the high mosquito treatment leaves, and higher in leaves with many midges (Fig 3.1).

Bacterial abundance was positively related to the number of midges ($P = 0.004$). There may have been a weak negative association between mosquito treatment and bacteria ($P = 0.08$).

Effects on temporal variability and persistence

Cyclidium had the lowest persistence times and highest temporal variability, on average, of the three microfaunal taxa (Table 3.1). However, neither measure of stability was significantly related to resources, predation or any of the covariates.

Colonizing mosquitoes increased the CV of *H. rosa* in the pre-manipulation period (Table 3.3, Fig 3.3), but had no effect after mosquitoes were manipulated. However, resources (ant additions) increased the CV of *H. rosa* populations during this period (Table 3.3, Fig 3.3). Both predation and resources also affected the persistence of *H. rosa* (Table 3.4). The strongest effect was a marked reduction in persistence (from an average of 16 days to 4 days) due to colonizing mosquitoes (Fig 3.3). Higher resources (ant treatment) also tended to reduce persistence, but this effect was only seen where mosquitoes were rare or absent (zero mosquito treatment, low colonization) (Fig 3.3). Where mosquitoes were more abundant, increasing resources increased persistence of *H. rosa*.

Colonizing mosquitoes increased temporal variability for *Bodo* populations prior to the mosquito manipulation (Fig 3.4), but predation had no effect on CV for *Bodo* in the post-manipulation period (Table 3.3). Predation decreased, and midges increased persistence times for *Bodo* populations (Table 3.4, Fig 3.4).

Table 3.1. Mean abundance and stability for the 60 study populations of *Bodo*, *Cyclidium*, and *H. rosa*. Incidence is proportion of leaves occupied by taxon. Mean density is no. per mL and mean abundance is no. per leaf. Temporal variability is CV calculated over sampling dates and persistence is the interval (in days) with consecutive non-zero counts. Summary statistics were calculated for each leaf, and then averaged across leaves. Temporal variability and persistence were calculated only for occupied leaves.

	Bodo	***Cyclidium***	***H. rosa***
Incidence	1.0	0.45	0.73
Density (SE)	9.24×10^4 (1.4×10^4)	145 (50.7)	22.5 (5.05)
Abundance (SE)	7.40×10^5 (1.3×10^5)	959 (301)	243 (54.5)
Temporal variability (SE)	1.77 (0.06)	3.38 (0.13)	2.61 (0.15)
Persistence (SE)	43.9 (2.1)	6.81 (1.22)	14.45 (2.10)

Table 3.2. Results of models testing for effects of resource and predator manipulations (Ant trt, Mosq trt) on abundance of microfauna for the pre- and post-mosquito manipulation periods. Covariates were mosquito colonization (Mosq col), natural resource capture rates (Capture), # midges and abundance of other microfauna.

Pre-manipulation

Taxon: ***Cyclidium***	Df	SS	F Value	Pr(F)
NULL	54	516.42		
Mosq col	2	10.08	0.63	0.54
Capture	1	16.06	2.02	0.16
Midge	1	10.83	1.36	0.25
Ant trt	2	57.60	3.61	**0.04**
Bodo	1	38.37	4.81	**0.03**
H. rosa	1	3.39	0.43	0.52
Ant trt * Mosq col	4	35.53	1.11	0.36
Capture*Mosq col	2	25.78	1.62	0.21

Table 3.2. Continued.

Pre-manipulation

Taxon: ***H. rosa***	Df	SS	F Value	Pr(F)
NULL	54	221.33		
Mosq col	2	40.79	6.06	**0.005**
Capture	1	0.35	0.10	0.75
Midge	1	0.71	0.21	0.65
Ant trt	2	4.84	0.72	0.49
Bodo	1	18.85	5.60	**0.02**
H. rosa	1	0.77	0.23	0.63
Ant trt * Mosq col	4	11.36	0.84	0.50
Capture*Mosq col	2	9.06	1.34	0.27

Post-manipulation

H. rosa	Df	SS	F Value	Pr(F)
NULL	54	196.81		
Mosq col	2	52.39	7.73	**0.002**
Capture	1	0.37	0.11	0.74
Midge	1	4.95	1.46	0.23
Ant trt	2	1.35	0.20	0.82
Mosq trt	2	5.26	0.78	0.47
Bodo	1	9.65	2.85	0.10
Ant trt * Mosq trt	4	3.42	0.25	0.91
Ant trt * Mosq col	4	1.66	0.12	0.90
Capture*Mosq trt	2	5.43	0.80	0.46
Capture*Mosq col	2	3.90	0.58	0.57

Table 3.2. Continued.

Pre-manipulation

Taxon: ***Bodo***	Df	SS	F Value	Pr(F)
NULL	1	75.36		
Zone	5	11.14	2.11	0.09
Mosq col	2	8.35	3.96	**0.03**
Capture	1	2.08	1.97	0.17
Midge	1	6.09	5.77	**0.02**
Ant trt	2	0.14	0.07	0.93
Cyclidium	1	0.22	0.21	0.65
H. rosa	1	2.97	2.81	0.10
Ant trt * Mosq col	4	8.24	1.95	0.12
Capture*Mosq col	2	0.26	0.12	0.88

Post-manipulation

Bodo	Df	SS	F Value	Pr(F)
NULL	53	92.34		
Zone	5	22.17	4.04	**0.007**
Mosq col	2	0.13	0.06	0.94
Capture	1	2.02	1.84	0.18
Midge	1	9.74	8.88	**0.006**
Ant trt	2	1.53	0.70	0.51
Mosq trt	2	11.76	5.36	**0.01**
H. rosa	1	0.14	0.13	0.72
Ant trt * Mosq trt	4	5.40	1.23	0.32
Ant trt * Mosq col	4	5.97	1.36	0.27
Capture*Mosq trt	2	2.62	1.20	0.32
Capture*Mosq col	2	1.23	0.56	0.58

Table 3.3. Results of models testing for effects of resource and predator manipulations on the temporal variability (CV) of microfauna for the pre- and post-mosquito manipulation periods. Covariates were mosquito colonization (Mosq col) , natural resource capture rates (Capture) and abundance of midges and other microfauna. Results for *Cyclidium* are not shown.

Pre-manipulation

H. rosa	Df	SS	F Value	Pr(F)
NULL	34	16.53		
Mosq col	2	3.64	4.88	**0.02**
Capture	1	0.85	2.27	0.14
Midge	1	0.23	0.62	0.44
Ant trt	2	0.02	0.02	0.98
Bodo	1	1.07	2.88	0.10
H. rosa	1	1.03	2.77	0.11

Post-manipulation

H. rosa	Df	SS	F Value	Pr(F)
NULL	20	9.43		
Mosq col	2	0.42	0.56	0.58
Capture	1	0.60	1.63	0.23
Midge	1	0.003	0.008	0.93
Ant trt	2	3.52	4.79	**0.03**
Mosq trt	2	0.77	1.05	0.38
Bodo	1	0.07	0.19	0.67

Table 3.3. Continued.

Bodo	Df	SS	F Value	Pr(F)
NULL	54	9.30		
Zone	5	1.13	1.76	0.15
Mosq col	2	1.35	5.24	**0.01**
Capture	1	0.04	0.28	0.60
Midge	1	0.27	2.12	0.15
Ant trt	1	0.76	2.97	0.06
Cyclidium	1	0.06	0.45	0.51
H. rosa	2	0.02	0.13	0.72
Ant trt * Mosq col	4	1.01	1.96	0.12
Capture*Mosq col	2	0.13	0.52	0.60

Bodo	Df	SS	F Value	Pr(F)
NULL	53	16.92		
Zone	5	2.96	2.34	0.07
Mosq col	2	0.76	1.50	0.24
Capture	1	0.07	0.26	0.61
Midge	1	0.23	0.90	0.35
Ant trt	2	0.32	0.64	0.54
Mosq trt	2	0.77	1.53	0.24
H. rosa	1	0.14	0.54	0.47
Ant trt * Mosq trt	4	2.44	2.41	0.07
Ant trt * Mosq col	4	1.16	1.15	0.36
Capture*Mosq trt	2	0.38	0.75	0.48
Capture*Mosq col	2	0.86	1.70	0.20

Table 3.4. Results of models testing for effects of resource and predator manipulation on the persistence of microfaunal populations. Covariates were mosquito colonization (Mosq col), natural resource capture rates (Capture) and abundance of midges. Results for *Cyclidium* are not shown, as no factor showed significant effects.

	Df	SS	F Value	Pr(F)
Bodo				
NULL	57	11.83		
Mosq col	2	1.01	3.64	**0.04**
Capture	1	0.003	0.02	0.88
Midge	1	1.00	7.17	**0.01**
Ant trt	2	0.63	2.29	0.11
Mosq trt	2	0.85	3.06	0.06
Ant trt * Mosq trt	4	0.88	1.57	0.20
Ant trt * Mosq col	4	0.93	1.67	0.17
Capture*Mosq trt	2	0.67	2.42	0.10
Capture*Mosq col	2	0.66	2.38	0.10
H. rosa				
NULL	38	61.99		
Zone	5	10.76	4.25	**0.02**
Mosq col	2	14.32	14.14	**0.0005**
Capture	1	0.01	0.02	0.86
Midge	1	0.21	0.41	0.52
Ant trt	2	4.89	4.83	**0.03**
Mosq trt	2	3.05	3.01	0.08
Ant trt * Mosq trt	4	7.56	3.73	**0.03**
Ant trt * Mosq col	4	8.75	4.32	**0.02**
Capture*Mosq trt	2	0.04	0.04	0.96
Capture*Mosq col	2	5.79	5.72	**0.02**

Figure 3.1. Effect of mosquito predators on *H. rosa* and *Bodo* abundances (mean ± SE). (a) Mosquito colonization lowered *H. rosa* abundances in pre- and post-mosquito manipulation periods. (b) Mosquito colonization and experimental additions lowered *Bodo* abundances. For mosquito manipulation, residuals are plotted (effects after the other factors have been entered into the model). Mosquito colonization categories were: Low (0-2 larvae) and High (> 2 larvae). The mortality category contains leaves where mosquitoes had died. Mosquito manipulations were the addition of 0, 5, or 10 larvae.

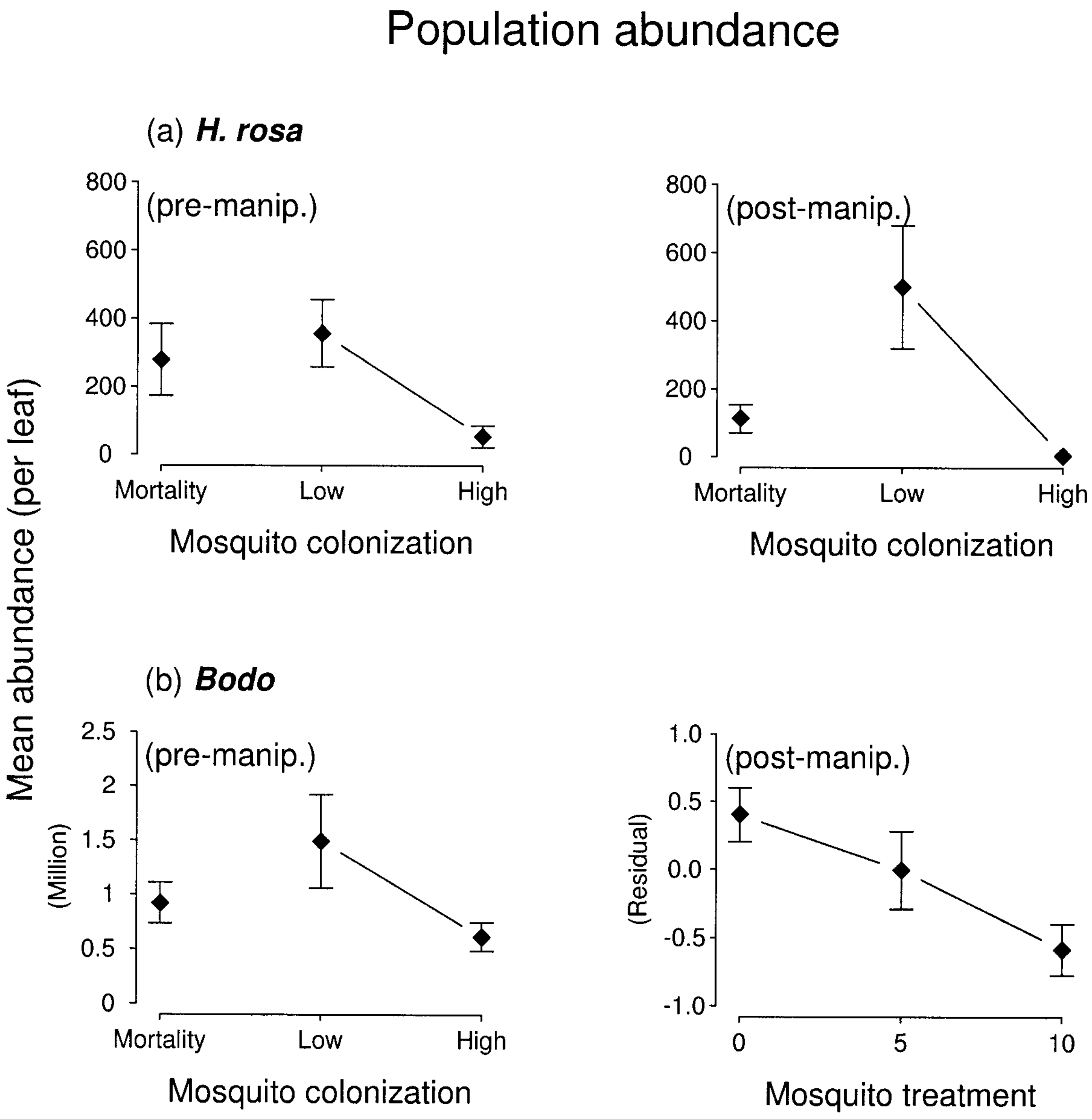

Population abundance
(a) H. rosa
(pre-manip.)
(post-manip.)
800
600
400
200
0
Mortality
Low
High
Mosquito colonization
Mean abundance (per leaf)
(b) Bodo
(pre-manip.)
2.5
2
1.5
1
0.5
0
(Million)
(post-manip.)
1.0
0.5
0.0
-0.5
-1.0
(Residual)
0
5
10
Mosquito treatment

Figure 3.1

Figure 3.2. Temporal dynamics of *H. rosa* at Low (0 – 2 larvae) and High (> 2 larvae) levels of mosquito colonization. Abundance estimates are averages and standard errors across leaves within each category. Dotted line indicates when mosquitoes were manipulated.

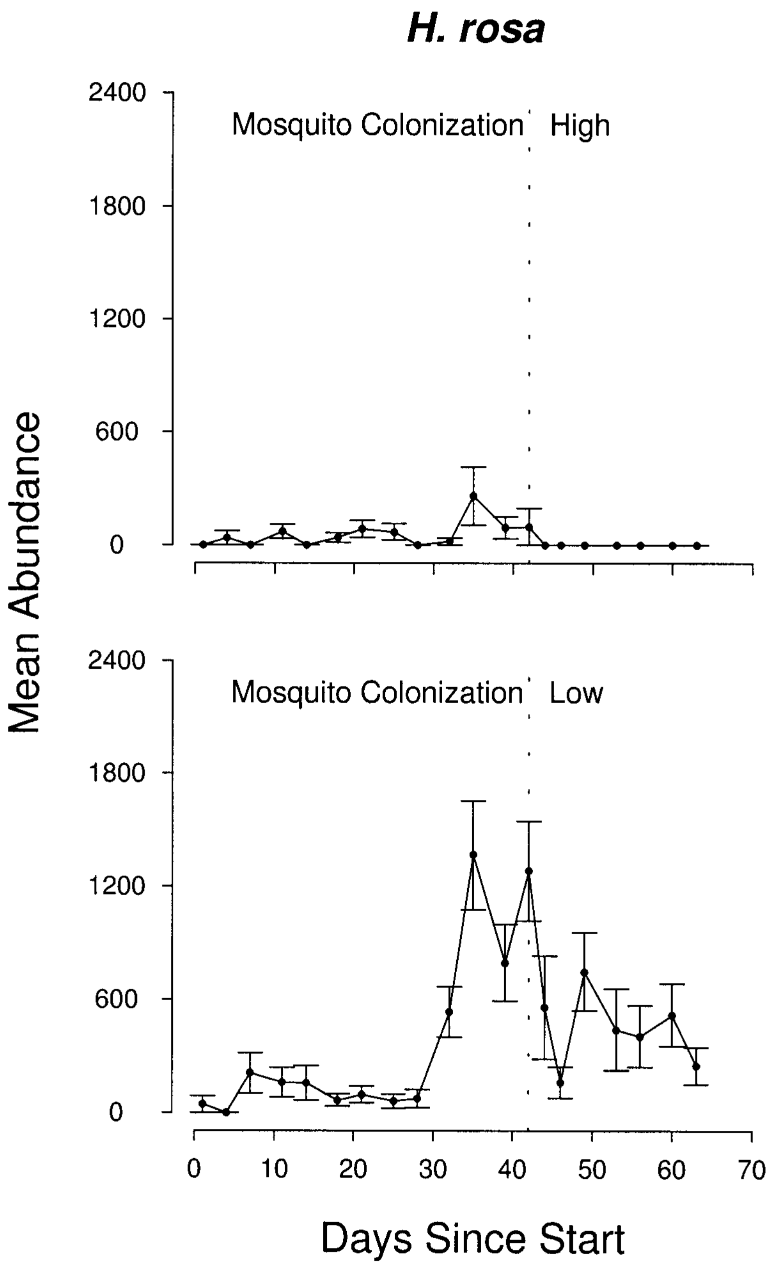

H. rosa
Mosquito Colonization High
Mosquito Colonization Low
Mean Abundance
2400
1800
1200
600
0
0
10
20
30
40
50
60
70
Days Since Start

Figure 3.2

Figure 3.3. Effects of predators and resources on the stability of *H. rosa* populations. Temporal variability (CV) increased with (a) mosquito colonization and (b) the addition of resources. (c) Persistence declined with mosquito colonization. (d) The effect of resources on persistence depended on predation. Low predation: leaves where no mosquitoes were added. High predation: leaves where 5 or 10 mosquitoes were added. Residuals are effects after the other factors were entered into the model. Error bars are standard errors.

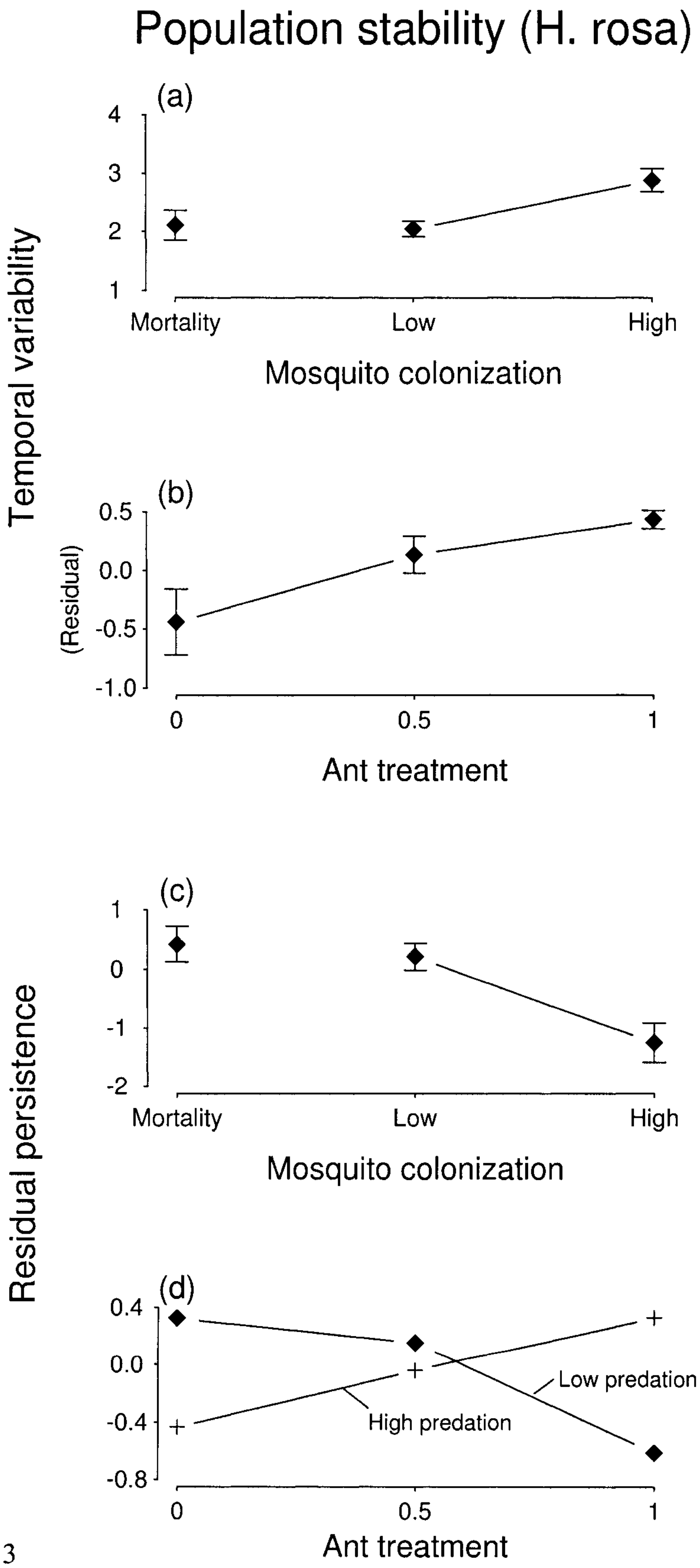

Population stability (H. rosa)
Temporal variability
(a)
4
3
2
1
Mortality
Low
High
Mosquito colonization
(b)
(Residual)
0.5
0.0
-0.5
-1.0
0
0.5
1
Ant treatment
Residual persistence
(c)
1
0
-1
-2
Mortality
Low
High
Mosquito colonization
(d)
0.4
0.0
-0.4
-0.8
Low predation
High predation
0
0.5
1
Ant treatment

Figure 3.3

Figure 3.4. Effect of mosquito colonization on the stability of *Bodo* populations. (a) Temporal variability (CV) increased with mosquitoes in the pre-manipulation period. (b) Persistence declined with mosquitoes. Residuals are effects after the other factors were entered into the model. Error bars are standard errors.

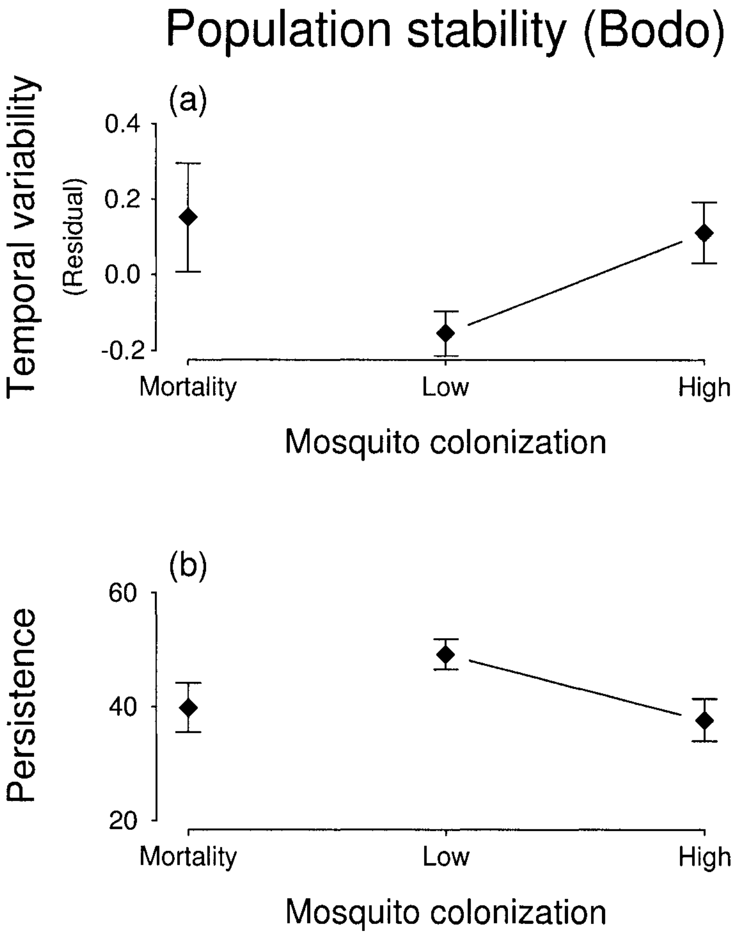

Population stability (Bodo)
(a)
Temporal variability
(Residual)
0.4
0.2
0.0
-0.2
Mortality
Low
High
Mosquito colonization
(b)
Persistence
60
40
20
Mortality
Low
High
Mosquito colonization

Figure 3.4

Figure 3.5. Summary of top-down and bottom-up effects on the stability of microfaunal populations in pitcher plants. A. Top-down (mosquito predation) effects were destabilizing. B. Bottom-up effects were stabilizing in the presence of predators, and destabilizing for *H. rosa* populations when mosquitoes were rare or absent.

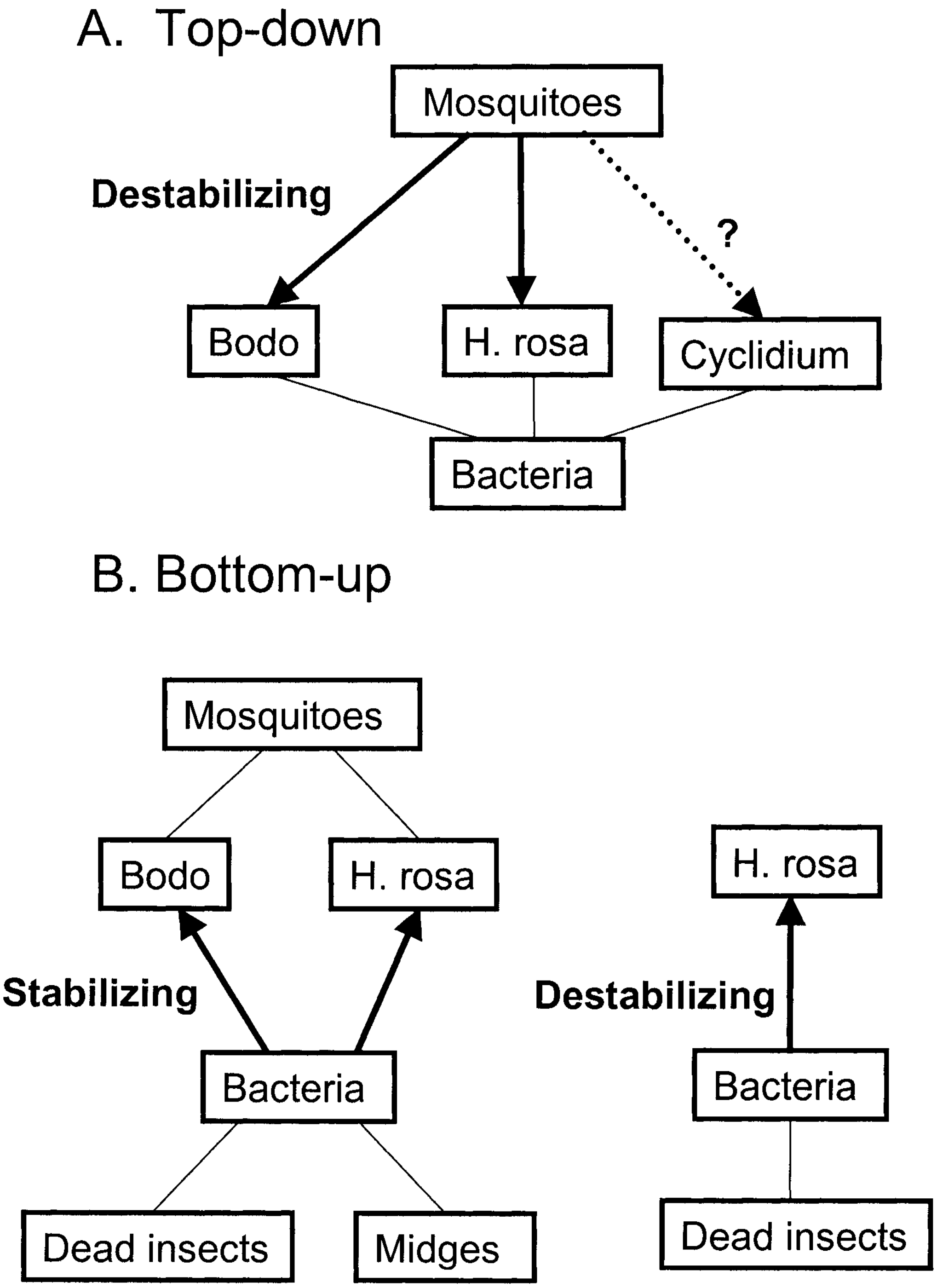

A. Top-down
Mosquitoes
Destabilizing
?
Bodo
H. rosa
Cyclidium
Bacteria
B. Bottom-up
Mosquitoes
Bodo
H. rosa
Stabilizing
Bacteria
Dead insects
Midges
H. rosa
Destabilizing
Bacteria
Dead insects

Figure 3.5

DISCUSSION

Food web structure varies from pitcher to pitcher as a consequence of variation in colonization. Here I show that variation in community structure leads to variation in the contribution of top-down and bottom-up factors to local dynamics, which has consequences for the local stability of pitcher plant microfauna (Fig. 3.5). Discussions of top-down and bottom-up effects in food webs have at least two quite distinct dimensions, (1) various (sometimes contradictory) predictions as to the effects of predation and resources on population stability and (2) a debate over the relative importance of top-down and bottom-up effects in determining the abundance of other trophic levels (prevalence of trophic cascades). Below I begin by examining the effects of resources and mosquito predators on the local stability of the pitcher plant microfaunal populations, and then discuss trophic cascades in pitcher plants. I found top-down effects to be destabilizing, and bottom-up effects to be stabilizing in the presence of predators and destabilizing in the absence of predators for one taxon (Fig. 3.5).

Bottom-up (resource) effects on population dynamics

I found that resource level affected the stability of two of the microfaunal taxa I examined, the rotifer, *H. rosa* and the microflagellate, *Bodo*. Addition of ants increased ciliate (*Cyclidium*) abundance, but had no influence on temporal variability or persistence. In pitcher plants, resources consist of detritus, principally dead insects captured by the plant. Bacteria feed on the detritus, and are consumed by the microfauna, as well as by mosquitoes.

Increasing resources experimentally (adding ants) tended to destabilize *H. rosa* populations, without affecting abundance (in leaves where mosquitoes were rare or absent). Temporal variability was greater and persistence times were shorter where resources had been added. This result is consistent with the well-known 'paradox of enrichment' model (Rosenzweig 1971), where increasing the carrying capacity of a basal species destabilizes the consumer species. Examples of the paradox of enrichment from natural communities are few, and a recent empirical study has suggested that the effect should only occur in simple food chains without omnivory, and with edible species

(Kaunzinger and Morin 1998). My study is consistent with this expectation; the destabilizing effect of resource addition occurred only in communities where the omnivorous mosquitoes were rare or absent. In leaves with significant numbers of mosquitoes, the opposite pattern was seen: increasing resources *increased* the stability of *H. rosa* populations. Many others have also shown the dependence of the paradox of enrichment on aspects of community structure (Abrams 1993, Grover 1995, Scheffer and de Boer 1995, Leibold 1996, McCann et al. 1998b, Murdoch et al. 1998, Morin 1999). For *H. rosa*, the paradox of enrichment disappears as top-down (omnivorous) effects become more important.

Bottom-up effects in pitcher plant communities depend not only on the number of captured insects within in the leaves, but are influenced by midges. Shredding activity by midges appears to increase the availability of resource material for bacteria (Heard 1994). Similar effects of shredding invertebrates on bacteria growth have been shown for other aquatic systems, due to increased available surface area and the production of faeces (e.g. Merritt et al. 1984). Midges strongly increased bacterial numbers in my study, and in fact, this was the only factor seen to significantly influence bacterial abundance. The dynamics of *Bodo* appeared to be strongly linked to the abundance and activity of midges. Both persistence times and average abundance of *Bodo* increased with midges, regardless of mosquito abundance. Increased stability as resource availability increased is opposite to the predictions of 'paradox of enrichment' models and to the response of *H. rosa* in the absence of predators (above). It is consistent, however, with many other empirical results from aquatic systems (e.g. McCauley and Murdoch 1990), and theory suggests that many characteristics of real food webs will eliminate the paradox of enrichment, including heterogeneity among species in edibility or vulnerability to predators, competitive interactions among consumer species, and spatial refuges (Leibold 1996, Murdoch et al. 1998, Scheffer and de Boer 1995, Grover 1995, Morin 1999, Abrams 1993, McCann et al. 1998a). I can only speculate as to which explanation might be most relevant. The microfaunal consumer level is clearly heterogeneous (different growth rates and food preferences), as is the basal level (various bacterial types). Heterogeneity at either level can eliminate the paradox of enrichment effect (Abrams 1993, Grover 1995, Leibold 1996). In particular, the activity of midges may act to alter available resources in a manner analogous to the influx of allochthonous resource modelled by Huxel and McCann (1998), favouring some bacterial types over others. Interactions within trophic levels (competition, intraguild predation) also affects stability (Leibold 1996, Morin 1999), and I detected competitive interactions between *Bodo* and *Cyclidium*, as well as a positive effect of *Bodo* on *H. rosa* that is suggestive of intra-guild predation.

Top-down (predator) effects on population dynamics

Variation in the abundance of mosquitoes was one of the most important causes of variation in the dynamics of the microfaunal taxa I examined. Mosquitoes affected the stability (temporal variability and persistence) of *H. rosa* and *Bodo* populations, and may have caused the extinction of *Cyclidium*. Predators can be stabilizing or destabilizing, depending on a plethora of assumptions with respect to predator and prey characteristics and community structure. Mosquitoes are generalist omnivores, feeding on bacteria as well as on microfauna. Omnivory can be destabilizing (Pimm and Lawton 1978), but there are circumstances where generalist predation and weak omnivory can stabilize food web interactions (Holt and Lawton 1994, McCann and Hastings 1997, McCann et al. 1998b). I found only destabilizing effects for mosquito predators. Populations of *Bodo* and *H. rosa* had larger temporal fluctuations and lower persistence times with increasing predation, results that are consistent with laboratory experiments showing that predators or omnivores increase temporal variability of protist populations (Lawler and Morin 1993). In addition, *Cyclidium* disappeared at or just after the peak oviposition period for mosquitoes. I do not know if predators were the cause, but mosquitoes can eliminate ciliate and other protist populations (Addicott 1974, Maguire et al. 1968). Instability and local extinctions may be common for prey of generalist predators in aquatic systems (Murdoch and Bence 1987), particularly where predator generation times are much longer than those of their prey.

Trophic cascades

There were clear top-down effects of mosquitoes on the two microfaunal taxa, *Bodo* and *H. rosa*. Mosquitoes, especially those colonizing naturally, had disproportionately large effects, causing about a 50% decline in *Bodo*, and eliminating *H.*

rosa later in the summer. Other studies have also found that mosquitoes decrease total microfaunal abundance (Addicott 1974), or the abundance of some taxa (Cochran-Stafira and von Ende 1998, Bledzki and Ellison 1998, Kneitel and Miller 2002, Miller et al. 2002) in pitcher plant communities.

Trophic cascades, where the effects of top predators are seen at the level of the basal species, have been documented in many aquatic communities (Carpenter and Kitchell 1993, Brett and Goldman 1996). Two recent studies of pitcher plant communities have also found a cascade; mosquitoes lowered microfaunal abundances, resulting in slightly higher bacterial densities. The cascade occurred through *H. rosa* in Kneitel and Miller (2002), and through ciliates in Cochran-Stafira and Von Ende (1998). I did not find a trophic cascade in this study. Mosquitoes had strong effects on both *H. rosa* and *Bodo*, but the effects did not translate into increased bacterial densities. In fact, there was a tendency for a decline in bacteria with increases in mosquitoes, probably due to direct feeding. There are numerous methodological differences between the studies, for example, community composition was homogenized and colonization eliminated in both Cochran-Stafira and Von Ende (1998) and Kneitel and Miller (2002), and the former study was conducted in a laboratory setting. However, I suspect that the principal reason that I found a truncated cascade was the presence of midges in my communities. Midges colonized all but one of the leaves in my study, and they have been present (and abundant) in every bog I have sampled in Nova Scotia and Newfoundland. In contrast, midges are absent in some southern bogs (Miller et al. 1994, Harvey and Miller 1996), and were not included in either of the studies demonstrating cascades (Cochran-Stafira and Von Ende 1998, Kneitel and Miller 2002). Midges in my study caused such a strong increase in bacteria that none of the microfauna had a detectable effect on bacterial densities, thus effectively stopping the cascade. Huxel and McCann (1998) find a similar result when they model the influx of a second resource; the heterogeneity in the consumer level causes the trophic cascade to become a trickle. In my study, the trickle is small enough that the direct effect of mosquito consumption on bacteria dominates.

When present, midges are clearly a key species in pitcher plant communities. Their effect on bacteria has consequences for mosquito survival and growth, and may explain part of the positive association usually seen for these arthropods (Heard 1994, Nastase et al. 1995, Trzcinski pers obs). Here I show that midges also affect microfaunal (*Bodo*) abundance and stability, and probably truncate a trophic cascade.

Conclusions

Both top-down and bottom-up factors influence the stability of pitcher plant microfaunal populations (Fig. 3.5). Top-down (mosquito predation) effects are strong and destabilizing for *Bodo*, *H. rosa* and perhaps *Cyclidium* populations. Bottom-up effects are more taxon-specific. Additional resources either stabilize or destabilize *H. rosa* populations depending on the predator regime. Indirect effects of midges on bacterial densities stabilize *Bodo* dynamics, while truncating the cascading effects of mosquito predation. I suggest that a regional process (colonization) sets the stage for this variation in local dynamics of communities occupying pitcher plant leaves. My results are broadly consistent with food web theory that suggests that heterogeneity within trophic levels has significant consequences for patterns of stability and trophic cascades.

CHAPTER 4

Population growth rate and community structure affect population synchrony

INTRODUCTION

The stability or persistence of metapopulations (where local populations are unstable) depends on the presence of mechanisms that maintain a degree of asynchrony among local populations (Reeve 1988, Hanski 1999). In models without local dynamics, colonization / extinction events are the source of the asynchrony (e.g. Levins 1969), while in models with local dynamics asynchrony is often produced by a spatially heterogeneous environment or by spatially uncorrelated environmental change (Harrison and Quinn 1989, Gilpin and Hanski 1991, Grenfell et al 1998). Increasing synchrony increases the risk of global extinction (Heino et al. 1997), and as a consequence synchrony is not only of theoretical interest but also of increasing concern in conservation biology (Earn et al. 2000, Cazelles et al. 2001).

Most of the work aimed at identifying the causes of spatial synchrony has focused on two principal mechanisms: dispersal and correlated environmental change or regional stochasticity (Bjørnstad et al. 1999). Local population dynamics can be synchronized by correlated changes in environmental conditions, a process commonly known as the Moran effect (Moran 1953, Royama 1992). The Moran effect is thought to be an important synchronizing mechanism in many populations, from butterflies to squirrels to sheep (Sutcliffe et al. 1996, Ranta et al. 1997, Grenfell et al. 1998). Dispersal also acts as a synchronizing force, making population dynamics less independent. High dispersal rates homogenize population growth rates (Engen et al. 2002), and consequently, local populations act as a single large population. To the extent that dispersal synchronizes local dynamics, it is a destabilizing force, but dispersal can also be the source of metapopulation stability, by 'rescuing' populations from low size (Brown and Kodrick-Brown 1977, Heino et al. 1997, Blasius et al. 1999).

Local dynamics can interact with synchronizing forces, reducing their effects. High local population growth rates generally lower population synchrony (Ranta et al. 1997, Heino et al. 1997, Lande et al. 1999, Earn et al. 2000). Local noise, chaos and particular patterns of dispersal can also reduce the effectiveness of synchronizing forces (Allen 1993, Heino et al. 1999, Earn et al. 2000). Lande et al. (1999) looked at the effects of local dynamics (degree of density regulation) on the spatial scale of population synchrony in a model where synchrony was generated by spatially correlated environmental stochasticity and by dispersal. They found that as density regulation increases, the scale of population synchrony decreases. Density regulation refers to the rate of return to equilibrium and is proportional to the maximum rate of increase in the logistic model (Beddington and May 1977). Spatial scale of synchrony refers to the distance at which the dynamics of local populations become uncorrelated (or reach a constant background level). Lande et al's (1999) results imply an important mitigating role of density regulation on population synchrony, and thus on metapopulation stability.

I used populations of a protozoan, *Bodo sp.,* living in the pitcher plant (*Sarracenia purpurea*) to test for the predicted relationship between density regulation and population synchrony. I monitored populations of *Bodo sp.* at six study sites over a period of three months. Leaves vary in resources levels and community structure and thus are likely to vary in the degree of density regulation (or maximum rate of increase). I used the time series to estimate the maximum rate of increase at each site, and then determined if populations at sites with higher rates of increase tended to have less synchronous dynamics.

METHODS

Pitcher plant leaves contain small aquatic communities composed of bacteria, protozoa, rotifers, and arthropods. Leaves fill with water during rainfalls and passively capture insects and other unfortunate creatures (Heard 1998). This decaying material serves as a food resource for the aquatic community and for the pitcher plant. Leaves contain a diverse protozoan assemblage (Addicott 1974, Miller et al. 2002), and as in many other communities, most species are rare. The three most common microfauna in this study were *Bodo sp.*, a small flagellate (8 – 10 μm), *Cyclidium sp.,* a ciliate (25 – 30 μm), and *Habrotrocha rosa*, a bdelloid rotifer (usually > 150 μm). The arthropod fauna is similar to that described in other studies (Bradshaw 1983, Heard 1994, Miller 1994), and is made up of three dipteran larvae: a mosquito *Wyeomyia smithii*, a midge *Metriocnemus knabi*, a sarcophagid fly *Blaesoxipha fletcheri*, and an aquatic mite *Sarraceniopus gibsoni*. Mosquitoes prey on bacteria and protists in the water column, while midges and mites feed on decaying material at the bottom of the leaf. In this study, I focused on the most abundant of the microfauna, *Bodo*, a small (5-12 μm) flagellate.

I selected two sites (35 x 35 m) in each of three bogs located at Duncan's Cove, Sandy's Cove, and Peggy's Cove Nova Scotia. I studied one leaf from 10 randomly chosen plants at each site for a total of 60 leaves. I collected water samples every 3 to 4 days from 6 July to 2 October 2000, for a total of 27 sampling dates over 89 days. Leaves were left open to natural colonization. I used the procedures outlined in the previous chapter to sample *Bodo* and to estimate abundance. On 8 August, after the peak period of mosquito oviposition, I manipulated mosquito density by adding five larvae to half the pitchers at each site.

Statistical analyses

The analysis consisted of four parts: (i) estimating the maximum rate of increase (r) (equivalent to density regulation), (ii) estimating the population synchrony at each site, (iii) testing for a relationship between synchrony and distance, and (iv) testing for relationships between synchrony, rate of increase and community structure.

I estimated the rate of increase (r) at each site with a linear mixed model using all 60 time-series.

$$y_{ijk} = \beta_0 + \beta x_{ijk} + \beta_{0i} + \beta_{1i} x_{ijk} + b_{j(i)} + \varepsilon_{ijk},$$

$$i = 1,\ldots 6,\ j = 1,\ldots 10,\ k = 1,\ldots 26$$

where $y_{ijk} = \log(N_{k+1}/N_k)$, $x_{ijk} = \log(N_{ijk})$, and i is site, j is leaf, and k is the time interval.

This model generalized a linear regression between the finite rate of increase ($\log(N_{k+1}/N_k)$ and population size ($\log(N_{ijk})$) by specifying leaf within site as a random effect ($b_{j(i)}$),and population size, site and their interaction as fixed effects The $b_{j(i)}$ and e_{ijk}'s are assumed to be independent random variables with $N(0, \sigma^2_b)$, $N(\epsilon, \sigma^2)$. This model fit a separate relationship between the finite rate of increase and population size for each site and allowed for variation in the intercept for each leaf. β_{0i} and β_{1i} are the intercept and slope or each site. The slope β_{1i} estimates the strength of density dependence (γ in Lande et al. 1999) and the y-intercept β_{0i} estimates the maximum rate of increase (r) at a site.

I estimated population synchrony as the pair-wise Spearman correlation coefficients for *Bodo* abundances over time in different leaves. Synchrony was measured for all possible pair-wise combinations of leaves within each site (10 x 10 matrix). Mean synchrony for a site was then the mean correlation of all unique pairs (Bjørnstad 1999). To look for synchronizing or desynchronising events, I plotted the temporal similarity in population abundance. That is, I compared the population size of a leaf with the average abundance of all leaves at a site (metapopulation size, $n = 10$). Lines near zero are synchronous with the dynamics of the metapopulation. Synchronizing events should cause the lines to converge at zero, whereas desynchronising events should cause divergence.

Mosquito abundances were manipulated partway through the experiment. However, site-level estimates of r and synchrony changed little when estimates were obtained using all leaves or using only unmanipulated leaves. Thus all leaves were included in the analysis, and the effect of the manipulation was to increase the range of mosquito densities in the sampled leaves.

I tested for a relationship between pair-wise synchrony and distance between leaves. The test was first conducted separately for each site, (max distance 35 m) and then sites were combined within bog to test longer distances (max distance 240 m).

I then tested for a relationship between the site-level estimates of $\underline{r}$ and synchrony in two models, the first including only the maximum rate of increase, $\underline{r}$, as the explanatory variable, and the second also including average mosquito and midge abundances as explanatory variables. In an attempt to further understand the influence of mosquitoes and midges on synchrony, I then tested if the variation (standard deviation) in mosquito and midge abundance affected mean synchrony at a site. These factors could not be included in the same model because of limited number of degrees of freedom (six sites).

Finally I tested for a relationship between site-level synchrony and stability, at the local (leaf) spatial scale and at the regional (site) spatial scale. I tested for a relationship between site-level synchrony and two measures of local population stability, (1) average temporal variability of *Bodo* abundances (CV), estimated for each leaf and then averaged across leaves within a site, and (2) average persistence time, also estimated for each leaf, and then averaged across leaves. I also used two measures of stability at the regional scale. The first was the temporal variability (CV) of *Bodo* abundances over time (abundances averaged across leaves within sites on each date). The second is a measure of the change in incidence over time. In a stable metapopulation the proportion of sites occupied should be at equilibrium (constant). *Bodo* populations did not go extinct at the regional scale at any site over the time course of the experiment. However, there was some indication of increasing instability, because incidence started out high (>80%) and decreased during the season. I used the slope of this decline at each site as a measure of stability.

RESULTS

The maximum rate of increase (r) of *Bodo* populations in this study was 2.62, averaged across all sites. Sites varied significantly in r (Table 4.1, interaction term), but bogs did not. The lowest rate of increase was 2.18, and the highest 3.14, both of which occurred at Peggy's Cove (Table 4.2). Variation in mean synchrony was also greater between sites than between bogs (Table 4.3).

There was no evidence that population synchrony declined with distance at the site or bog spatial scales (Figure 4.1). Synchrony did not decline with distance at any site (Table 4.4), or when all sites were combined ($r = 0.07$, $n = 268$, $P = 0.26$). When examined over longer distances within a bog (up to 240 m), there was still no evidence of a relationship between synchrony and distance (Table 4.5).

There was no relationship between site-level synchrony and the maximum rate of increase ($r = -0.37$, $P = 0.47$), with r as the only explanatory variable. However, when mosquito abundance, midge abundance and r were included, two of the three factors had a marginally significant and negative effect on site-level synchrony (Table 4.6). (Synchrony was not significantly correlated with the average abundance of mosquitoes or midges when considered independently ($r = -0.61$, $P = 0.20$, $r = -0.37$, $P = 0.47$).)

Part of the effect of mean mosquito abundance on population synchrony at a site appeared to be due to increased variation in abundance among leaves. Sites with more mosquitoes and midges also had greater variation in their abundance, and population synchrony decreased with increased variation in mosquito and midge abundance (Table 4.7).

Synchrony did not affect local stability. Neither temporal variability (average CV) nor persistence time was significantly related to synchrony ($r = -0.56$, $P = 0.24$, $r = 0.07$, $P = 0.89$). Synchrony was also not related to temporal variability at the regional scale ($r = 0.31$, $P = 0.55$). However, more synchronous sites showed steeper declines in incidence over the season ($P < 0.001$, Figure 4.3). Population incidence started out high (>80%) at all sites and steadily decreased during the season. Stability, when measured as the rate of decrease in population incidence, decreased as population synchrony increased ($P = 0.02$, Figure 4.4).

Table 4.1. Results from a linear mixed effects model of 60 time-series of *Bodo* population abundance. The variance estimates for site and leaf within site were 0.132 and 0.151 respectively, and the residual variance was 2.44.

	Coefficient	*d.f.*	F	P – value
Intercept	2.62	1	1.92	0.16
$\log(N_{ijk})$	-0.17	1	476.08	< 0.0001
Site		5	1.18	0.33
Site*$\log(N_{ijk})$		5	2.22	0.05

Table 4.2. Site-level estimates of the maximum rate of increase (r̲) and population synchrony.

		r̲		Synchrony	
Bog	Site	mean	range	mean	range
Duncan's	1	2.27	2.26 - 2.30	0.16	-0.50 - 0.81
	2	2.49	2.47 - 2.51	0.42	-0.18 - 0.89
Sandy's	3	2.96	2.94 – 3.00	0.17	-0.60 - 0.85
	4	2.66	2.65 - 2.68	0.23	-0.41 - 0.70
Peggy's	5	3.14	3.12 - 3.17	0.22	-0.54 - 0.72
	6	2.19	2.17 - 2.21	0.50	-0.23 - 0.88

Table 4.3. Bog-level estimates of the maximum rate of increase (r̲) and population synchrony.

	r̲		Synchrony	
Bog	mean	range	mean	range
Duncan's	2.38	2.26 - 2.51	0.30	-0.69 - 0.81
Sandy's	2.81	2.65 – 3.00	0.18	-0.60 - 0.85
Peggy's	2.67	2.17 - 3.17	0.23	-0.54 - 0.72

Table 4.4. Tests of the spatial scale of synchrony for each site. Pearson correlations between synchrony and distance (*n* = 45).

Bog	Site	Pearson correlation	*P* – value
Duncan's	1	-0.014	0.93
	2	-0.172	0.26
Sandy's	3	0.397	0.007
	4	0.073	0.63
Peggy's	5	0.057	0.71
	6	0.039	0.80

Table 4.5. Tests of the spatial scale of synchrony for each bog. Pearson correlations between synchrony and distance (*n* = 190).

Bog	Pearson correlation	P – value
Duncan's	-0.065	0.37
Sandy's	0.062	0.39
Peggy's	0.111	0.13

Table 4.6. The effects of mean mosquito density, mean midge density, and the maximum rate of increase ($\underline{r}$) on the synchrony of *Bodo* populations at a site.

	Coefficient	*d.f.*	*S.S.*	*F*	*P* – value
Null		5	0.100		
Mosquitoes	-0.012	1	0.037	14.36	0.06
Midges	-0.018	1	0.018	6.87	0.12
$\underline{r}$	-0.385	1	0.040	15.50	0.06

Table 4.7. The effects of three factors, standard deviation (σ) in mosquito density, standard deviation in midge density, and the maximum rate of increase ($\underline{r}$) on the synchrony of *Bodo* populations at a site.

	Coefficient	*d.f.*	*S.S.*	*F*	*P* – value
Null		5	0.100		
σ mosquitoes	-0.016	1	0.067	117.84	0.008
σ midges	-0.018	1	0.008	14.56	0.06
$\underline{r}$	-0.27	1	0.024	41.18	0.02

Figure 4.1. The effect of distance between leaves on the synchrony in population dynamics. First row of graphs are for sites at Duncan's Cove. Second and third rows are for sites at Sandy's and Peggy's Cove.

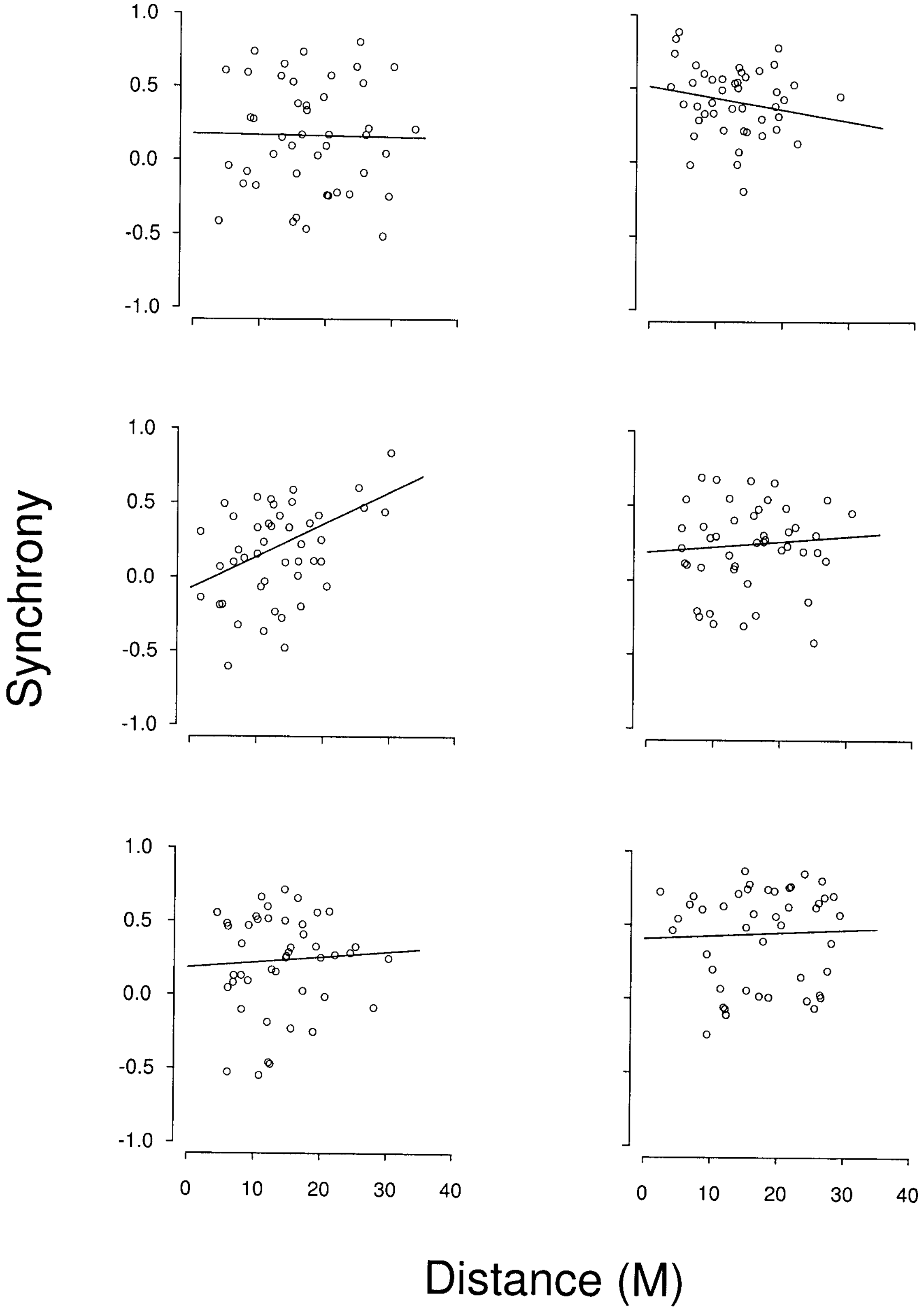


Figure 4.1

Figure 4.2. The effect of the maximum rate of increase on the synchrony of *Bodo* populations at a site. Numbers indicate site (Duncan's Cove: 1, 2, Sandy's Cove: 3, 4, Peggy's Cove: 5,6).

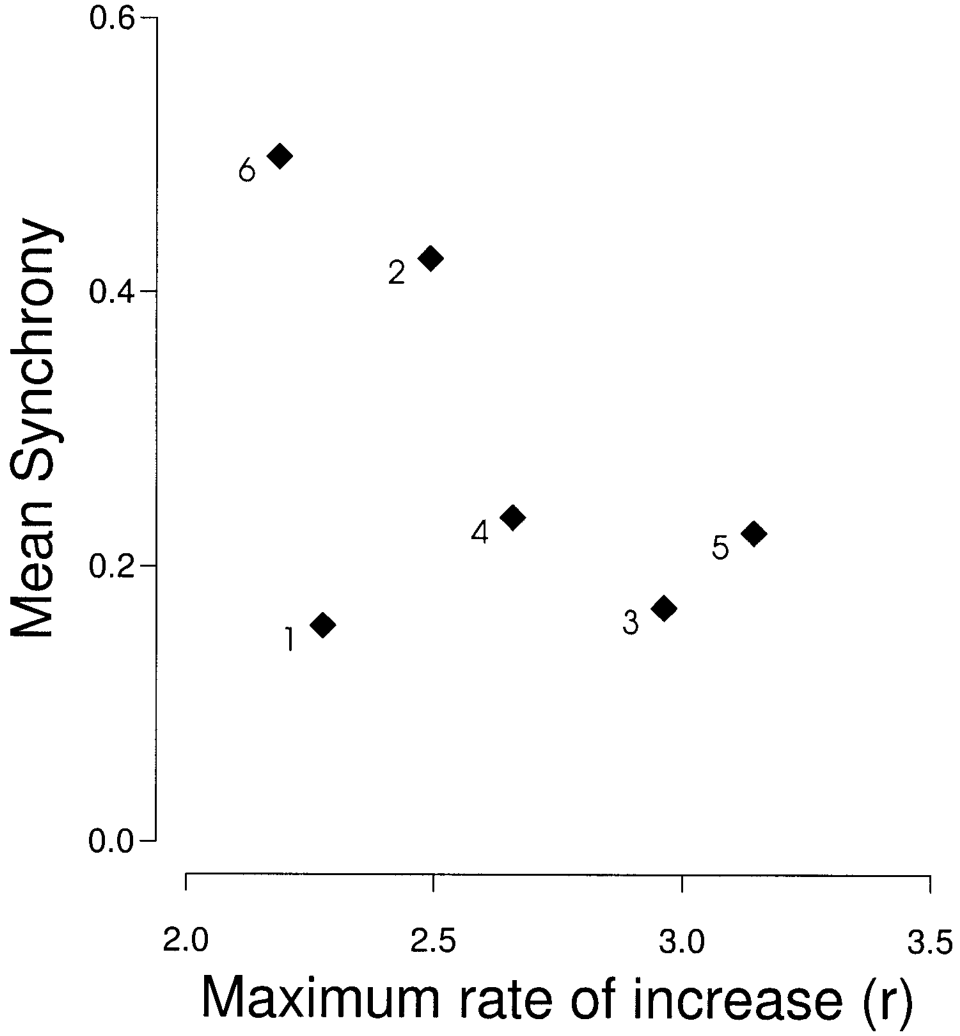

0.6
0.4
0.2
0.0
Mean Synchrony
6
2
4
5
1
3
2.0
2.5
3.0
3.5
Maximum rate of increase (r)

Figure 4.2

Figure 4.3. The temporal decline in population incidence. First row of graphs are for sites at Duncan's Cove. Second and third rows are for sites at Sandy's and Peggy's Cove.

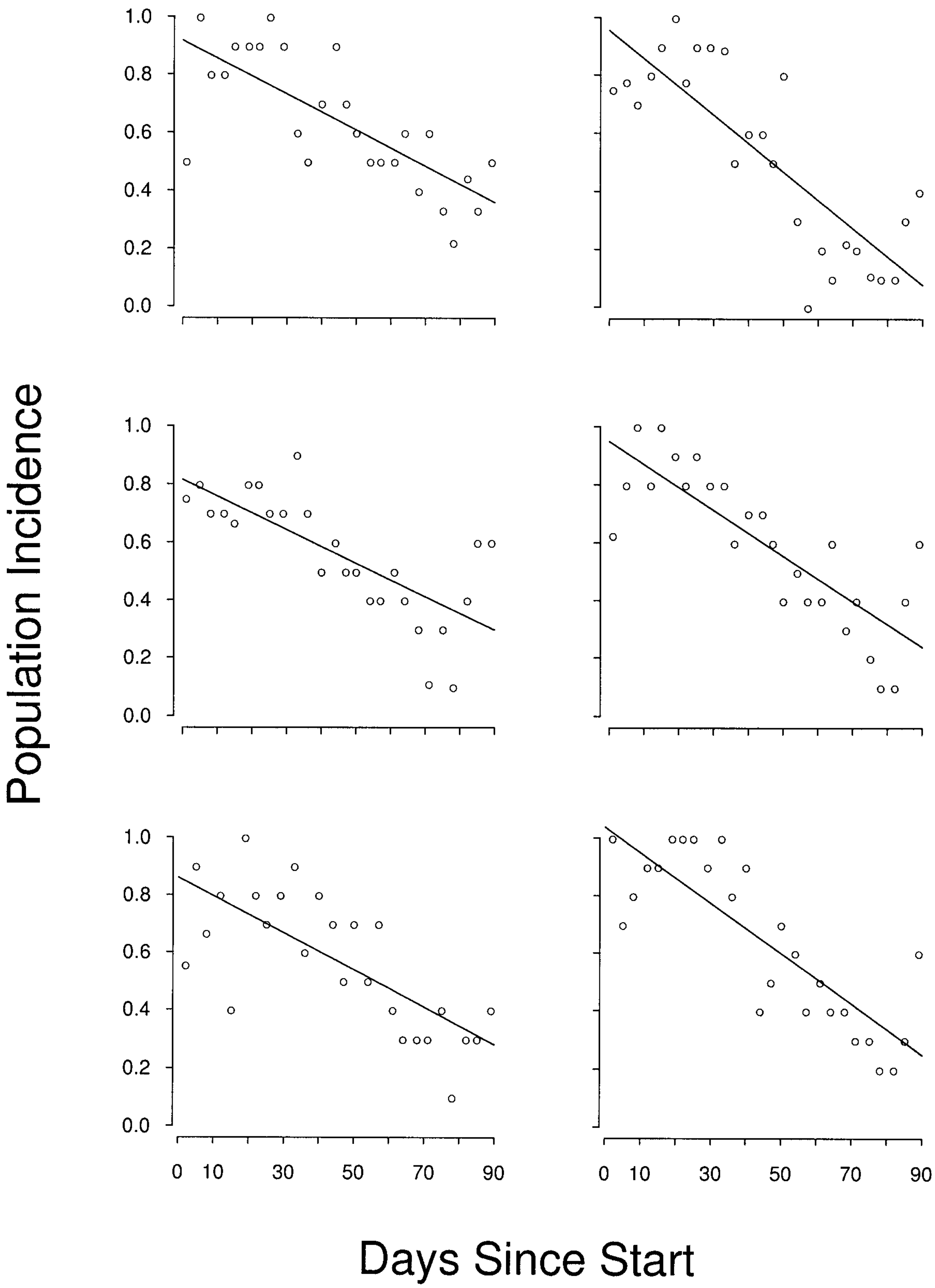

Population Incidence
1.0
0.8
0.6
0.4
0.2
0.0
0
10
30
50
70
90
Days Since Start

Figure 4.3

Figure 4.4. The effect of synchrony on the rate of decrease in *Bodo* population incidence. Each point is a measure of the population dynamics at a site. Numbers indicate site (Duncan's Cove: 1, 2, Sandy's Cove: 3, 4, Peggy's Cove: 5,6).

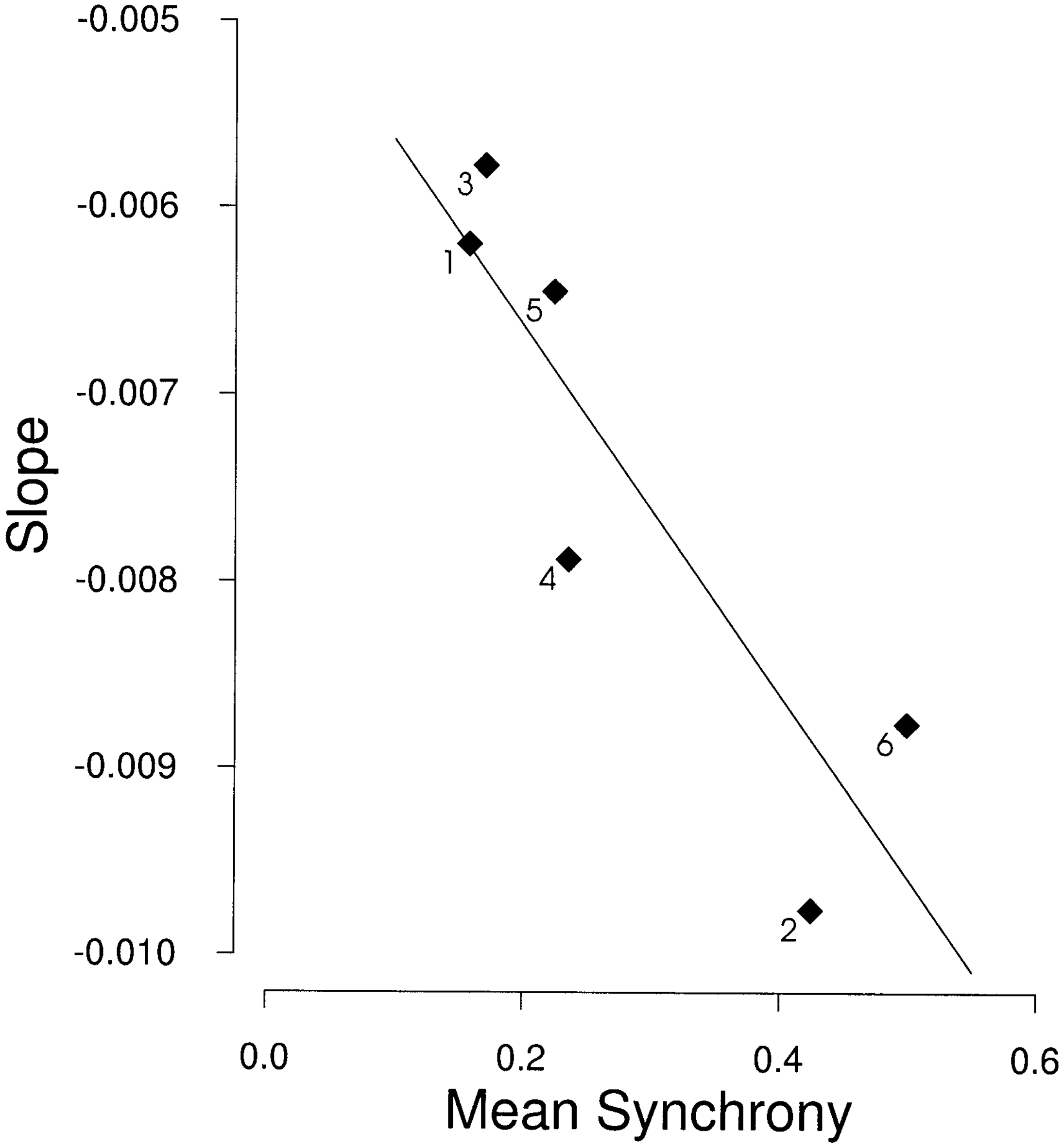

-0.005
-0.006
-0.007
-0.008
-0.009
-0.010
Slope
3
1
5
4
6
2
0.0
0.2
0.4
0.6
Mean Synchrony

Figure 4.4

DISCUSSION

The degree to which population dynamics are synchronized is a product of both regional synchronizing forces (dispersal and correlated environmental change) and local dynamics. Models by Lande et al. (1999) suggest that increasing the degree of local density regulation (increasing r) should reduce the synchronizing effect of dispersal. While there was no simple negative relationship between synchrony and the rate of increase at a site for *Bodo* populations in pitcher plant leaves, synchrony did decline significantly with r after accounting for variation in mosquito and midge abundances. Very high densities of either taxon resulted in lower than expected synchrony based on r. It thus appears that there is an underlying negative relationship between r and synchrony, but it is necessary to account for community structure in order to detect the effect.

Strong density regulation (or a high rate of increase) is expected to reduce the effectiveness of dispersal as a synchronizing force (Lande et al. 1999, Kendall et al. 2000). In their model Lande et al. (1999) showed this effect as a decrease in the spatial scale of synchrony. In my study I found no 'spatial scale of synchrony', as synchrony did not decline over the distances tested. However, I measured the *degree* of synchrony at a particular spatial scale, and found that synchrony was lower where density regulation was high (after accounting for mosquito and midge abundances). Density regulation lowers synchrony because it decreases the synchronizing effect of dispersal and/or correlated environmental change. Both synchronizing forces are generally expected to produce a pattern of declining synchrony with distance. Typically, distant populations exchange fewer individuals and experience favourable or unfavourable conditions at different times. In this study, *Bodo* population synchrony did not decline with distance. There are several possible explanations: 1) neither environmental correlation nor dispersal declined with distance 2) dispersal declined with distance, but the effect was overpowered by common changes in environmental conditions occurring at scales larger than that of the study, or 3) environmental correlation declined with distance but the effect was overpowered by global dispersal (at a scale larger than the study).

Little is known about the dispersal of *Bodo*. The genus is widely distributed and can be found in soil, marine and freshwater environments. Individuals may travel with insects, splashing water, or in the atmosphere (Maguire 1963, Rivera et al. 1992). I do not have a direct measure of dispersal rate, but *Bodo* is a rapid and nearly ubiquitous colonizer. *Bodo* was found in all 60 pitcher plant leaves monitored in this study and that of the previous year (Chapter 2), and all but two leaves of this study had *Bodo* present on the first or second date the leaf was sampled. Rivera et al. (1992) found that wind speed and direction affected the incidence of protozoan cysts, including *Bodo*, in air samples collected in Mexico City. If *Bodo* travels primarily in the atmosphere, then factors controlling propagule rain (wind patterns, leaf orientation) could influence spatial patterns of population synchrony. In this case, a more complex model than a simple negative correlation with distance would be required to explain the effect of dispersal on spatial patterns of synchrony.

Major environmental events are strongly correlated at the site and bog scales of this study, and there is probably a good correlation across the entire study area (75 km). Rainfall events and seasonal changes in temperature occur at similar times. Thus the spatial scale of environmental forcing is such that it is unlikely to produce a strong distance relationship within or among bogs. Both rainfall events and temperature changes are expected to synchronize *Bodo* populations. Rainfall produces and maintains the pitcher plant aquatic environment, and could synchronize *Bodo* populations by perturbing them at the same time. Rainfall increases water volume, decreases nutrient concentrations and probably pH levels. Some but not all rainfall events appear to be associated with increases in synchrony within sites (Fig 4.5). Heterogeneity in rain 'capture' due to leaf orientation or leaf size may reduce the synchronizing effects of rainfall. Common changes in temperature will also tend to synchronize population dynamics by causing correlated changes in bacterial and protozoan growth. The magnitude of the effect could vary among leaves or sites, however, due to fine-scale heterogeneity in temperature caused by shading (Kingsolver 1979). Correlated changes in the biotic environment experienced by *Bodo* also have the potential to be synchronizing forces. Both mosquitoes and midges influence *Bodo* numbers (Chapter 2), and simultaneous colonization of leaves could therefore induce correlated changes in *Bodo* abundance. However both mosquitoes and midges have an extended period of oviposition, which suggests that few leaves are colonized at the same time. Variation in the timing of mosquito colonization could cause asynchronous declines or even local extinctions, and therefore it is expected that mosquitoes are more likely to desynchronise rather than synchronize dynamics.

The effectiveness of the synchronizing forces, be they dispersal or correlated environmental change, depend on local dynamics (Lande et al. 1999, Hanski 1999, Kendall et al. 2000, Engen et al. 2002). In this study, two components of local dynamics, the rate of increase, r, and community composition (mosquito and midge abundance) influenced synchrony. Sites with high numbers of mosquitoes had lower synchrony than expected based on r. Sites with more mosquitoes and midges also had greater variation (among leaves) in abundance, and lower synchrony was associated with this greater heterogeneity in these two arthropods. Mosquitoes may interfere with the synchronizing effects of correlated environmental change or dispersal. For example, high numbers of mosquitoes in a leaf could eliminate a positive response to warmer temperatures, or prevent colonizing individuals from establishing a population, as seen by Miller et al. (2002). Sites with high midge abundances also had lower synchrony than expected based on r, but there was no association with higher variation in midge abundance. The effect of midges may be through their effect on *Bodo* population size. *Bodo* populations tend to be larger where there are more midges (see previous chapter), and dispersal is less effective at synchronizing large populations. However, *Bodo* populations typically remain at high abundances for only a week or two. An alternative explanation is that midges promote uncorrelated population explosions.

In this study I found an underlying negative relationship between the rate of increase (r) at a site and the degree of synchrony seen among populations at that site. Sites with high average growth rates have populations that are less synchronized, implying that synchronizing forces such as dispersal and correlated environmental change are less effective for populations with the potential to grow very rapidly. Under assumptions of logistic growth, the maximum rate of increase is equivalent to 'density regulation', or speed at which a population returns to equilibrium (Lande et al. 1999). High r or density regulation can be thought of as disrupting synchrony in at least two ways. High growth rates mean that a population returns back to equilibrium more quickly after being perturbed downward. Populations with high growth rate are thus more 'stable', spending more time near equilibrium or K. Dispersal is expected to have less effect on realized demographic rates in populations with strong density regulation (Engen et al. 2002). A quick look at the dynamics of individual *Bodo* populations (Figure 4.6) suggests that this is not likely to be the dominant effect of r in these populations. Populations spend very little time at high densities or near what might be considered carrying capacity. The magnitude of r also plays a fundamental role in determining patterns of local population dynamics, with higher r's leading to cycles and ultimately chaotic dynamics (May 1975). Several modelling studies have shown that as dynamics move into the cyclic or chaotic range, the effectiveness of dispersal or correlated environmental change in synchronizing population dynamics declines rapidly (Allen et al. 1993, Heino et al. 1997, Ranta et al. 1997, Lande et al. 1999). My estimates of r for *Bodo* populations in pitcher plants are high, suggesting the potential for unstable dynamics. The explosion/crash dynamics of individual populations also suggests instability at the local scale.

Population asynchrony has been identified as an important component of regional persistence; increasing synchrony is destabilizing (Harrison and Quinn 1989, Gilpin and Hanski 1991, Grenfell et al 1997, Heino et al. 1997). Both dispersal and correlated changes in the environment can synchronize populations, and thus tend to decrease regional stability. Dispersal can also increase stability via the rescue effect. *Bodo* colonizes a high proportion of leaves early in the season. The abundance at a site tends to increase then decrease as the season progresses (Figure 4.7), while at the same time incidence declines (Figure 4.3). I found that incidence decreased faster at sites where local populations were more synchronous (Figure 4.4). This result supports the prediction that population synchrony can have a negative effect on regional population stability.

Figure 4.5. Temporal similarity in population abundance. Each line is a comparison between leaf population size (xi) and the average abundance of all leaves at a site (n = 10). Arrows indicate rain events, and the dotted line shows the timing of mosquito manipulations. Lines near zero are synchronous with the metapopulation.

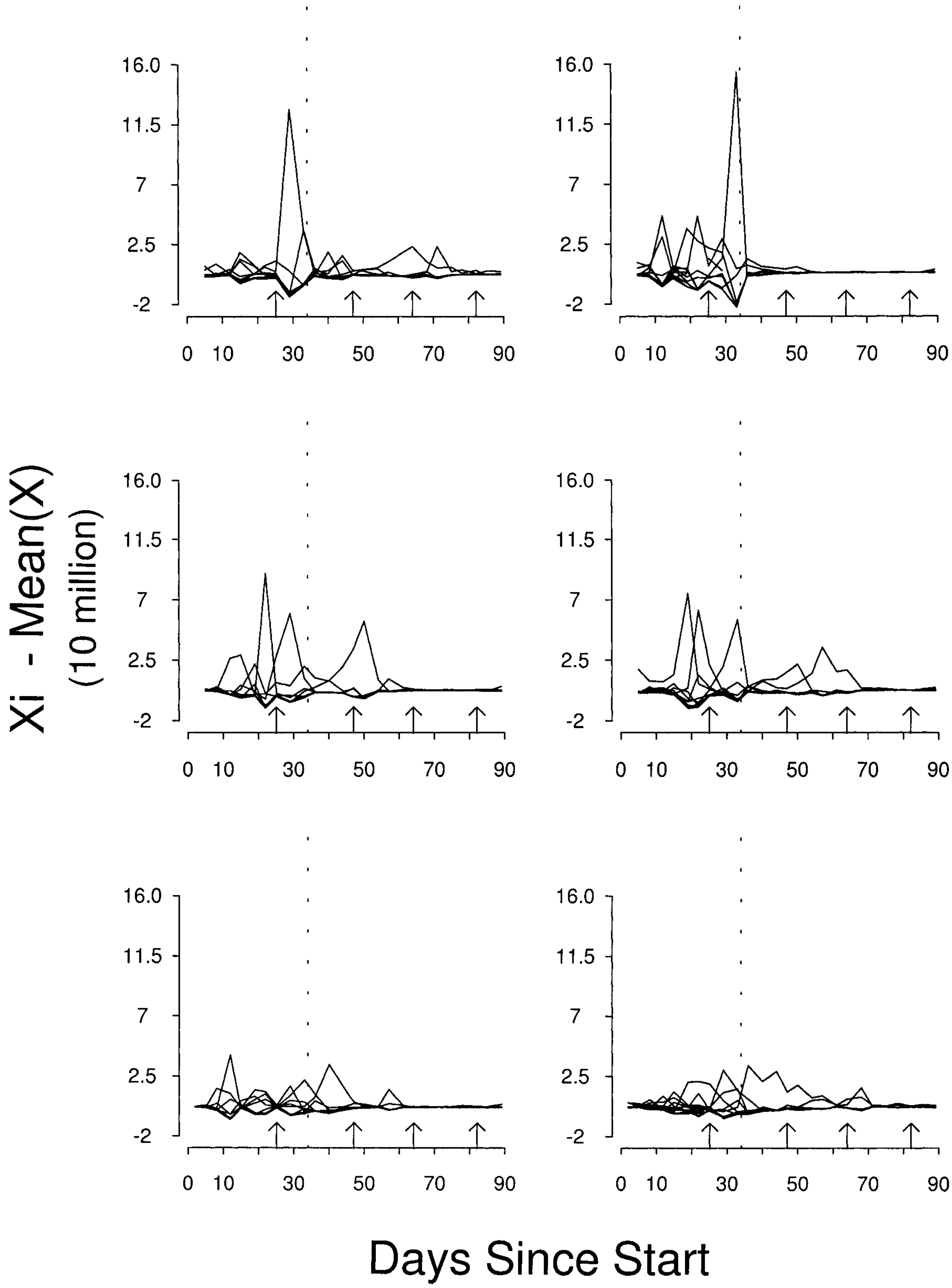

16.0
11.5
7
2.5
-2
0
10
30
50
70
90
Xi - Mean(X)
(10 million)
Days Since Start

Figure 4.5

Figure 4.6. Examples of *Bodo* population dynamics within six leaves. First row of graphs are for leaves at Duncan's Cove. Second and third rows are for leaves at Sandy's and Peggy's Cove.

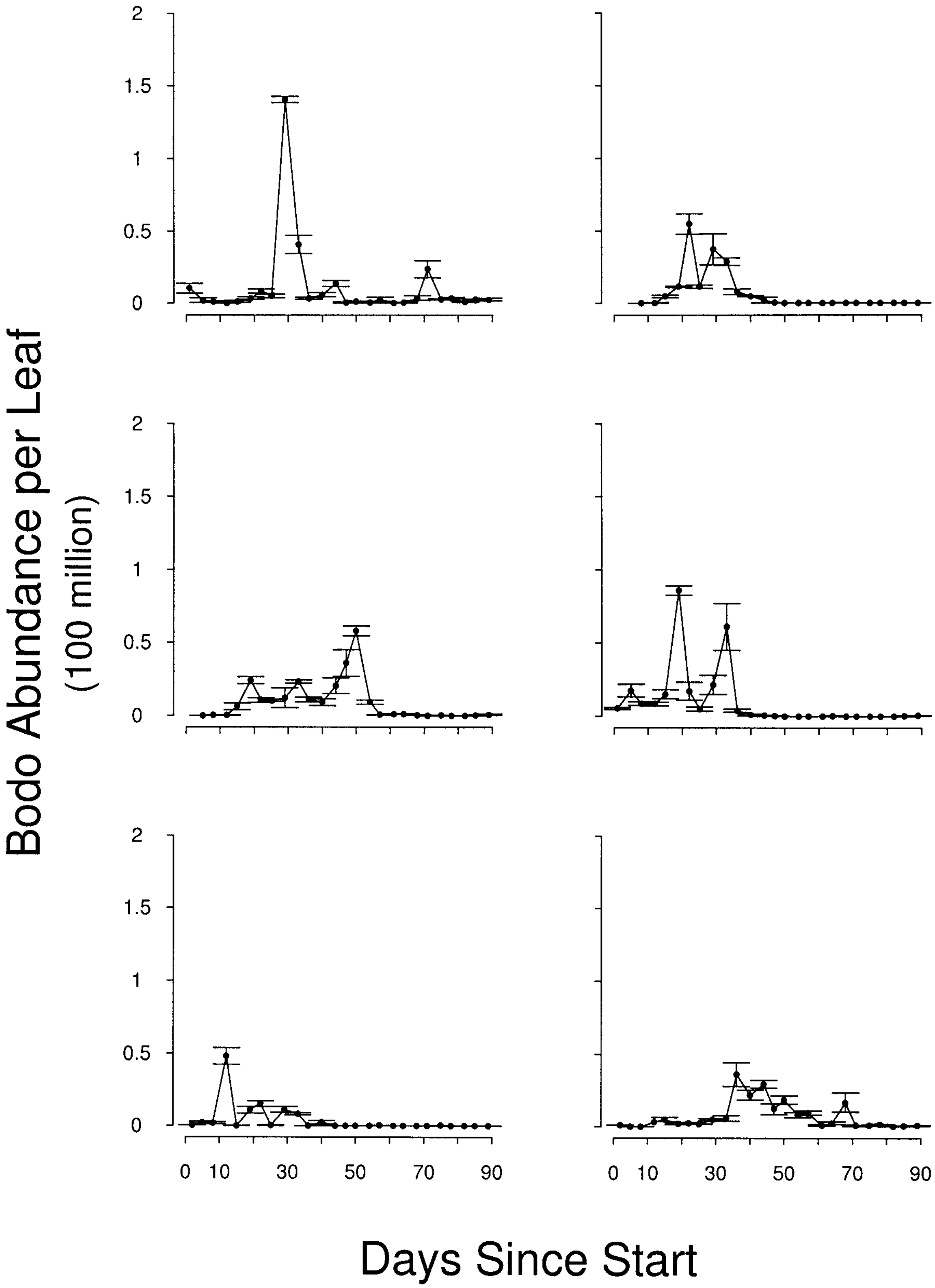

Bodo Abundance per Leaf
(100 million)
2
1.5
1
0.5
0
0
10
30
50
70
90
Days Since Start

Figure 4.6

Figure 4.7. The regional trend in *Bodo* abundance. Each line is the total abundance in 10 leaves at a site. First row of graphs are for sites at Duncan's Cove. Second and third rows are for sites at Sandy's and Peggy's Cove.

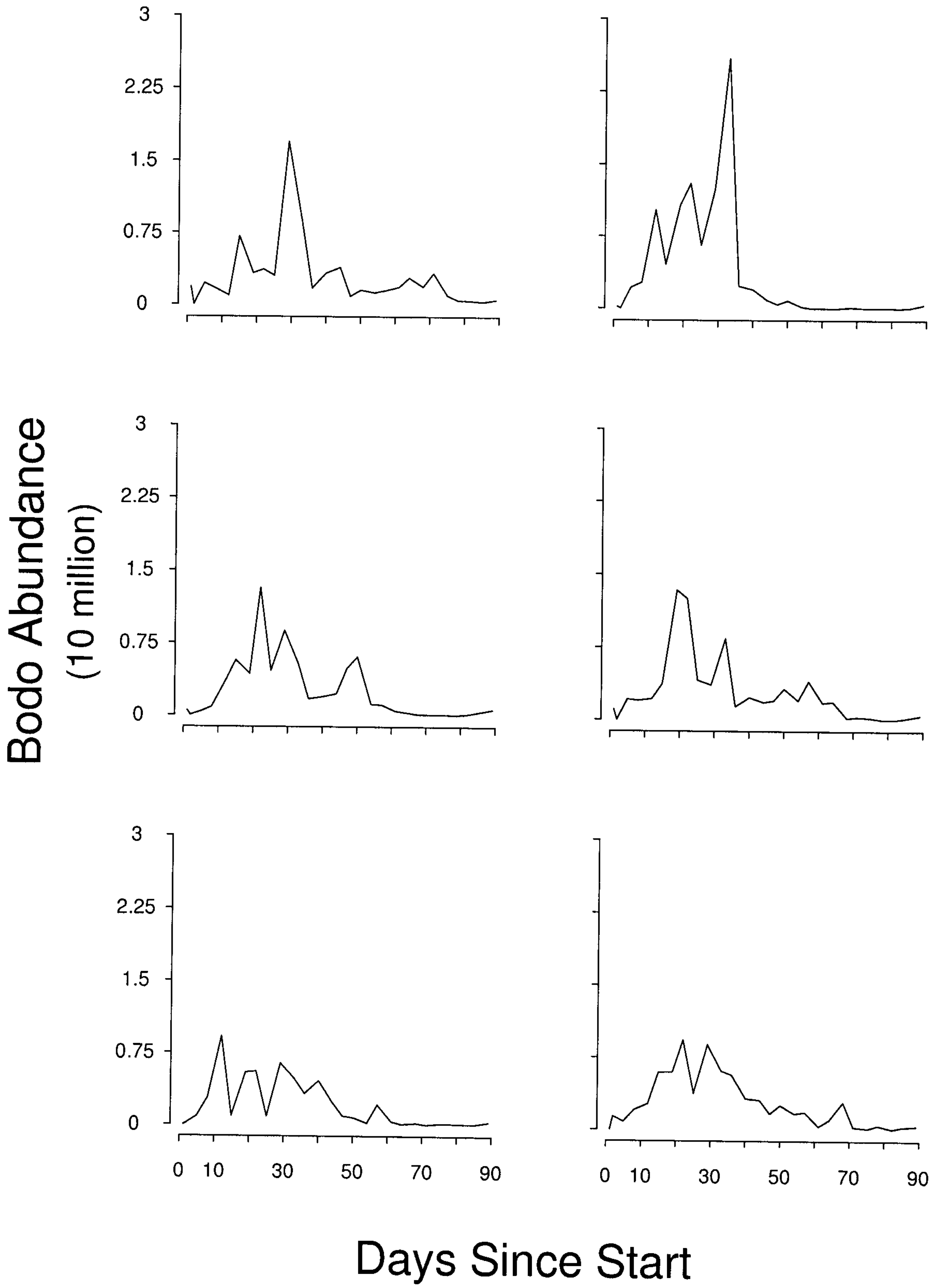

3
2.25
1.5
0.75
0
Bodo Abundance
(10 million)
0
10
30
50
70
90
Days Since Start

Figure 4.7

CHAPTER 5

Discussion

The study of pitcher plant communities has given me (and hopefully the reader) some insight into how local and regional processes affect population dynamics and community structure. In my study area, most leaves contain midges and mites, but many do not contain mosquitoes. When present, abundances in any leaf can vary widely. Patterns in pitcher plant colonization indicate some similarity or overlap in the leaves most colonized by these three arthropods. Mosquitoes, midges and mites more frequently colonized long leaves with high capture rates. The strength of the response depended on plant density, a meso-scale factor, with a stronger response where plants were sparse. Thus the process of community assembly depends not only on local factors but also to some extent on the meso-scale context.

The consequence of variation in community assembly is a heterogeneous array of local communities. Local interactions have the potential to change community structure during and after assembly. In pitcher plants, feeding by mosquitoes and midges affects the abundance and stability of the microfauna. Mosquitoes, which prey on bacteria and protists, decrease and destabilize the population dynamics of *Bodo*, *Cyclidium* and *H. rosa*. Midges feed on the detritus at the bottom of the leaf and increase bacterial densities. The response to resources depended on the taxa. *Bodo* populations were more stable in leaves with high midge density, indicating that midges facilitate *Bodo* growth. The effect of resources on the stability of *H. rosa* populations depended on predation rates. The addition of resources was destabilizing under low predation, but was stabilizing under high predation. Thus food-web interactions affect the population stability of pitcher plant microfauna.

The outcome of local interactions can affect regional dynamics. Models have shown that metapopulation stability is affected by extinction / colonization rates and the degree of population synchrony. Two studies predicted that as the strength of density regulation increased (≈ rate of increase, $\underline{r}$) population synchrony would decrease. For populations of *Bodo* in pitcher plant leaves, there was no relationship between the synchrony of and the maximum rate of increase ($r = -0.37$, $P = 0.47$), with r as the only explanatory variable. However, when mosquito abundance, midge abundance and r were included, all three factors had a significant and negative effect on site-level synchrony. These results show that local interactions along with a local process, i.e. population growth, can affect the stability of regional population dynamics.

Anyone who studies pitcher plant communities is impressed by the complexity of the interactions in such small space. I have demonstrated some of the ways that local and regional processes affect the population and community dynamics of pitcher plant microfauna. It is my hope that these results can be used to build a better understanding of the causes of community structure.

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