

CONSUMER SPECIES RICHNESS AND AUTOTROPHIC BIOMASS

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Abstract. We tested whether standing autotrophic (unicellular algal) biomass is sensitive to variation in initial consumer (nondecomposer, heterotrophic protistan) diversity in experimental microbial microcosms. Our results showed a strong, negative relationship between autotrophic biomass and consumer species richness. Additional microcosm experiments showed that this relationship was due largely to the direct and indirect trophic effects of consumers on autotrophs and decomposers. Collectively, these experiments suggest that standing autotrophic biomass is a function of community composition, trophic structure, and consumer diversity, the determining factors being the number of trophic levels, the discreteness of trophic levels, and the ecological equivalency of species within trophic levels. Our results suggest that ecosystem response to variation in consumer diversity can range from abrupt changes between “green” (high autotrophic biomass) and “barren” (low autotrophic biomass) states to relatively smooth transitions between these states.

Key words: *autotrophic biomass; biodiversity; community; ecosystem functioning; microcosm; protists; species richness; trophic structure.*

INTRODUCTION

Two issues are central to community ecology. These are, what governs variation in biotic diversity among ecosystems (the distribution and abundance of species) and what governs variation in standing biomass among ecosystems (the distribution and abundance of energy and materials among abiotic and biotic components)? Synthesizing these two yields a third; how does variation in biotic diversity among ecosystems govern variation in standing biomass among ecosystems? Many ecologists have addressed the more focused issue of how consumer, or nondecomposer heterotrophic diversity, either as the number of species or trophic groups, affects standing autotrophic biomass. That is, how does the composition of consumer communities affect how “green” or “barren” an ecosystem appears? This is the background for our study.

Although Elton (1927) first proposed a pyramidal distribution of biomass among trophic levels within an ecosystem, with autotrophic biomass at the base, this trophically based perspective implied no specific relationship between variation in consumer diversity and standing autotrophic biomass. Much later (1960), Hairston, Smith, and Slobodkin (HSS) would be the first to explicitly propose a relationship between variation in community composition and autotrophic biomass. HSS proposed that an ecosystem alternates between states of high levels of autotrophic biomass (“green worlds”) and low levels of autotrophic biomass (“barren worlds”) as numbers of trophic levels vary. Al-

though useful heuristic constructs for understanding community composition and biomass, neither Elton’s pyramid nor HSS patterns have proven to be universal features of ecosystems (Strong 1992, Abrams 1993, Del Giorgio and Gasol 1995). Thus, the association between consumer diversity and standing autotrophic biomass remains unclear.

We experimentally examined the association between variation in protistan consumer diversity and standing unicellular algal biomass in microbial microcosms to test for patterns of association between biotic diversity and autotrophic biomass. Our studies addressed the following questions. First, under equal levels of energy input, starting with equal quantities of nutrients and equal complements of decomposers, after many generations, would replicate ecosystems show different mean amounts of autotrophic biomass if consumer diversity differed among them? Second, would there be any pattern of variation in autotrophic biomass associated with variation in consumer diversity?

Three distinct perspectives in ecology provide testable hypotheses concerning the relationship between standing autotrophic biomass and consumer diversity. One perspective, which we will call the “systems” perspective, sees biomass distribution as a function of energy and material flows among “components” where components are functionally defined by their biogeochemical or trophic activities within ecosystems. That is, autotrophic biomass is a dependent function of ecosystem processes (energy and material flows), and the thermodynamic (Odum and Pinkerton 1955, Odum 1956, 1994, and papers in Higashi and Burns 1991) and stoichiometric (Reiners 1986, Sterner 1990, Sterner et al. 1992) principles that govern them. This per-

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spective regards biomass distribution as relatively insensitive to changes in diversity (Schulze 1995).

A second perspective, which we will call the "population" perspective, sees biomass distribution as a function of population dynamics. From this perspective, the assemblage of interacting species, or "community," within an ecosystem acts as the "engine" of an ecosystem's biogeochemical activity. Ecosystem response is a function of the pattern (structure) of interactions among species and stability is, in part, a function of this structure (e.g., MacArthur 1955, May 1973, Goodman 1975, Pimm and Lawton 1977, King and Pimm 1983, De Angelis 1992, Haydon 1994, Loreau 1995, McGrady-Steed et al. 1997, Naeem and Li 1997, Sterner et al. 1997). Autotrophic biomass is the cumulative product of such population-based processes. In contrast to the systems perspective, this population perspective sees such an enormous variety of possible responses to variation in consumer diversity that there is no way to generally predict autotrophic biomass (Del Giorgio and Gasol 1995). Rather, if autotrophic biomass is considered an ecosystem or community property, each species may have a unique impact on autotrophic biomass ranging from those with high to those with low "community importance values" (sensu Power et al. 1996).

A third perspective, which we will call the "trophic" perspective, focuses on food web processes. From this perspective, the distribution of biomass in ecosystems is determined by the structure of the food web, which regulates energy and material flow through trophically defined groups. The pattern of biomass distribution is therefore a function of trophic structure, nutrient loading, and energy input (Hairston et al. 1960, Oksanen et al. 1981, Pimm 1982, Carpenter et al. 1987, Wootton and Power 1993, Polis and Winemiller 1996, Wootton et al. 1996, but see also, Abrams 1993). This perspective sees biomass as suppressed in the presence of consumers and released from suppression when consumers are absent or suppressed by other consumers (Hairston et al. 1960, Oksanen et al. 1981, Wootton and Power 1993). As described above, a pattern of ecosystems alternating between "green" and "barren" states occurs with variation in numbers of trophic levels. The strength of this pattern, however, depends on the degree to which species aggregate cleanly into trophic classes (L. Oksanen, *personal communication*). Omnivory, invulnerable basal species, and diffuse trophic boundaries can prevent consumer suppression (e.g., Abrams 1993, Del Giorgio and Gasol 1995).

These contrasting perspectives all recognize autotrophic biomass as a dependent function of consumer diversity, but each makes different statements about the pattern of association expected as consumer diversity changes. These contrasting perspectives are not in conflict with one another; they address different aspects of ecosystem dynamics. Of interest are the relative con-

tributions of these different processes to biomass distribution.

From these perspectives, a null hypothesis emerges in which one would predict that, after many generations, at a fixed point in time no relationship between consumer diversity and autotrophic biomass would be found (the systems perspective, e.g., Schulze 1995). Trophic-based theory, however, predicts that a relationship between autotrophic biomass and consumer diversity would be found; in particular, autotrophic biomass would be suppressed with the addition of herbivore species and would be released from suppression if predators were added later (Hairston et al. 1960, Oksanen et al. 1981, Wootton and Power 1993). When species cannot be effectively coalesced into trophic groups, however, no necessary pattern of association is expected (e.g., Del Giorgio and Gasol 1995) even if autotrophic biomass is a function of consumer diversity.

Contrasting perspectives in theory such as the above are frequently addressed by empirical testing of the hypotheses each perspective generates. To examine the hypothetical relationship between consumer diversity and autotrophic biomass, however, requires manipulating community composition as an experimental factor while monitoring autotrophic biomass response and holding all other factors constant; such experiments are relatively intractable by traditional field methods (Wootton 1994, Naeem et al. 1995, 1996). As in most scientific disciplines, using experimental models to explore theory when field tests are impractical is an effective way to gain preliminary insight into the relative merits of contrasting ecological theory (Kareiva 1989, Lawton 1995, Drake et al. 1996, Lawler 1996, but see Carpenter 1996), and microbial microcosms have figured prominently in these methods (e.g., Gause 1934, Hairston et al. 1968, Vandermeer 1969, Luckinbill 1973, 1974, 1979, Drake 1991, Lawler and Morin 1993).

We followed in this tradition of using microcosms to test the different hypothetical relationships between consumer diversity and standing autotrophic biomass made by the three different perspectives in ecology. In the first experiment, we constructed aquatic, microbial microcosms containing small numbers of autotrophs (unicellular green algae) and decomposers (heterotrophic bacteria) and maintained them under uniform environmental conditions for many (>25) generations, but randomly varied the number of consumer species (heterotrophic protists) stocked in these replicate microcosms. Small numbers (<25) of consumers were added to microcosms and allowed to grow. Once algal densities stabilized (<14 d), we measured autotrophic biomass as a function of initial consumer diversity. If no pattern of association was found, this would support the null or systems-based perspective. A strong, negative association between consumer species richness and autotrophic biomass, however, was found. We

therefore conducted a series of additional experiments to explore how specific changes in the trophic structure of replicate microcosms explained the pattern observed in the first experiment. We varied the number of trophic levels, to test the trophic-based hypothesis by uncovering switching in autotrophic biomass between green and barren states if it occurred. We also varied the number of species and number of species per trophic level which would test the population-based hypothesis by uncovering autotrophic biomass sensitivity to variation in community composition if it occurred. By use of omnivores, we also manipulated the degree of discreteness of trophic levels which would test the trophic-based perspective that diffuse trophic structure would provide a pattern of association between autotrophic biomass and consumer diversity.

METHODS

Overview.—We constructed microcosms that contained autotrophs, decomposers, and dead organic and inorganic nutrients and varied the number of consumer species stocked in each microcosm. For simplicity, we refer to these nondecomposer heterotrophs as “consumers,” which includes herbivores, detritivores, omnivores, and top predators. Consumer species were all protists. Our decomposer species were bacteria whose primary source of energy and nutrients were from dead organic matter. Although decomposers might possibly have absorbed carbohydrates leaked from autotrophs, our experiments were conducted at low light levels (see below), which limited this possibility.

The rationale for this design is based on the principle that autotrophic biomass is determined by both biogeochemical and trophic processes in ecosystems. Harte and Kinzig (1993) identify autotrophs and decomposers as core biotic components and inorganic nutrients and dead organic material as core abiotic components universal to most ecosystems (Fig. 1). These core biotic components regulate the principal flows of energy and materials between the abiotic components and ultimately determine the standing autotrophic biomass. Consumers secondarily modify these flows (Fig. 1). Consumers typically represent trophic groups that either have autotrophs as basal species, decomposers as basal species, or omnivorous consumers that consume from different basal groups (Fig. 1). Flow of energy and materials among these “peripheral” components is governed by trophic links, such as herbivory, detritivory, predation, or omnivory (Fig. 1). Thus, variation in consumer diversity consists of changes in the number of consumer trophic levels and the number of species within these levels. These changes primarily affect autotrophic biomass by direct consumption (e.g., herbivory) and altering mineralization (return of nutrients to the inorganic pool).

Our autotrophic producer was a single species of green algae, *Chlamydomonas reinhardtii*. Our use of a single autotrophic species allowed us to unambigu-

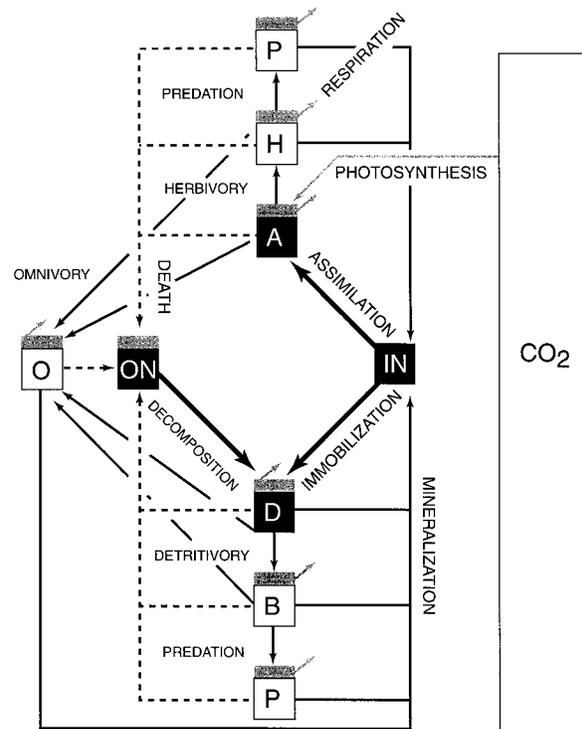


FIG. 1. A synthetic outline of a nutrient-delimited ecosystem derived from systems-, trophic-, and population-based perspectives. The core components are shown as black boxes: A = autotrophs, D = decomposers, ON = organic nutrients, and IN = inorganic nutrients. Ecosystem processes are photosynthesis, decomposition, mineralization (solid lines to IN), immobilization, nutrient assimilation, death (dashed lines to ON), and respiration (small upward arrows). Gray portions of boxes represent C derived from CO_2 via photosynthesis. Peripheral components consist of nondecomposer heterotrophs, or consumers, including H = herbivores, B = bacterivores or detritivores, P = predators, and O = omnivores. Trophic links (solid arrows directly linking biotic components) are herbivory, detritivory, predation, and omnivory. Note that another box representing O_2 , with arrows showing uptake by organisms and uptake and release by photoautotrophs, is left out for clarity.

ously estimate autotrophic biomass as a response variable representing autotrophic biomass. This experimental device eliminated complexities that might occur due to interspecific differences in competition and palatability among autotrophic species if more than one species was used.

Similarly, we did not manipulate decomposer diversity since our primary goal was to examine the effects of variation in consumer diversity on autotrophic biomass. We added three species of bacteria to all microcosms to ensure that each microcosm contained a sufficient complement of bacteria for decomposition to occur. Other species of bacteria, however, were undoubtedly present since completely sterile conditions could not be maintained. But such a potential source of random variation in decomposer species richness

should not affect the relationship between standing autotrophic biomass and consumer species richness.

Consumers were added as small initial populations (10–25 cells) of each consumer species after algal densities had stabilized (>14 d). The small size of this inoculum (a negligible biomass for a 50-mL system) was assumed to have no significant impact on the nutrient composition of the microcosm. We designed our experiment this way because this is typically how many communities begin, especially microbial communities—systems are colonized by a few individuals of each species. These few individuals grew to large numbers (millions, in some instances) and interacted not just with algae, but with bacteria and with each other. Thus, there is no reason, a priori, that any relationship between standing autotrophic biomass and consumer species richness should be affected by variation in the size of such small inocula.

Microcosms.—Microcosms consisted of polystyrene, disposable sterile petri dishes each filled with 50 mL (“large,” 100 mm diameter × 25 mm deep) or 20 mL (“small,” 60 mm diameter × 20 mm deep) of media. The medium was prepared by mixing one sterile Carolina Protist Pellet with 1 L of sterile Carolina Spring Water and inoculated with three species of fresh water bacteria (*Serratia marcescens*, *Bacillus subtilis*, and *Bacillus cereus*). Media were allowed to sit for at least 24 h to allow bacterial populations to grow. Sterile wheat seeds were added to each microcosm as a source of slowly released nutrients (Lawler and Morin 1993). Nutrients were not renewed, so the system was open only to energy (assuming CO₂ was not limiting). Light levels were (mean ± 1 SD) 124.2 ± 19.25 μmol photons·m⁻²·s⁻¹ produced by six 40-W fluorescent and two 25-W incandescent lamps with a 14 h:10 h light : dark cycle.

Ecosystem structure.—The core ecosystem consisted of a single species of autotroph (the green, unicellular alga *Chlamydomonas reinhardtii*) and bacterial decomposers consisting of three known species (see media preparation above). To this core ecosystem, trophically defined peripheral components were added. **Detritivores** consisted of the ciliate species, *Colpidium striatum*, *Spirostomum ambiguum*, and the flagellate *Chilomonas paramecium*, which consume particulate matter including bacterial decomposers (*Co. striatum* has been observed to consume *Ch. reinhardtii*, but we have not observed this in our experiments). For convenience, we use “detritivore” (consuming particulate matter, including bacteria) rather than “bacterivore” because these species more closely approximate detritivores in other ecosystems. **Omnivores**, or primary consumers of autotrophs, decomposers, and/or detritivores, consisted of the ciliates *Euplotes eurystomus* (consuming primarily autotrophs and detritivores), *Paramecium aurelia* (consuming primarily decomposers and some autotrophs), *Pa. caudatum*, and *Pa. multimicronucleatum* (both consuming primarily autotrophs and detriti-

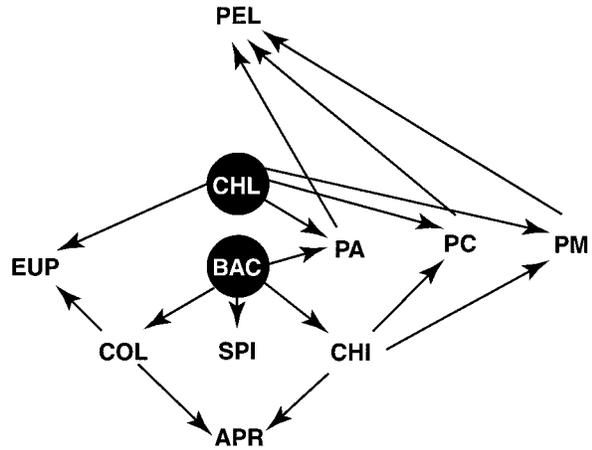


FIG. 2. Food web diagram of full diversity microcosm. Arrows indicate main direction of energy and material flow following scheme outlined in Fig. 1. Filled circles represent core species (autotrophs and decomposers). Decomposer-derived heterotrophs are below BAC (bacteria) while autotroph-derived heterotrophs are above CHL (*Chlamydomonas reinhardtii*). All microcosms contained *C. reinhardtii* (photoautotroph, unicellular alga), *Serratia marcescens*, *Bacillus subtilis*, and *B. cereus* (decomposers, bacteria). Species are abbreviated as follows: Detritivores: CHI = *Chilomonas* sp., COL = *Colpidium* sp., and SPI = *Spirostomum* sp. Consumers of either autotrophs or detritivores or both (omnivores): PA = *Paramecium aurelia*, PC = *P. caudatum*, PM = *P. multimicronucleatum*. Predators of consumers: EUP = *Euplotes* sp., APR = *Amoeba proteus*, PEL = *Pelomyxa carolinensis*.

vores), and the sarcodinid *Amoeba proteus* (consuming primarily detritivores). Note that although most of these omnivores also consume some bacteria, none with the exception of *Pa. aurelia* can grow on bacteria alone. Predators consisted of *Pelomyxa carolinensis*, which consumed omnivores (primarily species of *Paramecium*). These relations are shown in Fig. 2.

Autotrophic biomass.—We measured autotrophic biomass in the first experiment by counting algal cells in 10 fields 0.66 mm². We converted this to biomass per square meter by multiplying the number of cells by the constants $(\pi/6)(17.75 \mu\text{m})^3$, or the volume of a sphere, where the diameter of a *Ch. reinhardtii* cell = 17.75 μm, and assumed that algal cell biomass ≈ mass of an equivalent volume of water (Wetzel and Likens 1991). In the remaining experiments, we measured autotrophic biomass by recording images of algal abundance on the bottom of each microcosm using a microscope video camera. In large microcosms, 10 areas were recorded haphazardly, avoiding edges where image distortion was strongest. For small microcosms five images were recorded haphazardly. ImagePro Plus software was used to estimate total algal area and this was converted to biomass by transforming area to number of cells (area of one cell = 240.5 μm) and then converting number of cells to biomass by the above method.

Heterotrophic biomass.—Decomposer (bacteria) and detritivore (*Ch. paramecia* and *Co. striatum*) densities were estimated using 4'6-diamidino-2-phenylindole (DAPI) fluorescent staining methods for enumeration of microbes by epifluorescence microscopy following Porter and Feig (1980) and converted to biomass following Kemp et al. (1992). Biomass of other heterotrophs were estimated (in experiment 3 only) either by direct count (*Pe. carolinensis*) using a dissecting microscope or computer-based analysis of microscope images (*Pa. multimicronucleatum*). When using image analysis, one image was subtracted from another image taken 2 s later. This image subtraction yields images that show only moving cells. By using this method to remove stationary objects from the image, we could distinguish cells from debris more accurately. As with autotrophic biomass, average volumes of cells were determined by microscopy and biovolume determined by geometric approximations and assuming that biomass was equivalent to mass of water at estimated biovolume. Consumer biomass represented the sum of all consumers found in a microcosm.

Experiments.—Four experiments were conducted. In the first experiment, we directly manipulated consumer species as an experimental factor. In the second, we similarly altered diversity, but each level of species richness had a fixed combination of species. In the third and fourth experiments, we used a small number of species combinations to uncover the possible mechanistic explanations for the patterns we observed.

Duration of experiments ranged from 50 to 55 d, which was sufficient to allow autotrophic biomass to stabilize and consumers, including top predators, to reach stable compositions. Previous experiments have shown that autotrophic biomass stabilizes in <14 d in both 50- and 20-mL microcosms. Thus, consumers were added after 20 d when algal base was stable. Previous experiments have also shown that microcosms that do not contain autotrophs require nutrient additions every 7 d or consumer populations decline. Thus, each experiment was allowed at least 30 d from the point of inoculation of consumers to permit consumers to grow to levels where initial stocks of nutrients would become limiting and interactions among species were likely to have their effects on autotrophic and decomposer biomass. Omnivores were introduced 7 d after detritivore addition and top predators 7 d after omnivore addition at which point sufficient prey were present to sustain consumers. We have never observed omnivores to eliminate prey, but top predators typically reduce consumer densities after 7 d in the absence of alternate food sources. In summary, microcosms (including bacteria) were inoculated with algae on day 0, inoculated with detritivores on day 20, with omnivores on day 27, and inoculated with top predators on day 34 and terminated 16 or more days later.

Sampling date was chosen at ~50 d because it represents a period when such microbial microcosms are

relatively stable with respect to community composition (McGrady-Steed and Morin 1997), a state which occurs in ~6–7 d after addition of all species (McGrady-Steed and Morin 1997). Like most ecosystems, it is not likely that these systems are in “equilibrium” which is generally difficult to either determine or define and probably rarely occurs in nature (Lawler and Morin 1993). Rather, these microcosms are in relatively persistent states where interactions among species have been and continue to occur for many generations.

1. *Direct manipulation of species richness.*—In this experiment, a gradient in consumer species richness was established by choosing species combinations from a range of combinations using eight species of protists. The purpose of this experiment was to examine whether species richness showed a pattern of association with autotrophic biomass. The community structures are illustrated in Fig. 3. Each community structure was replicated three times. On day 20, 25 individuals of *Co. striatum* were introduced when selected for inclusion, but all other species were introduced as 10 cells per microcosm. This experiment was terminated on day 50 when populations were likely to have stabilized and biotic interactions were having effects.

2. *Species richness along a single pathway.*—In this experiment, we manipulated heterotrophic species richness by varying the number of protist species placed in a series of microcosms, but unlike experiment 1, species richness was increased by the addition of specific species rather than haphazardly drawing from the species pool (Figs. 3 and 4). The purpose of this experiment was both to confirm patterns observed in experiment 1 and to examine where in the process of community assembly does autotrophic biomass show significant changes. A total of 25 *Ch. paramecia*, 25 *Co. striatum*, and 60 individuals evenly distributed among the remaining protists were added to each microcosm.

We also deliberately varied temperatures among chambers to ensure that patterns we observed were robust to variation in temperature. After 20 d, to allow algal growth, each of four chambers were set at a different temperature, 15°, 20°, 25°, and 30°C, and detritivores were added. Omnivores were added 7 d later and top predators were added 14 d later. We pooled across chambers for analyses. This experiment was conducted for 38 d from the onset of temperature change (terminated 52 d from algal inoculation).

3. *Four trophic groups.*—In this experiment, we established a specific subset of the food webs used in experiment 2 to uncover possible mechanisms which explained the patterns observed in experiments 1 and 2. We used the smaller petri dishes for this experiment. Five replicates of each trophic structure were established in each of four growth chambers. Eight food webs were used (Fig. 5). The purpose of this experiment was to examine whether heterotrophs exerted their effects through herbivory or consumption of de-

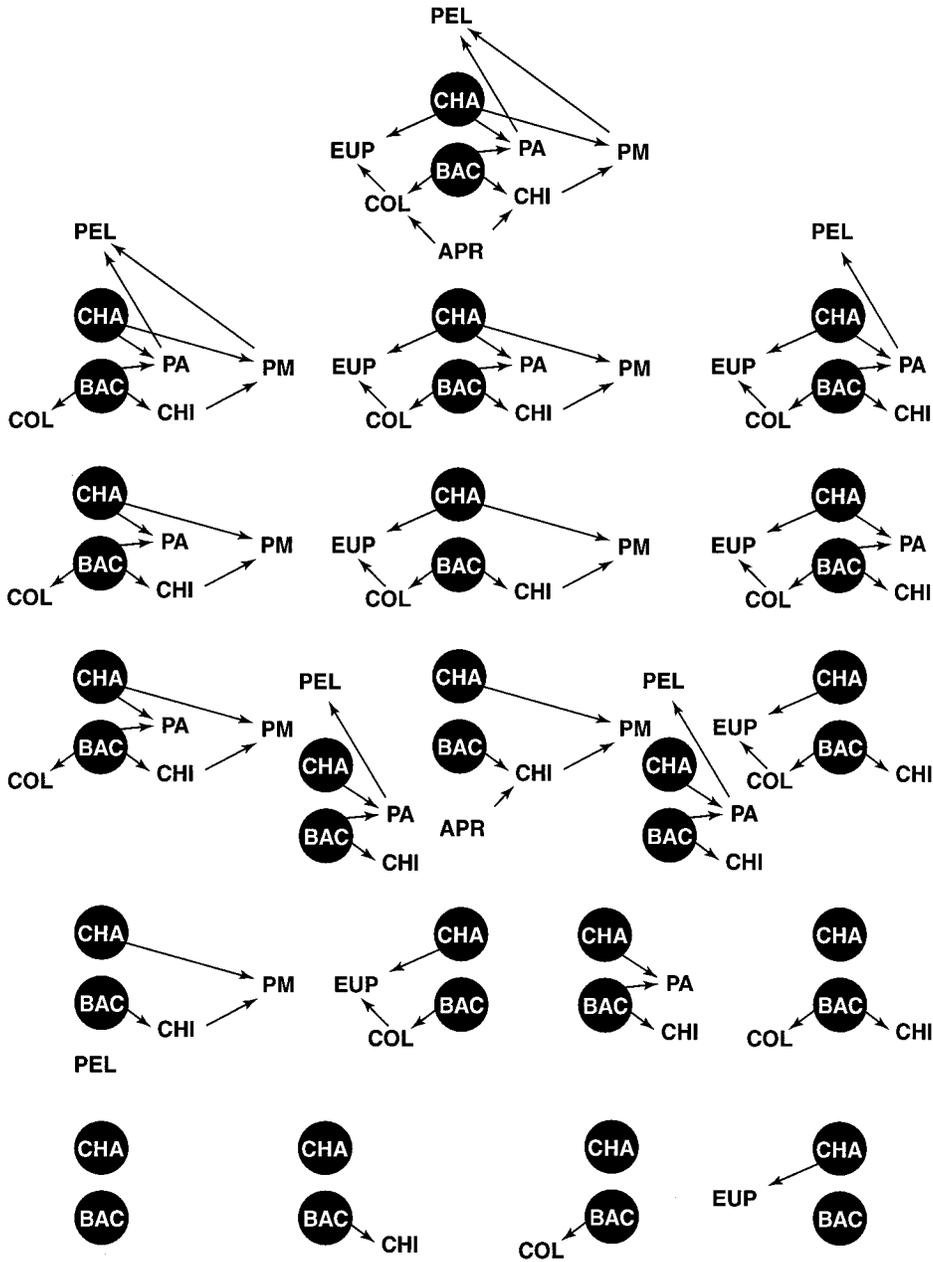


FIG. 3. Food web diagrams of experiment 1. Black circles show positions of core components (bacteria and *C. reinhardtii*). See Fig. 2 for full diversity microcosm and explanation of symbols and abbreviations. Note that each food web was replicated three times.

tritivores or both. We used *Pa. multimicronucleatum*, a generalist omnivore, in combination with *Colpidium* and *Chilomonas*, and *Pe. carolinensis*, an effective predator of *Pa. multimicronucleatum*. Detritivores were added on day 20, omnivores on day 27, and top predators on day 34, and the experiment was terminated on day 50.

4. *An autotroph with three trophic levels.*—In this experiment we manipulated diversity among replicate

microcosms such that either one, two, or three trophic levels were present. The purpose of this experiment was to test whether an omnivore could affect autotrophic biomass and whether the presence or absence of a top predator altered the effect. As before, *C. reinhardtii* served as the autotroph, but *Pa. multimicronucleatum* served as the omnivore, and *Pe. carolinensis* served as the predator (Fig. 6). This experiment was conducted for 55 d.

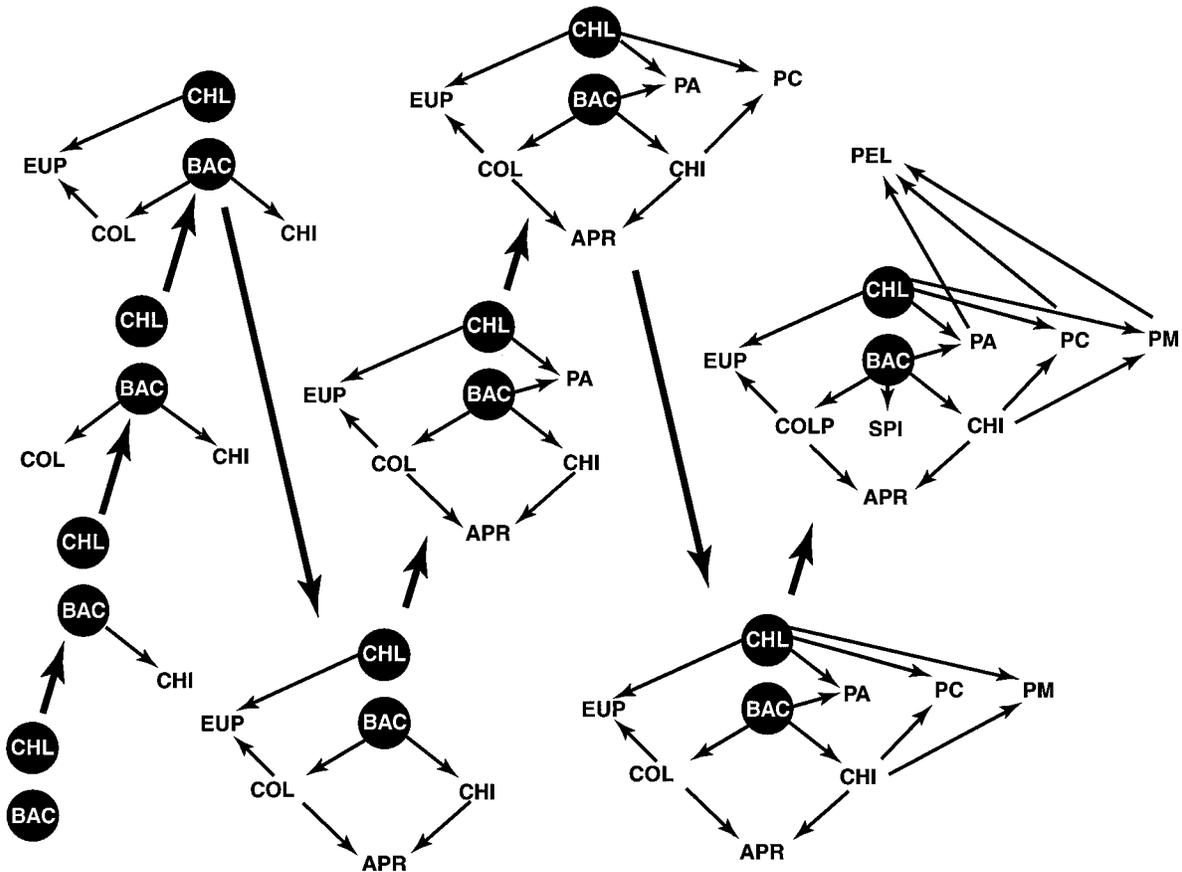


FIG. 4. Food web diagrams of experiment 2. Filled circles show positions of autotrophs and decomposers. Arrows indicate direction of increasing consumer diversity. See Fig. 2 for full diversity microcosm and explanation of symbols and abbreviations. Note that each food web was replicated four times, each under different temperature conditions as in experiment 2.

RESULTS

1. *Direct manipulation of species richness* revealed a well-defined decline in autotrophic biomass with respect to increasing consumer species richness (Fig. 7). This result rejects the hypothesis that autotrophic biomass is insensitive to variation in consumer diversity. A linear regression treating autotrophic biomass as the dependent variable, excluding microcosms without heterotrophs and microcosms from the maximum diversity treatment, revealed a significant negative relationship between autotrophic biomass and heterotrophic diversity (df = 1, 66; $R^2 = 0.34$; $P < 0.001$). We excluded the minimum diversity treatment because it did not contain consumers and our interest was in the interaction between consumers and standing autotrophic biomass. We excluded the maximum diversity microcosms because one would expect a lower variance for the highest diversity microcosms (it consisted of only one possible species combination) than other treatments. Such nonhomogeneity of variance would violate assumptions of a parametric regression model. Inclusion of this treatment, however, would not qualitatively alter results, as seen in Fig. 7. A Spearman rank cor-

relation, which is insensitive to nonhomogeneity of variance, provides further confirmation of a significant negative association between autotrophic biomass and consumer diversity ($r_s = -0.55$, df = 74, $t = 5.67$, $P < 0.001$).

2. *Species richness along a single pathway.*—This experiment revealed the same association between autotrophic biomass and heterotrophic species richness as observed in the direct manipulation of species richness (compare Figs. 7 and 8). A regression analysis of autotrophic biomass as a dependent variable of species richness, excluding replicates without heterotrophic species and ignoring temperature treatments, revealed a significant negative relationship (model: linear; $R^2 = 0.66$; $P < 0.001$; Fig. 7). Visual inspection of the data and theory (Oksanen et al. 1981) suggests a negative exponential with a nonzero asymptote might describe the relationship. Such a model also significantly fit the data, albeit only slightly better than the linear model (model: negative exponential; $R^2 = 0.67$, $P < 0.001$, Fig. 8).

The single pathway design of experiment 2 (Fig. 4) permits identifying possible mechanisms behind the

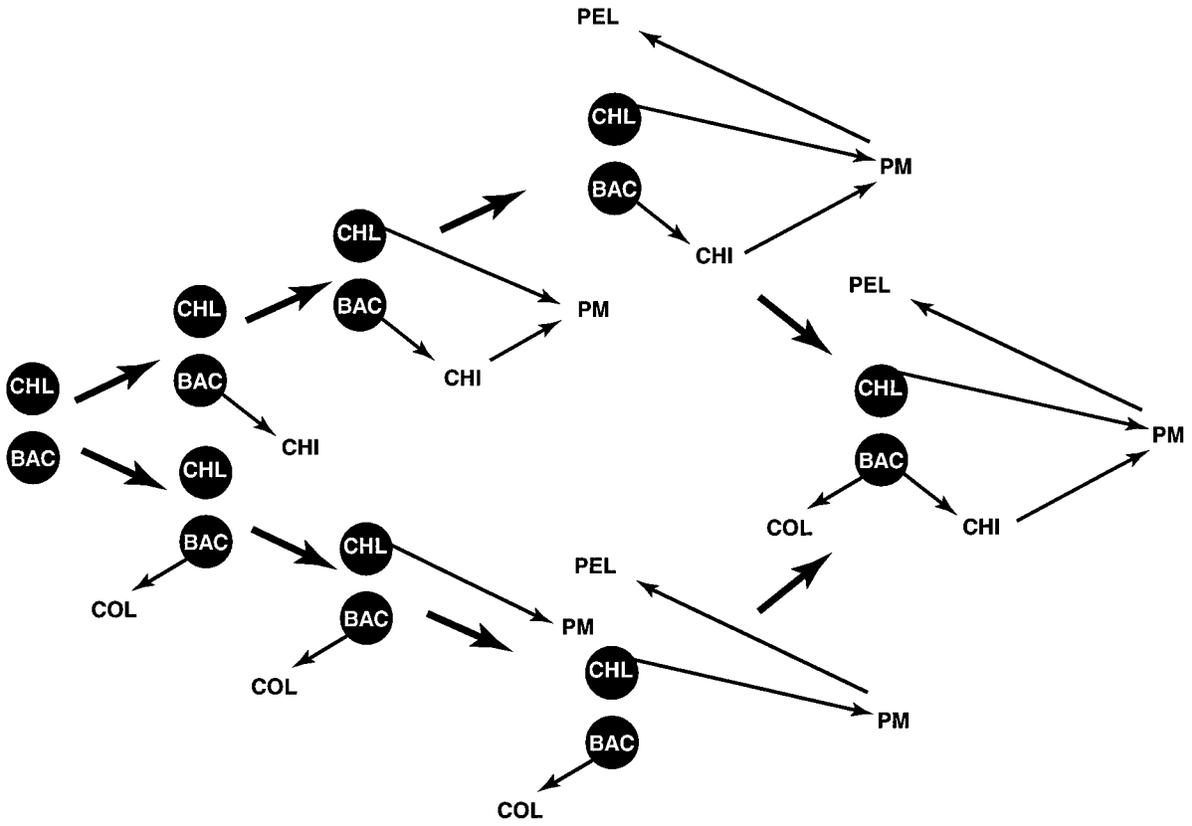


FIG. 5. Food web diagrams of experiment 3. Filled circles show positions of autotrophs and decomposers. Arrows indicate direction of increasing consumer diversity. See Fig. 2 for full diversity microcosm and explanation of symbols and abbreviations. Note that each food web was replicated five times, each under different temperature conditions as in experiment 2.

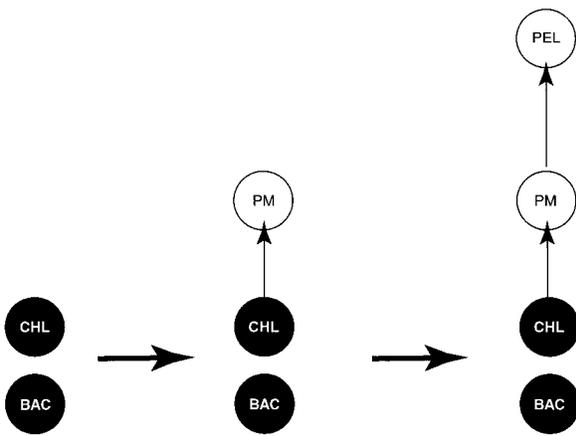


FIG. 6. Food web diagrams of experiment 4. Filled circles show positions of autotrophs and decomposers. Arrows indicate direction of increasing consumer diversity. See Fig. 2 for full diversity microcosm and explanation of symbols and abbreviations. Note that each food web was replicated five times, each under different temperature conditions as in experiment 2.

patterns observed in Figs. 7–8. Fig. 8 shows that autotrophic biomass was depressed in the absence of bacterivorous detritivores. The addition of bacterivorous detritivores, however, resulted in substantial increases in autotrophic biomass. This initial increase is most likely due to the indirect facilitation of algal growth provided by protistan bacterivory (e.g., Porter et al. 1985, Stone 1990, Rothhaupt 1992), a mechanism further supported by results from experiment 3 (below). That is, immobilization of nutrients by bacteria is reduced by bacterivory, thereby facilitating algal growth.

The addition of omnivores suppressed autotrophic biomass to levels comparable to those found in the absence of nondecomposer heterotrophs. This algal suppression supports the predictions of trophic-based theory. The mechanism for this algal suppression is possibly the increased apparent competition (*sensu* Holt 1977) between bacteria and algae for nutrients created by the addition of omnivores. In the presence of omnivores, algae and bacteria mutually support populations of their common enemies which leads to apparent competition. Further support for this hypothetical mechanism is provided by experiment 3 (below).

These results suggest that the consumption of detritivores or direct consumption of autotrophs may be the

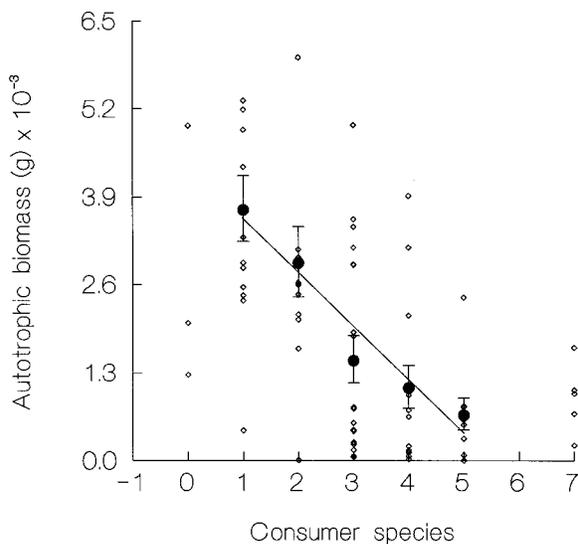


FIG. 7. The relationship between autotrophic biomass and heterotrophic species richness when community composition is varied randomly. Here, autotrophic biomass is represented as the estimated total biomass of algae per microcosm. Numbers of heterotrophic species correspond to those illustrated in Fig. 3.

mechanisms responsible for the negative association between diversity and autotrophic biomass. Note that these patterns were obtained over a wide range of temperatures (Fig. 8).

3. *Four trophic groups.*—Autotrophic biomass is reduced when decomposer bacteria are abundant independent of consumer diversity (Fig. 9). Bacterial biomass is reduced when numbers of trophic groups increase in microcosms. Heterotrophic biomass was highest when higher trophic levels (consumers of detritivores and/or top predators) were present (Fig. 9).

The design of this experiment permits identification of the two possible mechanisms which explain the negative associations observed between autotrophic biomass and non-decomposer heterotrophic diversity. Increasing numbers of trophic groups in this simplified set of microcosms was associated with decreasing densities of bacteria (Fig. 9, bottom). Autotrophic biomass showed highest levels when decomposer biomass was low and consumer biomass greater than zero (Fig. 9, compare middle with top and bottom). Treatment (numbers of trophic groups) effects were significant for autotrophic biomass (ANOVA; $F = 7.21$; $df = 3, 28$; $P < 0.01$), decomposer bacterial biomass (ANOVA; $F = 5.52$; $df = 3, 28$; $P < 0.01$), and consumer biomass (ANOVA; $F = 15.42$; $df = 3, 28$; $P < 0.001$).

Although the addition of detritivorous protists resulted in dramatic increases in algal biomass, the addition of omnivores did not significantly suppress algal biomass nor did the addition of a top predator result in a significant change in algal abundance (post hoc Bonferroni test of pairwise comparisons, $P > 0.05$).

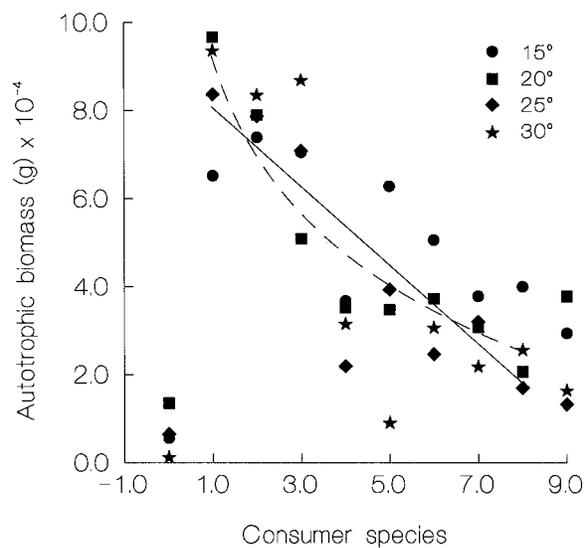


FIG. 8. The relationship between autotrophic biomass and consumer species richness when community composition is varied following a specific sequence. Here, autotrophic biomass is represented as the estimated total biomass of algae per microcosm. Numbers of consumer species correspond to those illustrated in Fig. 4. The solid line shows the linear, least-squares fit to the data; the dashed line shows the negative exponential fitted to data. Symbols represent replicate microcosms maintained at different temperatures as described in legend.

These results support removal of bacteria by detritivorous protists as the mechanistic bases for the observed release of algae from growth suppression when detritivores were added. Further, distinct HSS patterns were not observed in this system when averaging across microcosms that differed in species composition.

4. *An autotroph with three trophic levels.*—Results from this experiment revealed a significant effect of treatment (number of trophic groups) on autotrophic biomass (using means from chambers and ignoring temperature, ANOVA; $F = 21.3$; $df = 2, 9$; $P < 0.001$). This experiment differs from experiment 3 because each consumer level is represented by a single species and the omnivore is, in actuality, primarily an herbivore. The visible decline in autotrophic abundance created by the presence of omnivores (Fig. 10), however, was not significant (by post hoc Bonferroni pairwise comparisons). An increase in autotrophic biomass in the presence of omnivores (in this case, herbivores) and a top predator (Fig. 10), however, was significant (by post hoc Bonferroni pairwise comparisons, $P < 0.01$). These microcosms provided a more direct test of trophic-based theory by reducing the number of complex links among trophic groups. These results suggest that predation on omnivores can release autotrophs from suppression thereby producing an HSS-like pattern in agreement with trophic-based theory (e.g., Hairston et al. 1960, Oksanen et al. 1981).

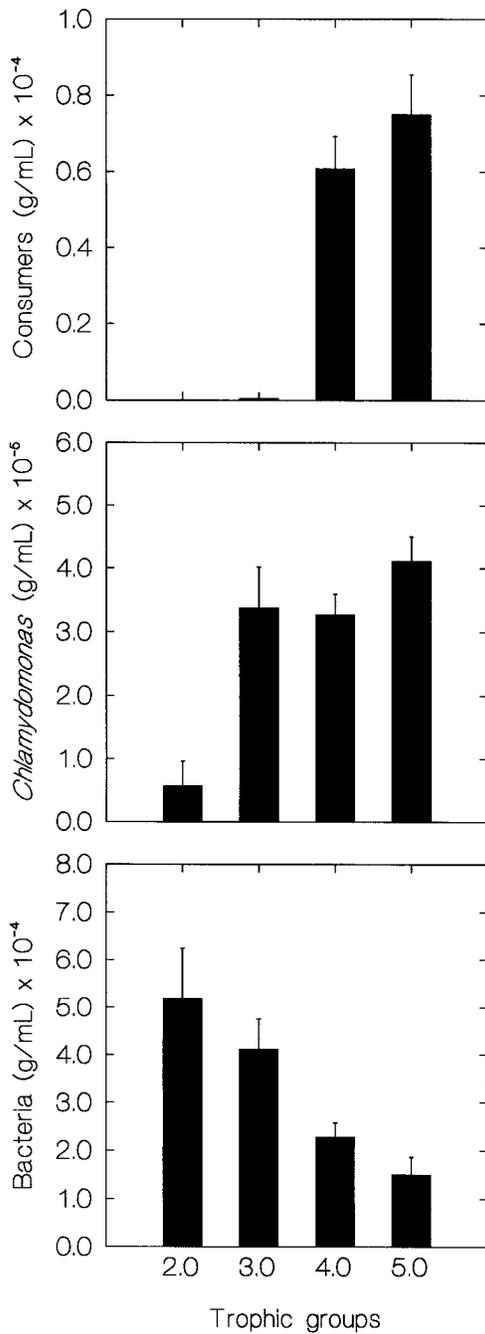


FIG. 9. Autotroph and decomposer (bacterial) densities associated with number of trophic groups (means + 1 SE). Values are for microcosms used in third experiment. In this figure, 2 = autotrophs and decomposers, 3 = groups in 2 + detritivores, 4 = groups in 3 + omnivores, and 5 = groups in 4 + a top predator.

DISCUSSION

After sufficient time to permit stabilization of microcosm community composition and trophic interactions to occur, standing autotrophic biomass showed a strong negative association with species richness of the

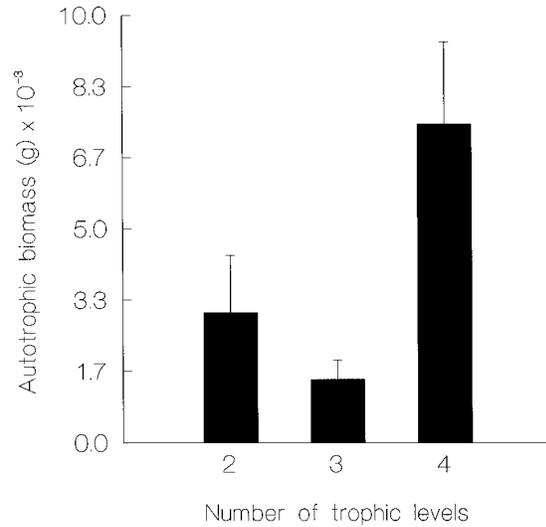


FIG. 10. Autotrophic biomass associated with number of trophic groups (means and 1 SE). Values are for microcosms used in fourth experiment. In this figure, 2 = autotrophs (producers) and decomposers, 3 = groups in 2 + detritivores, and 4 = groups in 3 + a top predator.

initial consumer (nondecomposer heterotrophic protists or herbivores, detritivores, omnivores, and top predators) inoculum.

In experiment 1, directly varying consumer species richness as an experimental variable had a significant effect on standing autotrophic biomass after several generations of population growth (30 d for detritivores, 23 d for omnivores, and 16 d for top predators). Autotrophic biomass declined with increasing consumer species richness (Fig. 7), a pattern confirmed in a second experiment (Fig. 8) and observed to be robust to considerable variation in temperature. This pattern was obtained whether constant densities of initial consumer species (experiment 1) or equal total density (experiment 2) of initial consumer species were used in the inocula.

This inverse association between autotrophic biomass and consumer species richness suggests that autotrophic biomass responds in a predictable way to variation in consumer diversity, which does not support the null, systems-based predictions of insensitivity (e.g., Harte and Kinzig 1993, Schulze 1995). The observed pattern also does not support the population-based predictions of high sensitivity (e.g., MacArthur 1955, May 1973, Goodman 1975, Pimm and Lawton 1977, King and Pimm 1983, De Angelis 1992, Haydon 1994, Loreau 1995). The observed linear or asymptotic response fits more closely with trophic-based predictions where trophic boundaries are diffuse (e.g., Hairston et al. 1960, Oksanen et al. 1981, Pimm 1982, Carpenter et al. 1987, Wootton and Power 1993, Polis and Wine-miller 1996, Wootton et al. 1996). It is important to note, however, that though our microcosms were run for a sufficient length of time to permit stabilization of

community composition and algal densities, they, like most ecosystems, were not necessarily at equilibrium. The theory we reference, however, predicts autotrophic biomass assuming equilibrium. Thus, it is difficult to relate our findings directly to equilibrium-based theory.

The mechanisms underlying the observed pattern provide insight into why the observed pattern fit no perspective perfectly. Experiments 2–4 identified two possible mechanisms operating in our microcosms, both of which are known to potentially affect autotrophic biomass in naturally occurring aquatic ecosystems. First, increasing numbers of consumer species directly reduced autotrophic biomass by increased consumption of autotrophs (e.g., Oksanen et al. 1981). Results from experiment 4 demonstrated that an omnivore (herbivore in this experiment) can reduce autotrophic biomass by its herbivory (Fig. 8). Such impacts of protists on autotrophic production are also known from natural aquatic systems. For example, ciliates are capable of consuming 20–60% of net annual primary production in aquatic ecosystems (Fahnenstiel et al. 1986, Pomeroy and Weibe 1988, Carrick et al. 1991, 1992, Laybourn-Parry 1992, Neilssen and Kjørboe 1994). Although our consumers were largely omnivores rather than strict herbivores, omnivores are known to affect resource species in nature (reviewed in Diehl 1993) as they did in our microcosms.

The second mechanism is based on the observation that autotrophic biomass was decreased indirectly by removal of bacterivorous detritivores. Bacteria are known to have potentially strong impacts on algal biomass by immobilizing available nutrients (e.g., Azam et al. 1983, Harte and Kinzig 1993). Consumption of bacteria by detritivores stimulates algal growth by releasing nutrients that had been immobilized by bacteria. Experiment 2 showed this pattern. Detritivores had substantial effects on autotrophic biomass, visible as a sharp rise in autotrophic biomass as detritivores were added (Fig. 8). Experiment 2 showed that adding consumers of detritivores (*Euplotes*) had a negative impact on autotrophic biomass, visible as a reduction in autotrophic biomass in systems that contained *Euplotes* (Fig. 8). Experiment 3 also shows the negative impact bacteria had on autotrophic biomass and the role of consumers in lowering bacterial biomass (Fig. 9). Such effects have been demonstrated in other studies. For example, protistan consumption of bacteria has been observed to stimulate primary production in ecosystems (Porter et al. 1985, Stone 1990, Rothhaupt 1992). Thus, it is not only the way in which consumers directly affect biomass by feeding, but also the way in which they regulate biomass indirectly by influencing the “antagonistic mutualism” between autotrophs and decomposers (Harte and Kinzig 1993).

Our microcosms were modeled after aquatic ecosystems which may show greater sensitivity of biomass to variation in biotic diversity than terrestrial systems. Donor-controlled systems, like many terrestrial eco-

systems, may show different patterns (Strong 1992). For example, model terrestrial systems (Naeem et al. 1995, 1996) in which consumer diversity was manipulated did not exhibit strong effects of herbivores, predators, or detritivores on autotrophic biomass.

Our experiments did not examine variation in decomposer and autotrophic diversity which may play important roles in biomass distribution. Several studies have shown that autotrophic diversity is positively associated with production (Bajpai 1996, Naeem et al. 1994, 1996, Tilman et al. 1996, and references therein) and autotrophic diversity may be positively associated with heterotrophic diversity (e.g., Oksanen et al. 1981). The effects of variation in decomposer diversity on biomass distribution are less well studied. Further research may demonstrate that biomass response to variation in consumer diversity may be affected by the diversity of core species.

In summary, our findings highlight two important features of ecosystems that govern whether they will reside in “green” or “barren” states. First, HSS patterns most likely occur when trophic levels are discrete. Such discreteness exists when the species within trophic levels are either strongly ecologically equivalent or strongly dominated by one species. Second, the decomposer chain (bacteria, detritivores, and predators of detritivores) can be equally important in determining autotrophic biomass as the grazing chain (algae, herbivores, and top predators). Given these findings, of the three bodies of community theory, population-, ecosystem- and trophic-based theory, the latter may provide a robust way of understanding the determinants of autotrophic biomass.

Our study provides insights into the fundamental differences among systems-, population-, and trophic-based perspectives that address the patterns of response of biomass distribution to variation in diversity in ecosystems. Each perspective focuses on a selection of the components and processes outlined in Fig. 1. In species-rich ecosystems, small changes in composition primarily alter the number of species within functional groups, but are not likely to alter the trophic and system linkages among components. If species are ecologically “equivalent” or “redundant” within functional groups (Walker 1992, 1995, Lawton and Brown 1993, Gitay et al. 1996, Naeem 1998), then autotrophic biomass may be insensitive to small-scale variation in consumer diversity and correspond more closely to systems-based perspectives. If species are singular (i.e., not redundant) and vary considerably in ecological importance values, then autotrophic biomass may be sensitive to variation in consumer diversity and correspond more closely to population-based perspectives. In either case, if variation in heterotrophic diversity involves the loss or addition of an entire trophically defined functional group, then shifts in autotrophic biomass from suppressed (“barren”) to released (“green”) states may be expected.

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