REPORT

Experimental evidence for alternative stable equilibria in a benthic pond food web

Jonathan M. Chase*

Department of Ecology and Evolution, University of Chicago, Chicago, IL 60637, USA Correspondence and present address: Department of Biology, Box 1137, Washington University, St Louis, MO 63130, USA
*Correspondence: E-mail: jchase@biology.wustl.edu

Abstract

Both local and initial conditions have been implicated in causing variation in the strengths of predator effects among natural communities. In this study, I performed a controlled mesocosm experiment using two common snails, *Physella gyrina* and *Helisoma trivolvis*, and their insect predator, *Belostoma flumineum*, to explicitly quantify and understand the causes of previously observed variation in food web interactions in natural ecosystems. The results from a controlled mesocosm experiment showed that: (1) at low productivity, snails were dominated by small-vulnerable species (*P. gyrina*), predator effects were strong and predator effects caused a trophic cascade extending to producers; (2) at high productivity, snails were dominated by large-invulnerable species (*H. trivolvis*), predator effects were weak and there was no trophic cascade to producers; (3) at intermediate productivity, alternative stable equilibria were implicated, such that depending on initial conditions, snails were dominated by either small-vulnerable or large-invulnerable species and predator effects were either strong or weak. Thus, this study represents one of the first to quantify how variation in food web structure can result from the local environment, initial conditions and their interaction.

INTRODUCTION

While most ecologists now agree that both resources and predators interact to structure natural food webs, it remains unclear why the relative strengths of food web interactions vary in space and time. Specifically, some studies have shown that predators can have strong effects on prey that cascade through the food web, while other studies find much weaker effects of predators (reviewed in Leibold *et al.* 1997; Persson 1999; Polis 1999; Chase 2000; Oksanen & Oksanen 2000). Some have proposed that local environmental conditions, such as the level of primary productivity, which vary in space and time, influence the relative strength of predation, and thus the equilibrium food web structure (e.g. Oksanen *et al.* 1981; Leibold 1996). Alternatively, others have proposed that initial conditions, such as the order in which species arrive in a community, create alternative stable equilibria in which the strength of predation varies (Paine *et al.* 1985; Bazely & Jeffries 1986; Petraitis & Latham 1999). An alternative stable equilibrium (sensu Lewontin 1969; May 1977) occurs when communities with identical environmental conditions can attain more than one equilibrium food web structure simply depending on the initial conditions of the community (e.g. the order in which species enter a community). Finally, there can be an interaction between the local environmental conditions and initial conditions, where alternative stable equilibria are predicted in some environments, but not in others (Van der Koppel *et al.* 1996; Chase 1999; Chase *et al.* 2000; Mylius *et al.* 2001).

Although a wide variety of theoretical models predict the possibility of alternative stable equilibria, few empirical demonstrations exist (but see e.g. Sait *et al.* 2000; Nelson *et al.* 2001; Scheffer *et al.* 2003). In previous research in the benthos of small pond food webs, I found a considerable amount of variation in the abundance, composition and strengths of food web interactions among ponds with intermediate levels of primary productivity (Chase 2003). These results were consistent with the concept of alternative stable equilibria at some, but not all levels of productivity. In addition, motivated by the observation that in these food webs, some prey species are small and always vulnerable to predators, while others could achieve sizes too large to be

eaten (Chase 2003), I developed a consumer-resource food web model to capture this complexity (Chase 1999). This size-structured food web model makes the following predictions about alternative stable equilibria, and the role of local environmental conditions and initial conditions on food web structure (see Chase 1999 for more detail).

At low primary productivity, prey growth is slow, and the benefits of a species growing to a size-refuge from predators is outweighed by the costs, in both longevity and reproductive output, resulting from the high likelihood of predation prior to achieving the refuge size. As such, smaller species that are superior competitors [in the sense of being able to maintain zero net growth on the least amount of resources; R* (Holt *et al.* 1994)] are able to persist, whereas larger, predator invulnerable species are driven extinct. In this case, the overall biomass of prey is predicted to be low and dominated by small-vulnerable prey species. Further, because the prey are uniformly vulnerable to predation, the relative effects of predators are predicted to be strong and cascade through the food web to producers.

At high productivity, prey growth is higher and the costs associated with growing to size-refugia become lessened relative to its benefits. As such, larger species that achieve a cost of large size by being poorer resource competitors are less vulnerable to predators [in the sense of being able to maintain zero net growth at a higher density of predators; P* (Holt *et al.* 1994)]. Here, the overall effect of predators on prey biomass should be weak because prey are dominated by large-invulnerable species. Prey biomass should be high and predator effects should not cascade to producers.

At intermediate productivity, dominance by either small or large prey species, and thus low or high prey biomass, can occur depending on initial conditions. That is, alternative stable equilibria are predicted. This is because when resources are intermediate, if the small prey species, which is a superior competitor, has higher initial densities (or enters a community first), it can drive resources below the level where the large prey species can invade the community and persist. Alternatively, if the large species, which is defended against predators as adults, but feeds predators as juveniles, has higher initial densities (or enters a community first), it can feed predators and increase their numbers such that the small prey species cannot invade the community and persist. In this case, the effects of predators on prey and their cascading effects to producers can be either strong or weak depending on which alternative state is realized.

MATERIALS AND METHODS

Study system

The two species of prey used in this experiment were the snails, *Physella gyrina* (hereafter *Physella*) and *Helisoma trivolvis* (hereafter *Helisoma*), which were two of the most abundant species of snails observed in surveys of natural ponds throughout south-western Michigan (USA) (Chase 1998, 2003). Both of these snail species are polyphagous and consume a variety of living algal cells, microbes and decaying plant and animal matter (Brown 1982), and like many species of pond snails, are sometimes able to have strong control over algal growth (Bronmark 1989; Chase 2003). The predator used in this experiment was the insect, *Belostoma flumineum* (Hemiptera: Belostomatidae) (hereafter, *Belostoma*); a common, and typically abundant predator that prefers snails to other prey items. *Belostoma* has several morphological attributes that enable them to effectively capture and subdue snails, including dexterous forearms and a long proboscis for invading snail shells. *Belostoma* eat snails throughout their life cycle; although they also readily consume other species (J. M. Chase unpublished data).

In addition to being some of the most common species in the natural pond systems (Chase 1998, 2003), these prey species and predators are ideal for testing the model of size-structured food web interactions discussed above (and in Chase 1999). *Physella* is small and highly susceptible to *Belostoma* (as well as other common species of predators; Chase 2003) at all size classes. Alternatively, *Helisoma* is vulnerable to *Belostoma* (and other predators; Chase 2003) as juveniles, but can grow to a predator-invulnerable size (Fig. 1). *Physella* and *Helisoma* can begin reproducing 1 and 2 months after hatching, respectively, and both have high reproductive rates (10–100 eggs per week). Thus, both species can complete at least two generations and should also approach their equililbria within these mesocosms in a single summer. Likewise, a single *Belostoma* male is able to mature 10–50 eggs per clutch complete its life cycle within
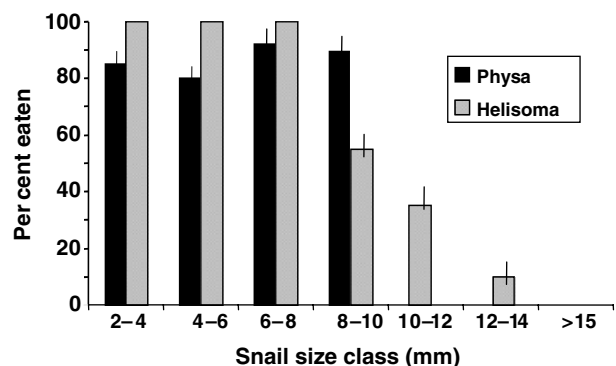

Figure 1 Susceptibility of different size classes of the snails, *Helisoma trivolvis* and *Physella gyrina*, to *Belostoma flumineum* predation in laboratory feeding trials. Five individual snails were placed with one adult *B. flumineum* for 48 h in a 15-l bucket. This was replicated five times for each snail species and size class. The average percent eaten (±1 SE) across all replicates is shown.

mesocosms in as quickly as 1 month, and have three to four generations in a single summer (J. M. Chase unpublished data). As the reproductive capacity of this species is much higher than the carrying capacity of a mesocosm, this species is able to approach equilibrium with a single season. Finally, the producers upon which this food web is based respond to variation in nutrient regimes and herbivory almost instantaneously through clonal growth, and thus also approach equilibrium within a single growing season.

Experimental design

I conducted a 3 × 2 × 2 factorial design mesocosm experiment manipulating primary productivity (three levels of nutrients), initial snail densities (two levels) and the presence or absence of predators (two treatments) at the Kellogg Biological Station (Calhoun County, MI, USA) pond lab facility. Each treatment was replicated four times. Mesocosms were 380-l polyethylene stock tanks filled with 2 cm of sand and nutrient poor well water to a uniform depth. Each mesocosm received a diverse inocula of naturally occurring planktonic and periphytic algae and zooplankton collected from 10 local ponds that varied considerably in environmental conditions. Zooplankton were introduced in order to maintain a nutrient balance between the pelagic and benthic food webs (e.g. Leibold & Wilbur 1992), the latter of which was the focus of this study. In addition, 50 g damp weight of the most common macrophyte, *Ceratophyllum demersum*, and 5 g each of the duckweeds *Lemna minor*, *Spirodela polyrhiza* and *Wolffia punctata*, and their associated epiphytes, were put into every mesocosm.

Primary productivity was manipulated by adding Phosphorus (P) in the form of NaH_2PO_4 and Nitrogen (N) in the form of $NaNO_3$ (keeping ratios constant), which are known to be limiting in this system, within the range of values observed from the natural survey (TP Range = 23–1337 μg/l; TN Range = 918–5888 μg/l). Low nutrient treatments received only well water (44 μg/l P: 935 μg/l N), intermediate productivity treatments received 5× ambient nutrient concentrations (220 μg/l P: 4675 μg/l N) and high productivity treatments received 10× ambient nutrient conditions (440 μg/l P: 9350 μg/l N).

In each mesocosm, a randomly chosen size-distribution of snails were stocked according to two treatments; (1) low density (=0.5× mean natural density; 12 *Physella* and eight *Helisoma* per mesocosm), (2) high density (=2× mean natural density; 48 *Physella* and 32 *Helisoma* per mesocosm). One week after snails were introduced, 10 second to third instar *Belostoma* nymphs were released into the mesocosms designated to receive predators.

Snails and *Belostoma* were counted approximately every 15 days to follow population growth and determine stability. At the termination of the experiment, all snails and

predators were enumerated and measured, and then converted to dry-weight biomass using length–weight relationships of those species from the mesocosms (Chase 1998). Macrophytes, duckweed and floating algae were removed, dried and weighed. Three subsamples (0.01 m²) of periphytic algae were scraped from the sides of each mesocosm, dried and weighed (this estimated the biomass of periphytic algae in the mesocosm, which is shown in the results).

Statistical analyses

I determined whether populations approached stability by comparing the difference in snail biomass from one 15-day census period to the next over the last 60 days of the experiment (when the populations of snails appeared to have levelled off). If the change in the biomass within a mesocosm over several census periods is significantly different from zero, then it can be concluded that the population is still changing. If, however, the relative change in biomass over several census periods is not significantly different from zero, then it can be reasonably concluded that the population has achieved some sort of quasi-stability.

As I was primarily interested in testing for the effects of predators and initial snail density on the biomass and composition of snails and producers under different levels of nutrients, I analysed each nutrient treatment separately to explicitly test my hypotheses. Within each nutrient treatment, I used ANOVA to test for treatment differences for each trophic level (predators, snails and producers) using predator and initial snail density treatments as factors. Next, I separated snails and producers into subgroups. Snail subgroups were *Helisoma* and *Physella*, and producer subgroups were macrophytes (which included the macrophyte, *C. demersum* and the duckweeds) and algae. The effect of the same factors, predators and initial snail biomass, on the biomass of snails and producers was analysed using MANOVA followed by univariate ANOVAs on subgroups when MANOVA was significant. Significant ANOVAs were followed by Tukey's HSD for pairwise comparisons among treatments.

All analyses were performed using Systat 7.0 for Windows.

RESULTS

For every mesocosm in this experiment, the relative change in snail biomass was not significantly different from zero over the last four census periods (60 days) of the experiment (*t*-tests: $P > 0.1$) and thus all mesocosms appeared to stabilize (Fig. 2). Furthermore, the size-structure of the population, in terms of the relative proportion of small and large individuals, did not change over the same
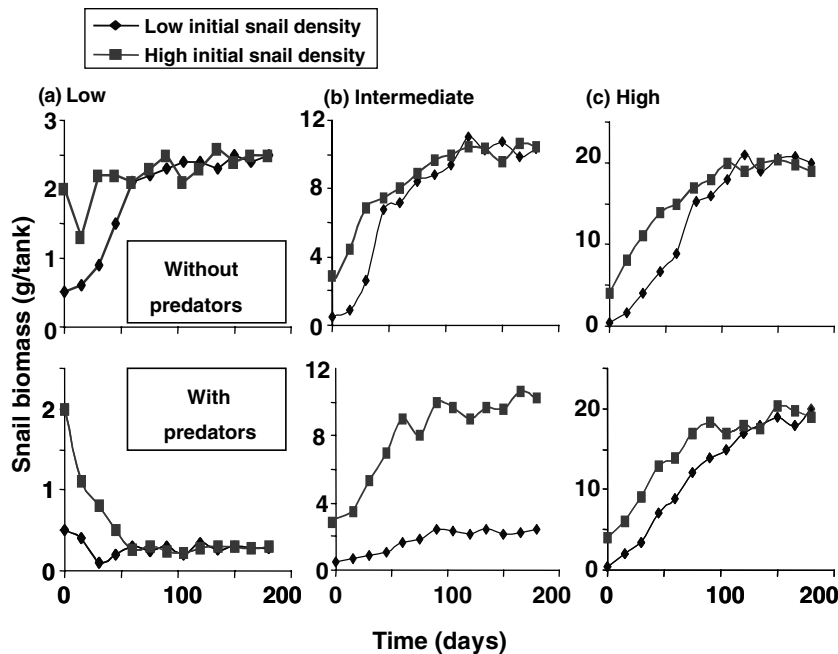
Figure 2 Upper panels represent snail biomass trajectories without predators present, while lower panels represent trajectories with predators for low (a), intermediate (b) and high (c) nutrient treatments. Symbols represent the mean estimated density at each census (high initial snail density treatment = squares, low initial snail density treatment = triangles); error bars are not presented for clarity.

four censuses (*t*-tests: $P > 0.01$). Because of this, I only used the final destructive census of producers and animals for the remaining analyses. I present MANOVA results in text and ANOVAs in Table 1. Furthermore, when analysed as the entire $3 \times 2 \times 2$ experimental design, results are identical.

In the low nutrient treatments, the initial snail density treatment had no effect on predator biomass (Table 1). Snail biomass was affected by predators (MANOVA; $F_{2,11} = 9.88$, $P < 0.004$), but not initial snail density treatment ($F_{2,11} = 0.48$, $P > 0.63$) or their interaction ($F_{2,11} = 2.41$, $P > 0.14$) (Fig. 3a). The overall negative effect of predators on snail biomass was solely due to the negative effect of predators on *Physella* (the small snail), because predators had no effect on the large snail, *Helisoma* (Table 1). Producer biomass was also affected by predators (MANOVA; $F_{2,11} = 6.87$, $P < 0.01$), but not initial snail density ($F_{2,11} = 1.32$, $P > 0.30$) or their interaction ($F_{2,11} = 0.26$, $P > 0.77$). The positive effect of predators on total producer biomass was solely due to the response of algae, because there were no effects on macrophytes (Table 1, Fig. 3b).

In the intermediate nutrient treatments, final predator biomass was higher in the high initial snail density treatment (Table 1). Final snail biomass was affected by predators (MANOVA; $F_{2,11} = 11.53$, $P < 0.002$), initial snail density ($F_{2,11} = 11.53$, $P < 0.002$) and their interaction ($F_{2,11} = 14.24$, $P < 0.001$). Snail biomass was lower with predators than without predators when initial snail density was low, but was unaffected by the predator treatment when initial snail density was high (Table 1, Fig. 3c). *Physella* was

uniformly less abundant in the presence of predators, regardless of the initial snail density treatment. However, *Helisoma* biomass was significantly higher in the presence of predators under high, but not low initial snail density (Table 1, Fig. 3c). Producer biomass was affected by the predator treatment (MANOVA; $F_{2,11} = 13.58$, $P < 0.001$), the initial snail density ($F_{2,11} = 8.14$, $P < 0.007$) and their interaction ($F_{2,11} = 21.49$, $P < 0.0001$). Both algae biomass and total producer biomass increased with predators under low initial snail densities, but was unaffected by the predator treatment at high initial snail densities. Macrophyte biomass was unaffected by both treatments and their interaction (Table 1, Fig. 3d).

In the high nutrient treatments, there was no effect of initial snail density on predator biomass (Table 1). Snail biomass was affected by predators (MANOVA; $F_{2,11} = 7.31$, $P < 0.01$), but not initial snail density ($F_{2,11} = 0.32$, $P > 0.74$) or their interaction ($F_{2,11} = 0.53$, $P > 0.60$). *Physella* biomass was lower with predators than without predators, whereas *Helisoma* biomass was higher with predators than without predators. There was no effect of predators on total snail biomass (Table 1, Fig. 3e). Producers were not influenced by predators (MANOVA; $F_{2,11} = 0.11$, $P > 0.89$), initial snail density ($F_{2,11} = 1.34$, $P > 0.36$) or their interaction ($F_{2,11} = 0.60$, $P > 0.57$) (Table 1, Fig. 3f).

DISCUSSION

There has been much debate and confusion surrounding the definition of, existence of, and criteria for alternative stable

Table 1 Results from ANOVA on the effect of predators (P) and initial snail density (I) on the biomass of snails (and the subgroups, *Physella* and *Helisoma*) and producers (and the subgroups, macrophytes and algae). These are analysed separately at each level of productivity

Response	Effect	d.f.	Productivity								
			Low			Intermediate			High		
			MS	F	P	MS	F	P	MS	F	P
Predator	I	1	0.01	0.27	0.62	0.05	0.05	0.02	0.01	0.53	0.49
Snail	P	1	5.40	4.69	0.05	226.69	15.39	0.002	63.22	1.53	0.23
	I	1	0.12	0.10	0.76	367.07	24.92	0.0001	6.93	0.17	0.69
	P × I	1	1.66	1.45	0.25	456.76	31.01	0.0001	7.26	0.18	0.68
Physella	P	1	1.60	16.31	0.002	2.78	10.74	0.007	1321	54.89	0.0001
	I	1	0.09	1.00	0.34	0.21	0.84	0.38	0	0	0.99
	P × I	1	1.08	2.79	0.16	0.01	0.05	0.84	0.03	0.01	0.97
Helisoma	P	1	1.19	1.15	0.30	278.96	18.22	0.001	1962	134.5	0.0001
	I	1	0.42	0.44	0.52	384.88	25.13	0.0001	6.87	0.47	0.51
	P × I	1	0.41	0.42	0.53	461.32	30.13	0.0001	8.27	0.57	0.47
Producers	P	1	875.57	6.03	0.03	486.84	12.15	0.005	259.20	2.93	0.11
	I	1	427.89	2.95	0.11	246.54	6.15	0.03	81.51	0.92	0.34
	P × I	1	69.74	0.48	0.50	788.14	19.67	0.001	57.52	0.65	0.44
Algae	P	1	900.36	7.14	0.027	86.15	27.97	0.0001	7.91	0.12	0.74
	I	1	352.90	2.79	0.12	454.02	16.15	0.002	152	2.28	0.16
	P × I	1	66.47	0.53	0.48	1249.1	144.47	0.0001	0.40	0.01	0.94
Macrophyte	P	1	0.17	0.08	0.78	35.69	2.51	0.14	259	2.93	0.11
	I	1	3.61	1.65	0.22	31.42	2.21	0.16	81.06	0.91	0.36
	P × I	1	0.04	0.18	0.89	52.96	3.72	0.07	57.52	0.65	0.44

equilibria. An alternative stable equilibrium only occurs when a system can follow one of several trajectories, as a result of differences in some sort of initial conditions, although the environmental conditions are identical. Thus, when different communities form in different environments, they are different equilibria, not alternative stable equilibria (Connell & Sousa 1983; Young *et al.* 2001). In addition, a variety of cases where a community cycles between one state and another due to intrinsic factors, are not true alternative states; instead, the community cycles periodically between states. For example, Persson *et al.* (2003) showed how a community periodically alternates between a state where cannibalistic adult top predators control juveniles, which cascades through the food web, and a state dominated by juveniles that control their prey.

True alternative stable equilibria have been discussed in several contexts related to community and ecosystems ecology: (1) Alternative densities or dynamical trajectories of a group of coexisting species can occur under differing initial conditions; here, the identity of species remains the same, but the density and dynamics differ among states (e.g. Schoener 1974; McCauley *et al.* 1999). For example, Nelson *et al.* (2001) demonstrated that the population dynamics of an herbivorous zooplankter (*Daphnia pulex*) and their algal food resource followed one of two trajectories, one dominated by a high biomass of herbivores, and the other by a low biomass of herbivores. (2) Interspecific interactions

between similar species (e.g. competitors) within a community can lead to alternative stable equilibria when the order in which species enter a community can influence final community structure because early colonizers can preclude invasion by late colonizers (e.g. Law & Morton 1993; Luh & Pimm 1993; Samuels & Drake 1997; Law 1999; Scheffer *et al.* 2003). For example, Drake (1991) showed that, in some cases, different communities of zooplankton established among otherwise identical microcosms, and this effect was caused by differences in the order in which species colonized (see also Drake *et al.* 1993). (3) Interspecific interactions interact with ecosystem level variables to create alternative states that are manifest at the ecosystem level, such as differences in the standing crops of entire functional groups or trophic levels (e.g. Petraitis & Latham 1999; Dent *et al.* 2002). For example, Scheffer (1998) discussed how shallow lakes could transition between dominance by macrophytes and clear water, or by algae and turbid water, and that this effect was likely to be an alternative stable equilibria.

While each of the above cases represents alternative stable equilibria in the conceptual sense, biologically, each has quite different effects on the system of study. The results of the alternative stable equilibria that I observed in the pond benthic food web might be some combination of the later two types. Initial conditions altered which species were favoured, and in some cases, influenced which
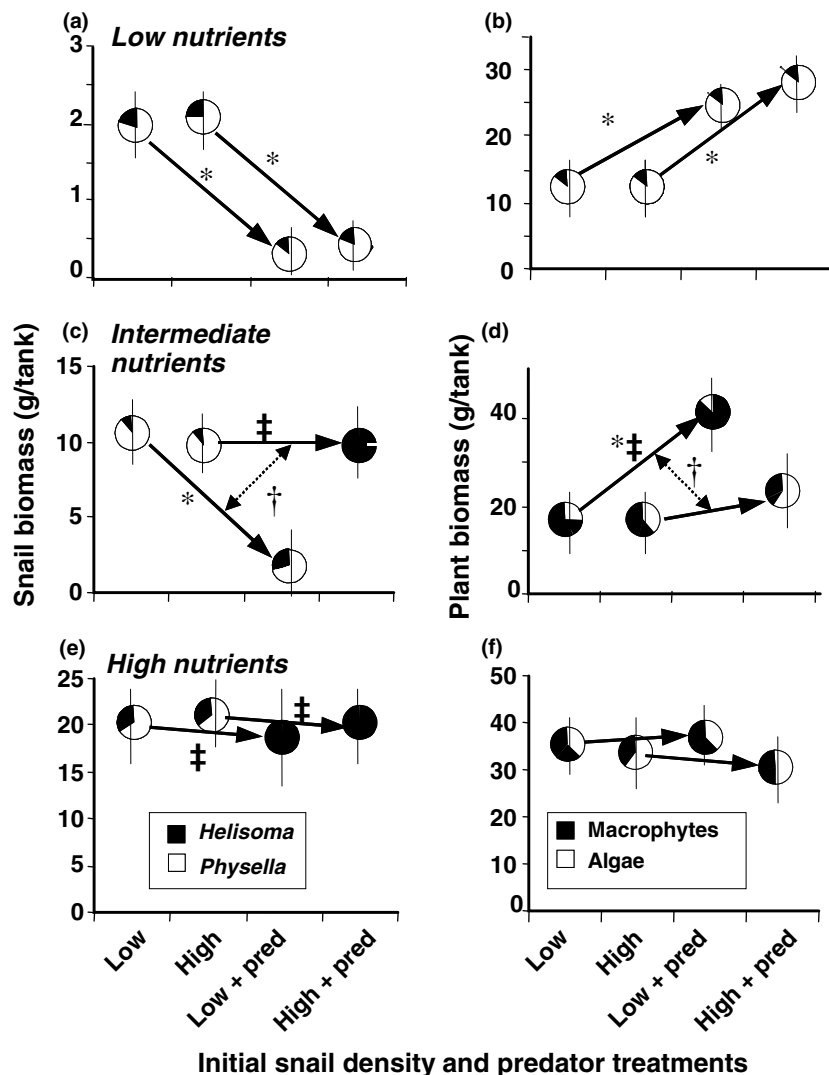
Figure 3 Final biomass and composition of snails (left panels) and producers (right panels) from mesocosm experiment in each nutrient treatment (a and b are for low nutrients, c and d are for intermediate nutrients, and e and f are for high nutrients). Total biomass is represented by the position of the circle on the graphs, while composition is represented by the proportions in the pie charts. SE bars are represented for total biomass only (not composition). Solid lines with arrows lead from each initial density treatment (low or high) without predators to its respective initial density with predators. Asterisks (*) next to an arrow represent a significant difference in total biomass (herbivores or producers) ($P < 0.05$), double-crosses (‡) denote significant differences in the composition of both groups of herbivores or producers (i.e. a shift in compositional dominance) ($P < 0.05$). Crosses (†) next to a dotted line with an arrow denotes a significant effect of the initial condition treatment on the final outcome of both herbivore and producer biomass and composition (see Table 1).

species persisted. This effect, in turn, created variation at the ecosystem level in terms of the level of standing biomass of primary producers and secondary consumers. However, alternative states at the ecosystem level are often discussed in the context of very long time and very large spatial scales, which my study did not do. Furthermore, I have no evidence of switching between states, which appears to occur at least in some systems, particularly after catastrophic disturbances (Carpenter 2001; Scheffer *et al.* 2001).

One of the most difficult tasks in devising a food web experiment that truly tests a theoretical framework is to make certain that the biological components of the system allow congruence with the assumptions of the model (e.g. allowing for numerical responses of predators and prey, enough time for equilbrial dynamics to be expressed, etc.). For this reason, I chose to use the two snails and insect predator (along with algal and macrophyte food resources)

because I knew they could thrive and complete their life cycles in a relatively short time period within the confines of the artificial mesocosms. Indeed, the length of the experiment (180 days) allowed a minimum of two generations of each species at the lowest productivity, and up to five generations of some species at the highest productivity. Because of the fecund nature of both prey and predators, this time period appeared to be long enough to allow for considerable population responses. Connell & Sousa (1983) presented very stringent criteria for detecting stability, and in particular, the possibility of alternative stable equilibria in ecological communities. Specifically, they suggest that experiments must encompass a time period of several generations of the interacting species, and that species abundances appear relatively stable over much of this time.

I suggest that the variation in community structure observed at intermediate levels of nutrients in this mesocosm experiment represents experimental evidence

for the lasting effects of initial conditions leading to alternative stable equilibria, rather than transient phenomena. This is because: (1) the high fecundity and rapid generation times of the organisms within the experiment ensured a minimum of three to five generations of each species; (2) the observed stability in snail population densities over the later half of the experiment, despite considerable births and deaths (Fig. 2), as well as the stability in snail size structure over the same period; (3) the fact that variation in initial snail density had no influence on final community structure under many conditions (Figs 2 and 3). In addition, alternative stable equilibria only appeared under certain environmental conditions, suggesting an interaction between environmental and initial conditions.

Despite the strong suggestive evidence that this community can persist in alternative states, I cannot say for certain whether these represent two alternative stable states, or whether one of the states is a saddle point which is neutrally stable, but which will revert to the other state upon small perturbations. In order to test this, I would have had to perform small-scale perturbation experiments on each of the states, to see whether they reverted back to the original state, and thus they were stable, or whether one or the other state no longer persisted. However, based on the fact that I have found similar potentially alternative states persisting among a wide variety of natural systems in my field studies (Chase 2003), I believe these communities are more likely to reflect alternative stable states, rather than a stable and a saddle point.

This experiment appeared to support most of the qualitative aspects of the general food web model with size-structured interactions (Chase 1999). (1) At low nutrient input, the herbivore community was always dominated by small herbivore species and predator effects were large and cascaded to the producer trophic level; (2) At intermediate nutrient input, when predators were present, the initial conditions of the herbivore community played a large role in determining whether communities were dominated by small herbivore species and had large predator effects, or were dominated by large herbivore species and had smaller predator effects; (3) at high nutrient input, the herbivore community was dominated by large species in the presence (but not absence) of predators, and predators had little overall effect on plant biomass or composition.

Although the results of this study are consistent with the predictions of the size-structured food web model of Chase (1999), I cannot rule out a variety of other mechanisms that lead to the same set of results. For example, several other models predict the same patterns of alternative stable equilibria only at intermediate, but not low or high, levels of productivity. Mechanisms that predict this pattern include predator swamping, where prey become so abundant that

predator efficiency declines (Van der Koppel et al. 1996), intraguild predation, where top predators eat and compete with intermediate predators (Holt & Polis 1997; Diehl & Feißel 2000; Mylius et al. 2001), and prey tolerance, where prey regrow (individually or at the population level) following consumption by predators (Holt et al. 1994; Chase et al. 2000).

Most ecologists agree that food web interactions can often be highly variable through space and time, but few studies have been explicitly designed to examine causes of this variation. Indeed, meta-analyses in both aquatic (Brett & Goldman 1996, 1997) and terrestrial (Schmitz et al. 2000; Halaj & Wise 2001) systems look for an overall effect of trophic level manipulations, ignoring the importance of variation in those effects (Leibold et al. 1997). Recently, Shurin et al. (2002) reviewed the evidence for the relative strengths of trophic cascades among different types of ecosystems and found important variation among ecosystems. For example, trophic cascades in the benthos of aquatic ecosystems, such as those considered in this study, tended to be much stronger than in other types of ecosystems. Although meta-analyses such as that presented by Shurin et al. (2002) provide important information about variation in the strengths of trophic interactions across ecosystem types, there is a considerable amount of variation within ecosystem types, such as the benthic pond ecosystems considered here. The key results from my study show that the variation in the strengths of food web interactions within an ecosystem type is driven deterministically both by environmental conditions (e.g. nutrient inputs) and initial conditions. As such, I suggest that in order to determine the relative importance of consumer- vs. resource-limitation of food webs, and how those interactions act to structure natural communities, it is essential to explore the causes and consequences of the spatial and temporal variations often observed in food web interactions within ecosystem types.

In this study, there were many more complexities of species interactions that are beyond the scope of the current paper, but which will importantly influence these sorts of food web interactions. For example, the producer community shifted from dominance of filamentous algae when herbivory was weak to dominance of macrophytes when herbivory was intense. Such results are expected in benthic food webs, because macrophytes are inedible to a majority of herbivores, whereas algae are favoured (e.g. Bronmark 1989; Chase 2003). Similarly, I manipulated nutrients (N and P) so as to maintain ratios constant, whereas variation in nutrient ratios, as well as light, can have profound effects on the nature of the interactions between aquatic herbivores and their algal food resources (e.g. Urabe et al. 2002). Finally, although I have focused only on the living food web, of producers, herbivores and predators, the herbivores I have considered (snails) also consume a considerable

amount of detritus. Recent evidence from a terrestrial system has shown differential indirect effects and trophic cascades between living and detrital food webs (Dyer and Letourneau 2003), and such differences may complicate the overall picture of the benthic food web discussed here.

Several previous studies have implicated size-refugia as a mechanism leading to alternative stable equilibria in a variety of natural systems (e.g. Paine 1976; Paine *et al.* 1985; Bazely & Jeffries 1986; Dublin *et al.* 1990). However, the empirical evidence presented here provides the first conclusive evidence for the occurrence of alternative equilibria in such a system. Specifically, in these pond food webs, the mechanism of size-refugia influences how food web structure responds to environmental conditions (i.e. primary productivity), initial conditions and their interaction. As the mechanism of size-refugia is commonly observed in several natural systems and is one of several mechanisms that can lead to alternative stable equilibria, I suggest that both environmental and initial conditions might play a larger role in determining the structure of natural food webs than was once suspected. In fact, many theoretical models predict an interaction between environmental and initial conditions in structuring food webs when a species embedded within a food web has greater per capita effects on the other species than on its own species (interspecific effects are greater than intraspecific effects) (e.g. Holt *et al.* 1994; Van der Koppel *et al.* 1996; Chase *et al.* 2000; Mylius *et al.* 2001). As such, I suggest that empirical ecologists will gain a better understanding of the factors that influence the structure of natural food webs by considering both environmental and initial conditions that vary naturally among localities.

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