DISTURBANCE, GRAZING AND SUCCESSION: AN EXPERIMENTAL APPROACH TO COMMUNITY ANALYSIS

by

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Computer simulations and freshwater microcosms were used to investigate the basis for two models proposed to explain the increase of community diversity with disturbance. The competition model predicts that intermediate levels of disturbance increase diversity by disrupting competitive exclusion. The evolutionary model predicts that diversity is highest at the historical rate of disturbance.

Computer simulations demonstrate that the competitive model depends on the assumption that r and K are inversely related. If this condition is not true, diversity declines monotonically with disturbance. If it is true, equitability (one component of diversity) increases with moderate disturbance frequencies even if competitive coefficients are set to zero.

The effects of microcrustacean grazers on algal succession were studied in microcosms of algae and associated microfauna. Replicated microcosms were grown under slightly different light and temperature regimes in two growth chambers. In each chamber, microcrustacean grazers (Chydoridae) were removed from six cultures. The successional sequence in all cultures was from a green algae community (dominated by *Scenedesmus quadricauda*) to a blue-green community (dominated by *Phormidium* sp.). The effect of grazing was to slow the rate of succession. Diversity of the communities fluctuated but was highest at the transition from one successional state to another.

The interaction of exogenous abiotic disturbance with grazing was investigated using minimally controlled freshwater microcosms. The disturbance was a 50% reduction in biomass of each culture. Three frequencies of disturbance were used. The experiments were conducted outdoors between June and September in 1981 and 1982. Disturbance increased diversity by increasing the rate of succession, but timing of observation and the age of the community affected this result. Initially, *Scenedesmus* dominated, but later communities were dominated by *Ankistrodesmus* sp. or *Phormidium* spp. The *Phormidium* state was correlated with the extinction of grazers, presumably due to disturbance.

The results of all three studies indicate that disturbance increases diversity by a number of mechanisms. The importance of competition has been much overstressed. Instead, the number of species which can exploit different successional stages and the degree to which disturbance initiates successional change may be the most important considerations.

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TABLE OF CONTENTS

LIST OF TABLES

Table Page

Chapter 2

Chapter 3

Chapter 4

LIST OF FIGURES

Figure Page

Chapter 2

Chapter 3

Chapter 4

CHAPTER 1

OVERVIEW

> I was, then, not only watching the much-vaunted wonders in a drop of pond water; I was also, with mingled sadism and sympathy, setting up a limitless series of apocalypses. I set up and staged hundreds of ends-of-the-world and watched, enthralled, as they played themselves out. Over and over again, the last trump sounded, the final scroll unrolled, and the known world drained, dried, and vanished.
>
> Annie Dillard
> (Teaching a Stone to Talk, p. 106)

If there is such a thing as a biological law then one must be that change is inevitable. This is probably as true for the paradigms used by ecologists as it is for the systems they study, although inertia does often seem to slow down the rate of change of the former. Thus, while community ecologists have long recognized that disturbance was an important component of ecosystems. it was generally treated as noise which interfered with the patterns of succession (see any treatment of the subject in textbooks published before the mid-seventies, such as Allee et al, 1949). A widely-held view was that species diversity increased during succession (e.g., Odum 1969). Only in the last ten years has disturbance been treated as a widespread phenomenon that acts as an organizing force which may maintain the high diversity of many communities (and only in the last few years has this concept appeared in textbooks, such as Ricklefs 1983).

The objective of this study was to scrutinize this supposed relationship between disturbance and community structure. To do this, I have made use of computer simulations and algal microcosms. Here I give a brief rationale of the experimental design and methodologies employed, some motivating questions that link the separate studies and a caveat concerning the prejudices of the experimenter.

Experimental Systems

The systems used and the questions asked are arranged in order of increasing complexity. The simplest is a deterministic mathematical model of several populations, based on which computer simulations have been performed. In the other experiments, replicated freshwater microcosms of algae and associated microfauna were used. Microcosms are ideal units of ecological study in the sense that they are small, can be replicated and possess many of the attributes of larger systems (e.g. trophic levels, succession). No less importantly, the relevant events occur within the time frame of the average graduate student. Allen and Starr (1982, p. 211) state that "... algae offer the smallest and in a sense the simplest biological model for testing fundamental ecological theory. For verifying and developing ecological hypotheses in such areas as succession, algae often offer the biological system of choice."

Lest the reader be inspired to throw out his or her transect lines and increment borers and stock up on flasks, I offer the following caveats:

(1) It is difficult (if not impossible) to distinguish between

age classes of algae. To some extent, smaller algae are younger within a population but there are also size differences between populations. This only becomes a problem when one tries to generalize the results to other communities, as terrestrial ecologists usually distinguish between size and/or age classes.

(2) Sampling is truly unbiased in the sense that there is no . chance for subjective evaluation before sampling. What one sees on a slide under magnification is all the information one has about the species in the community. In the sense that subjective evaluations are self-deceiving, this is a strength of microcosms. However, subjective evaluations can be valuable as they suggest patterns of organization such as patchiness or predator behavior. It is very difficult to determine anything about the physical and spatial structure of the microalgal community.

(3) While microcosms may be small, they are not simple. A typical community in this study might have 12 species of algae, the same number of protozoans, several species of metazoa and uncounted numbers of bacteria and fungi. Additionally, events may occur too quickly to be detected by the observer (Allen and Starr 1982).

(4) Algae have many different forms. In this study, the algae consisted of single cells, coenobia (a fixed number of cells), loosely organized masses of cells and filaments. Is an individual coenobial alga equivalent to a filamentous one? Some algal ecologists convert to standard cell volumes (available in the literature for some species), but the size variation between individuals of the same species was so great that I did not feel it would solve the problem. Conver-

sion to biomass or biovolume would probably change some of the specific results but not the general conclusions.

Experimental Design Rationale

Diversity of a community usually means species diversity but there is no good reason to assume that the species is the most relevant entity. Shelford (1911) argued that the growth forms of plants "...are the expression of the conditions of existence for the plants of a definite area. The formation is the fundamental unit of the ecology of communities and carries with it *no consideration of species whatever*." This issue has been raised again by Allen and Starr (1982) who state: "If we insist on reifying species as the necessary attributes of communities, then community behavior can appear exceedingly complicated."

While I believe that the points expressed by these authors have much validity, I have chosen not to eschew the taxonomic approach to diversity altogether. Instead, diversity is treated hierarchically. To some extent, growth form differences are the basis for taxonomic categories particularly at the level of phylum, class or even family. At the genus and species level, differences are more minute. Insofar as growth form represents the response of the organism to environmental variables, then competition between higher taxonomic groups should be less severe than between species. Darwin (1859, p. 84 in the New American Library Edition) made the observation:

> "...as the species of the same genus usually have...much similarity in habits and constitution, and always in struc-

> ture, the struggle will generally be more severe between them ... than between the species of distinct genera."

This suggests that the actual species diversity of the community conveys different information from the diversity of higher levels.

Three studies are used to examine the effects of grazing and exogenous disturbance on community structure:

(1) In Chapter 2, I use a deterministic difference equations model to examine through computer simulation some assumptions of competition-based disturbance theory. Even this very simple population model shows that the emphasis by some theorists (Levin and Paine 1974; Connell 1978; Huston 1979) on competition is unwarranted as the relative values of other life-history parameters are more important to the conclusions of the model.

(2) Chapter 3 describes a laboratory study of the effects of grazing by microcrustaceans in algal microcosms. The response of the community to grazing is measured by the species composition and diversity at successive ages.

(3) The effects of an exogenous abiotic disturbance on community structure are discussed in Chapter 4. The interaction of this disturbance with grazing and with succession are considered.

Motivating Questions and a Prejudice

In the final chapter, the results of these three studies are synthesized and used to examine some larger and more general questions. The order of these questions is significant. They represent the motivations of the author at various stages of this study.

(1) Assuming that a general theory of community structure is feasible, is there any reason to assume that competition is its basis?

(2) Can biotic and abiotic disturbances be equated with regard to their effects on a community?

(3) Can the measurement of community diversity tell us anything about the processes at work in the community? Can it be used to distinguish between the effects of endogenous and exogenous factors?

I must admit that, to a certain extent, question 1 grew out of a certain prejudice against population biology which at times seems absurdly reductionist from the perspective of a community ecologist. The theory of communities can be approached at two different levels: (1) at the level of the community itself, and (2) at the level of the populations that make up the community. In the jargon of computer programming, the first is a "top-down" approach, the second is "bottom-up", and any good programmer can tell you which is better.

CHAPTER 2

A CONSIDERATION OF THE ASSUMPTIONS OF SOME NONEQUILIBRIUM COMMUNITY MODELS

Within the last decade nonequilibrium community models have become increasingly important in ecological theory (Connell 1978). Disturbance has been shown to be an important influence in many communities where diversity is highest at some intermediate frequency of disturbance. This chapter addresses the assumptions inherent in some of the models of disturbance. In particular I am concerned with models that attempt to explain local diversity on an ecological time scale. I will examine how assumptions about life-history strategies determine the effect of disturbance on diversity.

The central concept of nonequilibrium community models is that diversity is maximized at some level of disturbance. The models of Levin and Paine (1974) and Huston (1979) differ in details, but both assume that the increase in diversity is due to the disruption of competitive exclusion. In the absence of disturbance, the dominant species will exclude the competitively inferior species and thus reduce diversity. Disturbance can increase diversity when it affects the dominant species more than the others, but it also increases diversity when all the species are affected proportionately (Huston 1979).

Levin's and Paine's (1974) is a spatial model in which disturbance introduces heterogeneity by opening up patches in late successional communities. Huston (1979) showed that the disturbance-diversity relationship could be explained by conventional competition theory and could apply to homogeneous environments. He developed a general model of disturbance in communities of species behaving according to the rules of Lotka-Volterra competition equations. The general form of these equations is

$$dN_i/dt=r_iN_i(K_i-N_i-\sum_j^S a_{ij}N_j)/K_i$$

where N_i=population size of species i, r_i=intrinsic rate of increase of species i, K_i=carrying capacity of species i and a_{ij}= the competitive effect of species j on species i. Disturbance was defined as a 50% reduction in the population size of each species. In computer simulations of interacting species, disturbance slowed the rate of competitive exclusion and thus diversity increased. The rate of disturbance that maximized diversity was dependent on the rate of competitive displacement.

Here I will show that in a model using Lotka-Volterra equations and 50% mortality the relationship between r and K determines the effect of disturbance on diversity. Moreover,

(1) all frequencies of disturbance lower diversity in those cases of competitive exclusion where r and K are not inversely related, and

(2) disturbance may increase diversity even in communities with no competition.

The dynamics of the model were explored using a computer simulation. Number of species and r, K and a for each species were entered at the beginning of each run. Initial population sizes were 10 for all species. The simulation was allowed to run for 400 iterations or, if there were only two species in the community, until one species became extinct. Disturbance level was held constant at 50% mortality but the frequency was varied between runs by changing the interval between disturbances.

First, I give the results for two competing species using four different combinations of the parameters (Table 1). Competitive exclusion occurs in each case but the winner is changed by rearranging the parameters, and the effect of disturbance is different in each case (Figure 1). Species 1 is the better a-competitor ($a_{12}<a_{21}$) but in the absence of disturbance it only wins when it has the higher K value (cases 3 and 4).

If time to extinction can be lengthened then the average diversity of the community is increased. In two cases (1 and 3), persistence of the competitively inferior species is increased by disturbance. However, the frequency that produces the highest diversity is higher in case 3 than in case 1. In both, r and K are inversely related.

These results are quite similar to models of non-selective predation (Slobodkin 1961; Caswell 1978). In those models, the disturbance is continuous whereas here it is discrete. Non-selective predation leads to coexistence if r of the inferior competitor exceeds r of the dominant species, but only at intermediate rates of predation. The relationship between rate of competitive exclusion and disturbance has been discussed by Caswell (1978, 1982).

While this simulation only considers two species, these results hold for communities of many species as well. This is easily seen by

TABLE 1. Population parameter values for four runs of the simulation.

	Species	r	K	a_{ij}
CASE 1	1	0.8	600	0.8
	2	0.4	1200	1.8
CASE 2	1	0.4	600	0.8
	2	0.8	1200	1.8
CASE 3	1	0.4	1200	0.8
	2	0.8	600	1.8
CASE 4	1	0.8	1200	0.8
	2	0.4	600	1.8

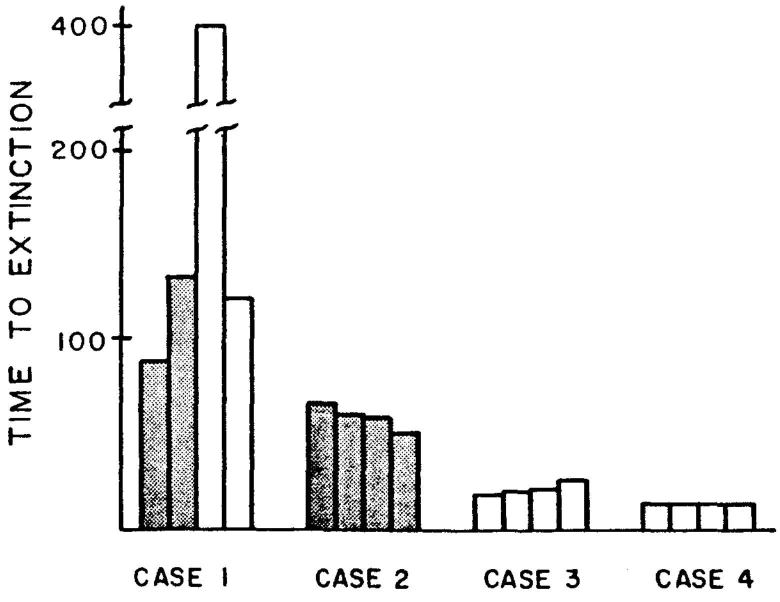


FIGURE 1. Time to extinction is shown for each case given in Table 1. Initial population sizes are 10 for both species. Four different disturbance frequencies are shown for each case. Within a set of bars, disturbance frequency increases from left to right. The no disturbance situation is given on the left followed by intervals between disturbances of 20, 10 and 5. The simulation was run until one species was extinct or until t=400. Shaded bars indicate that species 1 lost, open bars that species 1 won.

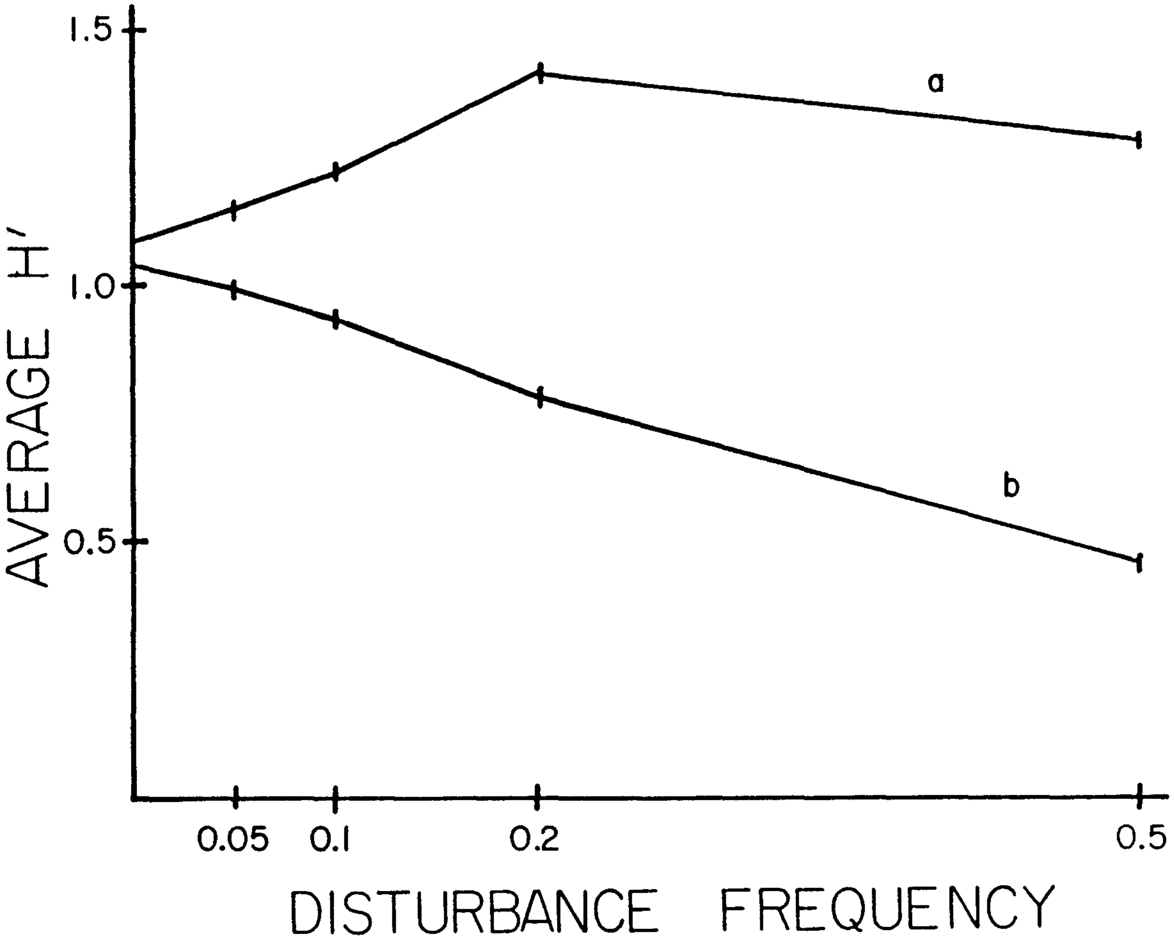
considering the results of the model using a hypothetical group of species that do not compete with each other (Figure 2).

When r and K are inversely related, diversity is highest at some intermediate frequency of disturbance (curve a). When r and K are positively related (that is, high-K species also have the highest r) diversity declines monotonically as disturbance increases (curve b).

In the first community (curve a), species conform to the r-K continuum model. Thus some species are slow growing but have high carrying capacities; these species can be expected to dominate when disturbance is absent or very low. At the other extreme are species with high growth rates which are capable of responding rapidly to reductions in population size.

The results of the noncompetitive model are consistent with the results of the competitive 2-species situation. Only when r and K were inversely related (cases 1 and 3 in figure 1) did disturbance increase diversity. In the absence of competition, diversity can only increase if equitability increases. This is exactly what happens in case 1. As disturbance frequency increases the slow growing species can not respond to reductions in population size as quickly as the faster growing species. Thus average population sizes become more similar. If disturbance occurs too often, the slow growing species are eliminated entirely and diversity decreases.

The assumption that species can be ordered along an r-K continuum is more important in this model than the notion that competitive exclusion is occurring. When competition is a factor, diversity



SPECIES:	K	r (case a)	r (case b)
1	1200	0.2	1.2
2	300	0.8	0.8
3,4,5	100	1.2	0.2

FIGURE 2. Average diversity (H′ is Shannon-Wiener index) over a time period of 400 is shown here as a function of disturbance frequency (1/interval between disturbances). (a) A 5-species community where r and K are inversely related. (b) Here the same values of r and K are used but r and K are positively related. Competition coefficients are 0. The distribution of maximum species abundances (K) will affect the magnitude of the outcome of this simulation but not the basic conclusions. Here a pattern typical of many natural communities with one dominant and several less abundant species is used.

changes because the average number of species and the equitability both increase, so the response might be more pronounced. However, disturbance models are also consistent with non-competitive community models if r-K selection can be assumed.

Thus, competitive exclusion can occur under a variety of conditions, and the rate of exclusion depends on r and K values as well as a. According to r-K selection arguments, there is an energetic trade-off between r and K so that r and K tend to be inversely related (MacArthur and Wilson 1967; Pianka 1970). Gill (1974) added that competition coefficients are similarly subject to selection but only at the expense of r and/or K.

In a review of r- and K-selection, Stearns (1977) pointed out several theoretical and empirical problems with this approach to populations. Of the theoretical flaws, perhaps the most important here is that K is impossible to define in terms of life-history traits. "Thus r and K cannot be reduced to units of common currency" (Stearns 1977) and if there is a trade-off between r and K it is not clear that it would be expressed demographically. Caswell (1982) reexamined life-history theory in relation to nonequilibrium models and argued that two distinct types of populations may be selected for, depending on the degree of disturbance. One population type tends to spend most of the time increasing and has a suite of traits traditionally considered r-selected; the other type spends most of its time declining and resembles K-selected populations. Selective pressure tends to reduce r in this second group. Caswell has established a theoretical basis for the assumed negative relationship between r and

K, thus correcting the theoretical flaw.

However, Stearns also reviewed the data for evidence of r-K selection. He found that only half of the data fit the predictions of r-K selection theory. Thus it is by no means clear that all communities can be expected to be made up of species with inversely related r´s and K´s.

Although controversy still exists over this mandatory trade-off in r, K and a, it is widely used both explicitly and implicitly in models of communities and population dynamics.

Levin and Paine (1974) model disturbance as the birth and death of patches of various sizes in space-limited communities. While they do not use r-K selection explicitly, the notion is implicit in some assumptions of the models. A mixture of patches of different ages allows the coexistence of transient, fast-growing species with the slower-growing dominants. The former fit the concept of r-selected species while the latter are K-selected (Pianka 1970).

In order for diversity to increase in a disturbed community, organisms with a variety of combinations of life-history strategies must be a part of the system. Competitive ability is only one aspect of life-history. Differential growth rates and different carrying capacities may be more important in determining the post-disturbance diversity.

CHAPTER 3

A STUDY OF THE ROLE OF GRAZERS IN THE DYNAMICS OF MICROCOSM DIVERSITY

Introduction

Mathematical models demonstrate that competing species may coexist if predators are present (Slobodkin, 1961; Caswell, 1978). This result holds only if the predator is nonselective or preys preferentially on the competitive dominant. If these models describe the real world, then predation must be an important factor in determining the structure and diversity of communities. However, extension of the predation hypothesis to communities necessitates the consideration of many other factors, both biotic and abiotic (Glasser 1982).

Field tests of the predation hypothesis have produced mixed results. Floristic diversity may be maintained by grazing (Harper 1977, Chapter 14) or by fungal predators (McCauley and Cook 1980). Fish, gastropods, sea urchins and other marine predators may increase the diversity of sessile inter- and subtidal communities (Paine 1966; Dayton 1971; Sousa 1979a) but may reduce the diversity of algal patches (Day 1977; Robles 1982). Predaceous fish reduced insect diversity (Campbell and Denno 1978) and mosquitos reduced the number of protozoan species in pitcher plant leaves (Addicott 1974). On the other hand, predation of freshwater fouling communities altered species composition without affecting diversities (Mook 1981).

Diversity should not be treated as a static parameter as it may vary in space and time. Communities may be characterized by several predators feeding on the same group of prey species. Often these predators will have very different effects (Ayling 1981; Thiery 1981) which may result in fluctuating diversities. Seasonal and successional changes in algae result in fluctuations in algal diversity (Porter 1977); grazing certainly plays a role in this (Crumpton and Wetzel 1982). However, the timing and intensity of predation may determine the effect on prey diversity in seasonal communities (Porter 1973).

The predation hypothesis is based on the assumption that in the absence of predation, competitive interactions will lead to extinction of some species and thus lower diversity. However, if community diversity is considered over time, the role of predation becomes more complicated. The direct effects of predation are the deaths of individuals, but prey diversity may also be affected indirectly by changes in the physical environment due to the activities of the predators. The secondary effects of predators have been noted in a few systems. Digging by predatory rays in soft-bottom communities results in a rapid succession of species on the disturbed sediments (van Blaricom 1982). The initial effect is the removal of competitors but this sets off a series of events which van Blaricom suggests are more related to temporal changes in the quality of resources than to competition. The secondary effects of grazers in plant communities include local stimulation of plant growth around dung and urine patches and physical disturbances by hoof marks or burrowing and digging (Harper 1977, pp.

449-456). Tilman (1982) has hypothesized that a decrease in the abundance of blue-green algae in Lake Trummen was due to increased nutrient recycling by unusually high zooplankton numbers one year.

The function of predation in communities, then, goes beyond the traditional population model role as an agent of mortality. Perhaps a better description is offered by Harper (1977, p.449) who suggests that the effect of grazers is to disrupt "any trend to monotony within vegetation. Once heterogeneity exists the activities of animals tend to exaggerate the variations within a community."

This study is of the interaction between grazing and diversity in successional microcosms of freshwater algae and microcrustacean grazers. Although protozoa and rotifers are also present they are not considered here. Most species appeared to be bactivorous and the populations were transient. The hypotheses to be tested are

(1) grazing slows down the successional change from a community dominated by green algae to one dominated by blue-green algae, and

(2) grazing increases algal diversity.

These hypotheses were empirically derived from two years of observations of these communities. While no mechanism is suggested in the hypotheses, possible mechanisms will be discussed. Also, the species composition of the algal community will be examined with respect to the grazing regime and culture methods.

Materials and Methods

Experimental Design and Methods

Three factors were identified as possible determinants of community structure: presence or absence of grazers, age of culture and differences of the two series (Table 1). Series differences included variation in species composition of the inoculum and in growth conditions. Two aspects of community structure -- diversity and species composition -- were studied. A bifactorial design was used in which the two factors were presence/absence of microcrustacean grazers and starting date/conditions. Changes over time were determined by sampling at 2-3 different times.

Each series was set up in the same way but at different times and under slightly different conditions. Each system consisted of twelve

TABLE 1. Bifactorial experimental design. Number of replicates in each treatment is given.

	Series I	Series II
	Started mid-April Cool-white light	Started mid-May Warm-white light
With microcrustaceans	6	6
Without microcrustaceans	6	6

200 ml cultures kept in growth chambers for a period of 60 days. The growth chambers were garbage cans with 9 inch circular fluorescent lamps mounted in the lids. The algal cultures were on the floor of the can 45 cm from the light source. The photoperiod was kept at 16:8 L:D for the duration of the experiment. Room temperatures fluctuated between 22 and 24 C. The growth chamber temperatures were as much as 5 degrees higher when the lights were on.

Cultures were initiated by adding 10 ml of inoculum to 200 ml of distilled water. The inoculum came from an outdoor concrete tank that contains standing water year round (average depth less than 30 cm). Two grains of rice were the nutrient base of each culture. An organic nutrient source was used instead of one of the more commonly used inorganic media because this experiment was concerned with investigating succession. Conversion of the rice grains into nutrients resembles the breakdown of organic detritus that occurs in natural systems. This process could affect the successional pattern of the algae. An inorganic medium might have reduced the variance in this system.

The cultures were examined daily until microcrustaceans began to appear. A control set of six cultures without microcrustaceans in each series was obtained by adding 5% rotenone powder. Rotenone is a plant-produced insecticide that is toxic to fish and many crustaceans but not to algae (Smith 1940). It breaks down in a few days when exposed to oxygen and light. Many bacteria are capable of transforming it to various metabolites (Sariaslani and Rosuzza 1983). The microcrustaceans are so sensitive to rotenone that the entire population of grazers in a culture could be killed by dipping the moistened tip of a capillary tube in the rotenone and stirring the culture with it. A second dose of rotenone was added a week later when more eggs had hatched and grazers were again found in some of the jars.

One set of twelve cultures was started in mid-April (Series I), a second set in mid-May (Series II). Although in both cases inoculum was drawn from the same tank, the initial numbers of microcrustaceans were quite different and the relative abundances of algal species were slightly different. Also, a cool-white lamp was used in Series I, a warm-white in Series II. This resulted in slightly higher temperatures in Series II (2° higher than Series I at maximum temperature).

Protozoan, metazoan and algal species were identified in each culture after 14 days. Species diversity of each culture was determined from 2-ml samples at 40 and 60 days; also, diversities were determined at 20 days in Series II cultures only. Approximately 1000 individuals (cells, coenobia, filaments) were counted from each sample at 160X magnification after the samples had been sonicated for 5 seconds to break up clumps of filamentous algae. Whenever possible, identification was to species according to the taxonomic classification system used in Edmondson (1959) and Prescott (1954). In most cases, genera could be determined except for some diatoms, which could not be identified to this level. However, as diatoms were much less abundant than other algae and in most cultures either only one species occurred or was very much more abundant, the results were not significantly affected by treating diatoms as one group.

Initially, the numbers of grazers were estimated by inspecting each culture every two days and counting the number of animals visible without magnification. When densities greater than 20 per flask were reached it was no longer possible to estimate densities in this manner. At this point, grazer densities were estimated every 14 days by stirring the flask and withdrawing ten 2ml samples. Individual animals could be counted in the pipette. The samples were saved and returned to the flask after all had been counted. The ungrazed samples were also stirred, ten 2ml samples removed and then returned as a control for effects from handling.

Statistical Methods

Principal components analysis was used to determine differences in species composition at 60 days in both systems. Rotated factor scores for the first three axes were analyzed by a 2-way analysis of variance with grazing and series as treatments. The percentage of the total community represented by blue-green algae was transformed (arcsine) and compared by analysis of variance for all three factors.

Community diversity was measured by an estimation of the Shannon-Wiener index,

(1) $H'=-\sum_{i}^{S} p_i \ln(p_i)$ where p_i =relative frequency of species i in a sample, and S = the number of species in the sample. This index is sensitive to changes in the number of species and in equitability of species. It is often desirable to calculate these separately. However, in a sampling scheme such as this the two are confounded. Since a fixed number of individuals is counted, as species become increasingly rare the probability of including them in the sample de-

creases. Thus a community may seem to have few species with high equitability when actually it may have many rare species and low equitability. Algal communities are characterized by a few dominant species and many rare species (Sager and Hasler 1969); thus, as sample size increases and more species are discovered, H' changes very little. The change in H' is due to the offsetting effects of increasing the number of species while decreasing the equitability. The estimator of H' underestimates true diversity; this is not important here as sample sizes are the same for all communities and relative differences rather than true diversities are of interest.

The Shannon-Wiener index can be partitioned hierarchically (Pielou 1977), so that the relative contributions of different taxonomic levels to overall diversity can be determined. Species diversity in these communities was expected to be primarily determined by two factors: (1) the successional change from a community dominated by green algae to one dominated by blue-greens, and (2) changes in the numbers of or the relative abundances of species because of succession and grazing. There are three times as many species of green algae as blue-greens in this system, so that the contribution of the two taxonomic divisions to H' is asymmetric. Thus the relative abundances of divisions (Cyanophyta, Chlorophyta and Chrysophyta) will influence the species diversity. Partitioning diversity gives

(2) $H' = H'(D) + H'_D(S)$.

$H'(D)$, the division diversity, is given by

$$-\sum q_j \ln(q_j),$$

where q_j =proportion of all individuals in division j. $H'_D(S)$ is the weighted mean of the species diversity in each division:

$$-\sum_{j} q_j \sum_{i}^{S_j} p_i \ln(p_i),$$

where S_j= number of species in division j and p_i = relative frequency of species i in division j. The sum of division diversity and the average species diversity gives the same value as calculated in (1). The distribution of H' is asymptotically normal (Hutcheson 1970), so parametric statistics were used in all analyses. Three-way analyses of variance for H', $H'(D)$ and $H_D'(S)$ were run to test the effects of grazing, age and culture.

All statistical analyses were performed on a DEC 1091 computer using BMDP statistical software (Dixon 1981).

Results

Community Composition

The majority of the species in these communities are green algae (Table 2). The primary pattern of algal succession in these cultures was a change from a community dominated by green algae and diatoms to one dominated by blue-green algae. This pattern was apparent in both grazed and ungrazed systems, but the rate of replacement of greens by blue-greens was much faster in the ungrazed communities (Table 3). Scenedesmus quadricauda was the most abundant species in the early successional assemblage; a Phormidium species was the most abundant in the late successional group.

Grazers also showed some successional variation, cladocera appearing first, often in great densities. Their numbers tended to

TABLE 2. Common algae in the communities. Genera or species names are given where known.

Chlorophyta	
Scenedesmaceae	*Scenedesmus quadricauda*, *Scenedesmus* sp. 2
Hydrodictyaceae	*Pediastrum boryanum*
Desmidiaceae	*Cosmarium* sp.
Oöcystaceae	*Ankistrodesmus* sp., *Chlorella* sp., and very small coccoid alga, probably *Palmellococcus*
Oedogoniaceae	*Oedogonium* sp.
Chrysophyta	
Diatoms, probably Fragilariaceae	
Cyanophyta	
Oscillatoriaceae	*Phormidium* sp.
Nostocaceae	
Rivulariaceae	*Gloeotrichia* sp

TABLE 3. Average frequencies of major algal families represented in communities from both series at 40 and 60 days. Percentages less than 1% but greater than 0 are indicated by --.

	Grazed				Ungrazed			
Series:	1		2		1		2	
Age (days):	40	60	40	60	40	60	40	60
Scenedesmaceae	50%	29%	48%	21%	17%	8%	17%	10%
Hydrodictyaceae	6	4	3	1	2	1	1	1
Oöcystaceae	9	8	19	20	5	6	2	1
Diatoms	15	11	2	2	16	9	12	4
Oscillatoriaceae	15	43	28	50	49	68	47	64
Nostocaceae	3	3	--	5	7	5	17	16
Rivulariaceae	1	2	--	1	3	2	3	5

decline and copepods and ostracods became more abundant. However, the later grazers never attained the high densities that the cladocera did. In general, the ostracods and copepods are much larger than the cladocera (2-4 times as large). The cladoceran species were all chydorids (*Alona costata* and *Chydorus* sp.) and ranged in size from 300 to 500 µm. It is likely that smaller individuals were missed in counting and actual densities could have been much higher.

The grazer densities in a community varied, and the long period between counts is another source of error. Series I and II also differed in grazer densities. Grazers had reached very high densities within the first 2 weeks in Series I but developed more slowly in Series II (Figure 1). For each culture, I determined the maximum density observed in each jar and the day on which that maximum occurred. The average maximum density in Series I cultures was 23 animals per 20ml sample and the average time of peak density was 35.8 days; in Series II, average density was 42 per 20ml sample at 21.5 days. Thus the Series II communities experienced earlier and more intense grazing pressure.

The first three axes of principal components ordination explained 74% of the variance in species composition in 60 day old communities. These three axes, explaining 41.6, 19.6 and 12.5 percent of the variation, were chosen as recovering species patterns (Gauch 1982). Additional axes each explained less than 10% of the variance.

Factor loadings of the major species indicate that the major pattern was a negative association between greens and blue-greens (Table 4), but they also reflect differences in the timing of peak

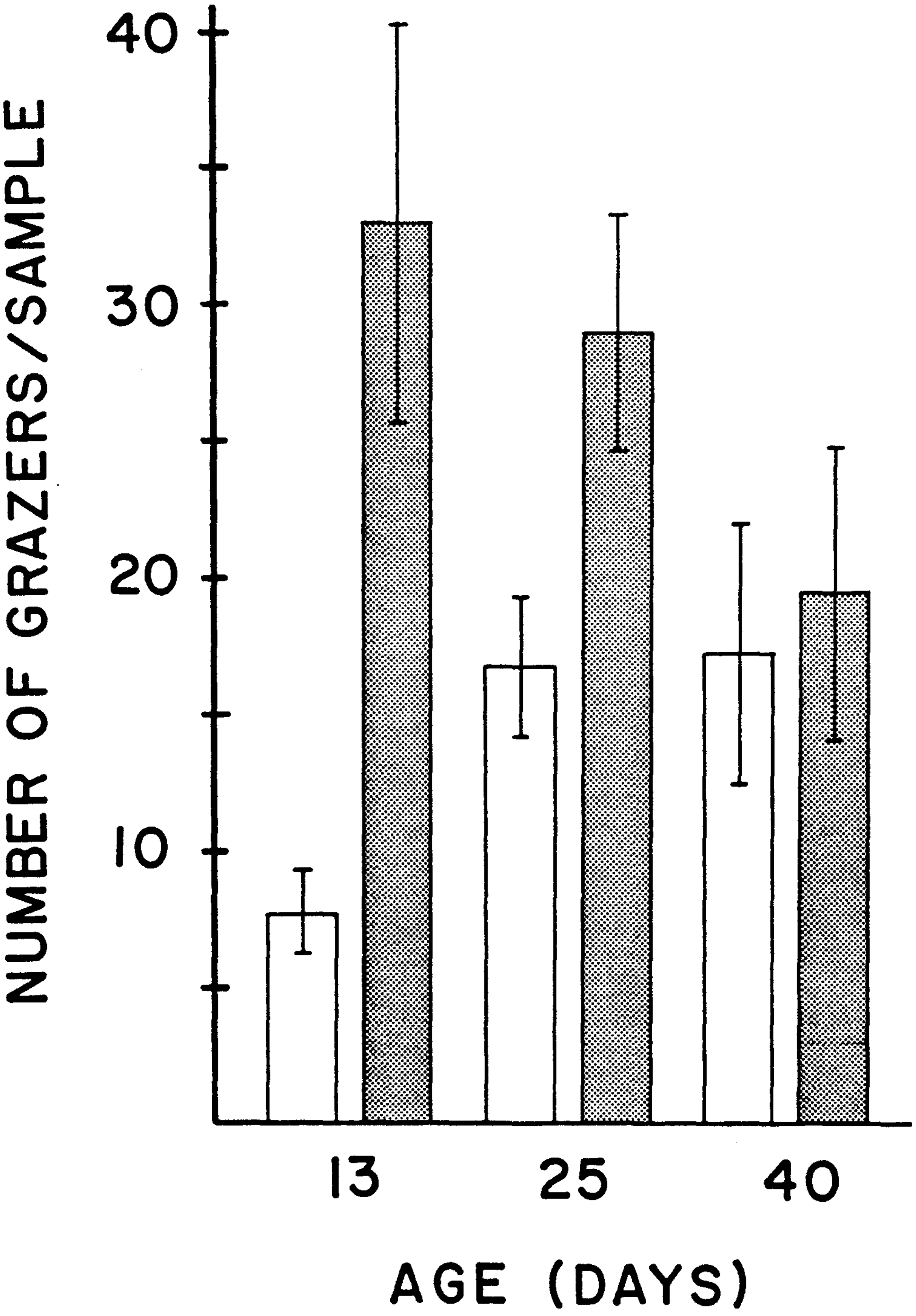


FIGURE 1. Average number of microcrustacean grazers in 20-ml samples from six replicates at three different times shows that series 2 (shaded bars) had more intense grazing pressure during the first few weeks than did series 1 (open bars). By the 40th day, grazer densities were nearly the same. Standard errors are indicated by vertical lines.

TABLE 4. Rotated factor loadings of major species on first three axes of principal components analysis.

Species	Factor 1	Factor 2	Factor 3
Scenedesmus quadricauda	0.926	-0.002	-0.124
Scenedesmus 2	0.721	0.451	-0.107
Pediastrum	0.564	0.481	-0.267
Ankistrodesmus	-0.033	0.439	-0.667
Coccoid green	0.097	-0.836	-0.376
Chlorella	0.627	0.585	-0.057
Diatom	0.201	0.712	-0.230
Phormidium sp.	-0.876	0.058	0.248
Nostocacean sp.	-0.185	0.000	0.874
Rivulariacean sp.	-0.367	0.185	0.714

densities within these subcommunities. Axis 1 separates the two *Scenedesmus* species from the *Phormidium* sp., while the third axis separates two Oöcystacean species from two blue-green species. *Scenedesmus* is the early dominant in the green subcommunity while *Ankistrodesmus* and other members of the Oocystaceae tend to occur later; similarly, *Phormidium* is the first blue-green to appear while the Nostocacean and Rivulareacean species become more abundant later. Axis 2 separates the small coccoid green from diatoms and several other green species.

Analyses of variance of the factor loadings show that the first and third axes also separated grazed from ungrazed communities (Table 5), and the third axis separated Series I cultures from Series II cultures. There was a significant interaction between series and grazing on the second axis, so main effects were not tested. Thus,

TABLE 5. Analyses of variance of factor scores for 60 day old communities partitioned between grazing treatments and series.

	source	SS	df	F	
Factor 1	series	0.122	1	0.13	ns
	grazing	4.190	1	4.57	*
	sXg	0.961	1	1.05	ns
	error	18.343	20		
Factor 2	series	8.623	1	31.51	--
	grazing	0.291	1	1.06	--
	sXg	3.012	1	11.01	**
	error	5.473	20		
Factor 3	series	6.184	1	10.42	**
	grazing	4.775	1	8.04	*
	sXg	0.545	1	0.92	ns
	error	11.875	20		

-- = not tested, ns=not significant, *=0.01<P<0.05, **=0.001 <P<0.01
***= P<0.001

grazing and series appear significant in determining species composition.

Division diversity H′(D) (Figure 2) was significantly affected by series differences and by the interaction between grazing and age (Table 6). Average species diversity $H'_D(S)$ (Figure 3) was significantly affected by age and by an interaction between series and grazing (Table 7). Interactions of grazing with both age and series (Table 8) were significant for the total diversity H′ (Figure 4). This ANOVA was rerun using a log transform but the interaction terms remained significant. From this it is concluded that a linear model is inappropriate for this system.

The relative frequency of blue-greens was greatly affected by

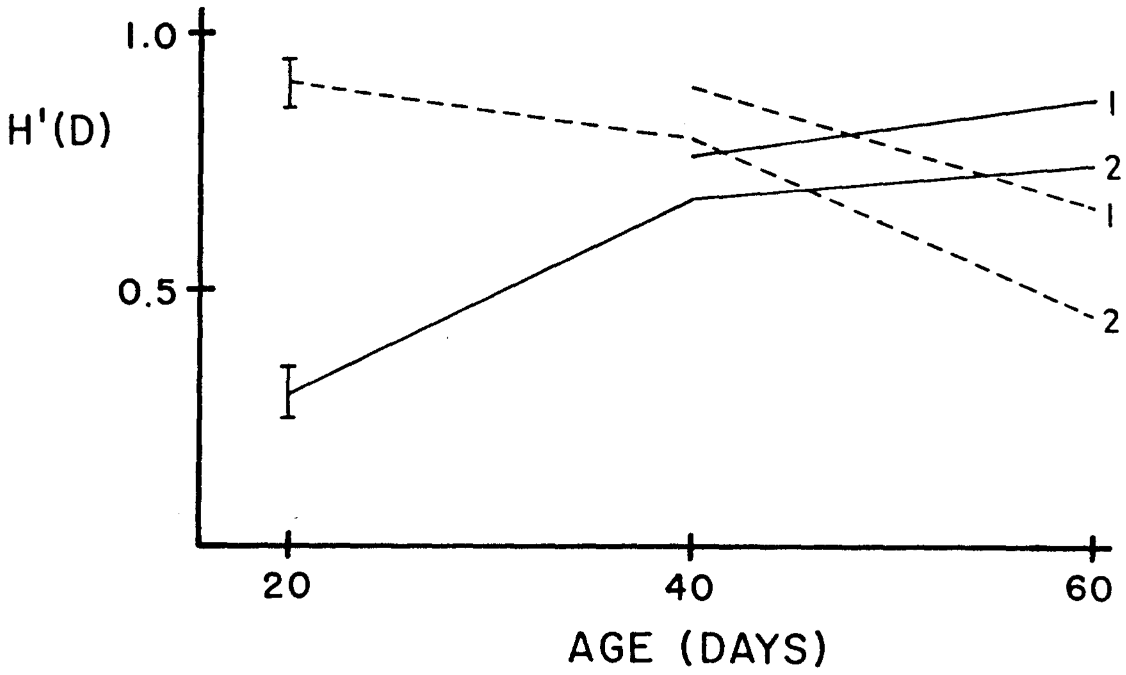


FIGURE 2. Means of division diversity in grazed (solid line) and ungrazed (dashed line) cultures from series 1 and 2 (indicated by number) vary with time. Standard errors of 20 day old communities are indicated; these were not used in analysis of variance (see Table 5).

TABLE 6. Analysis of variance of effects of grazing, age and series on division diversity, H′(D).

Source	SS	df	F	Significance level
Grazing	0.044	1	1.66	--
Age	0.105	1	3.95	--
Series	0.205	1	7.68	**
G x A	0.412	1	15.44	***
G x S	0.006	1	0.23	ns
A x S	0.016	1	0.59	ns
G x A x S	0.004	1	0.17	ns
Error	1.067	40		

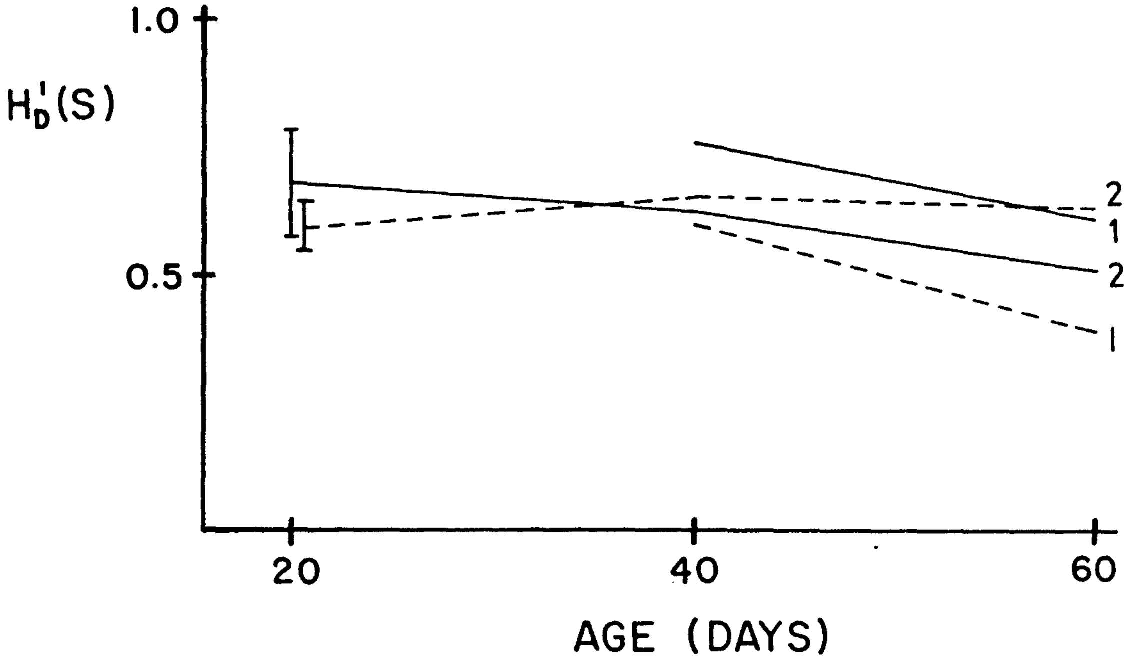


FIGURE 3. Means of average species diversity tend to decline over time. See Figure 2 for explanation of symbols.

TABLE 7. Analysis of variance of effects of grazing, age and series on the weighted average species diversity ($H_D'(S)$).

Source	SS	df	F	Significance level
Grazers	0.038	1	3.24	--
Age	0.192	1	16.51	***
Series	0.002	1	0.16	--
G x A	0.001	1	0.05	ns
G x S	0.224	1	19.34	***
A x S	0.031	1	2.63	ns
G x A x S	0.018	1	1.57	ns
Error	0.464	40		

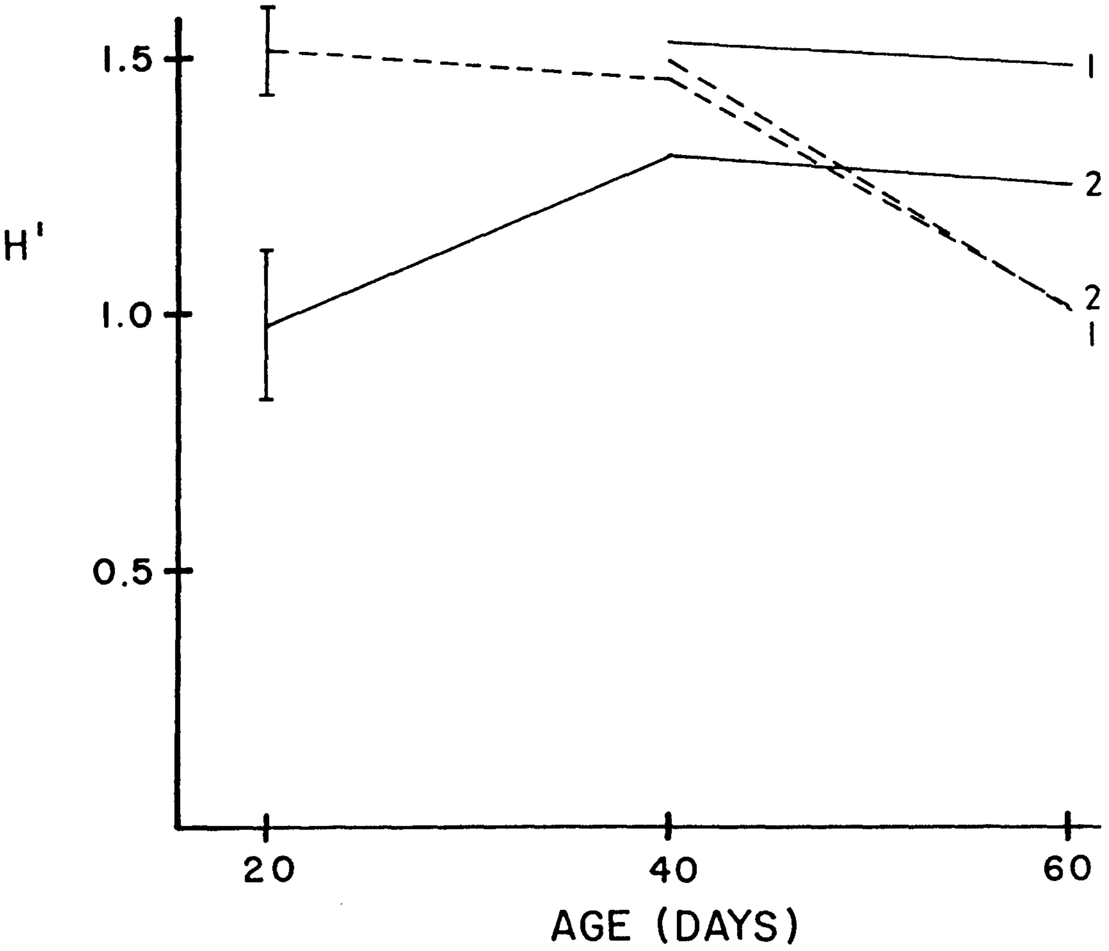


FIGURE 4. Means of diversity reflect the trends shown by the subcomponents, $H'(D)$ and $H_D'(S)$. Symbols same as for Figures 2 and 3.

TABLE 8. Analysis of variance of effects of grazing, age and series on total diversity, H'.

Source	SS	df	F	Significance level
Grazing	0.164	1	5.16	--
Age	0.585	1	18.46	--
Series	0.170	1	5.36	--
G x A	0.382	1	12.06	**
G x S	0.156	1	4.93	*
A x S	0.003	1	0.08	ns
G x A x S	0.005	1	0.15	ns
Error	1.267	40		

grazing and age. Series differences were also important though not as much (Table 9). The percentage of blue-greens was lower in grazed communities and in younger communities (Table 10). Series I had fewer blue-greens than Series II; this may be due to differences in temperature, light quality or the initial inoculum.

These results are consonant with the hypotheses that grazers slow the rate of succession and increase H'.

TABLE 9. Analysis of variance of effects of grazing, age and series on the average relative frequency of blue-greens.

Source	SS	df	F	Significance level
Grazing	2.007	1	62.03	***
Age	1.039	1	32.11	***
Series	0.150	1	4.64	*
G x A	0.019	1	0.60	ns
G x S	0.001	1	0.03	ns
A x S	0.022	1	0.69	ns
G x A x S	0.000	1	0.00	ns
Error	1.294	40		

TABLE 10. Average diversities of the green and blue-green subcommunities. Average relative frequencies of the subcommunities are also shown in parentheses.

	Series		Grazed	Ungrazed
		H′(gr) :	0.749 (92.1%)	0.711 (50.8%)
20 DAYS	II	H′(bg) :	0.039 (6.5%)	0.557 (37.7%)
		H′(gr):	1.085 (63.2%)	1.065 (22.1%)
40 DAYS	I	H′(bg):	0.538 (21.9%)	0.587 (61.9%)
		H′(gr):	0.873 (69.5%)	0.915 (21.2%)
	II	H′(bg):	0.068 (28.2%)	0.712 (66.7%)
		H′(gr):	1.060 (41.0%)	0.933 (14.9%)
60 DAYS	I	H′(bg):	0.425 (48.4%)	0.351 (76.3%)
		H′(gr):	0.800 (42.6%)	0.510 (11.3%)
	II	H′(bg):	0.310 (55.3%)	0.674 (84.6%)

Discussion

Species Composition

There were no major differences in the species assemblages of the communities, so the patterns revealed by principal components analysis are due to differences in relative frequencies. Series I cultures tended to have more diatoms than Series II, especially when grazed communities were compared. Ankistrodesmus was also more common in Series I while a Nostocacean blue-green was more abundant in Series II. The interaction effect on the second axis is probably due to the relatively high frequency of a small coccoid green alga and the very low frequency of diatoms in grazed Series II cultures.

The role of grazers in retarding the rate of increase of blue-greens is shown in several ways. The significance of grazing on the first and third axes factor loadings and the negative association of greens and blue-greens with these axes shows a relationship between grazing and the relative frequency of blue-greens. This is borne out by the results of the analysis of variance of the relative frequency of blue-greens.

There are exceptions, however. One ungrazed culture showed a smaller decrease in greens than the other ungrazed cultures. It was one in which grazers had not been entirely eliminated or had hatched from eggs after the last application of rotenone. Although no grazers were seen at 40 days, by 60 days they were abundant and large enough to be noted. This is the only "ungrazed" culture that is consistently grouped with the grazed cultures. On the other hand, one of the grazed cultures in Series I tends to be grouped with the ungrazed cultures. There is no obvious explanation for this and it serves to illustrate the variability of the system.

Community Diversity

All three treatment effects -- grazing, successional state and series -- were important determinants of diversity, but interactions between treatments complicate interpretation of results. These results are best understood by first looking for patterns in the diversity data and then examining the statistical analyses.

Total diversity, H', tends to be higher in Series I grazed cultures than in Series II. Apparently this is due to a decrease in $H_D'(S)$ in Series II, since $H'(D)$ is lower in Series II than in Series I regardless of grazing effects. The intense grazing pressure (see Figure 1) in Series II communities decreased diversities of both the greens and blue-greens (Table 10). Between series differences in grazing pressure do not appear to affect the relationship between grazing and $H'(D)$, so factors such as differences in inoculum, light quality, temperature or some combination of these must be responsible for the lower division diversity.

Effects due to grazing depend on culture conditions and age. $H'(D)$ is suppressed by grazing at 40 days but increased by grazing at 60 days. Moderate grazing increases $H_D'(S)$ regardless of age, while early heavy grazing suppresses it. Thus, in Series II average $H_D'(S)$ at 60 days in the ungrazed cultures was higher than in the grazed while the opposite pattern is seen in Series I (Figure 3).

H' declines as succession progresses but the rate of decline is less in the grazed systems, even when grazing is intense as in Series II. This is partially due to the suppression of blue-greens by grazers. The subcommunity of green algae contributes a greater proportion to $H_D'(S)$ and since it is more diverse than the blue-green subcommunity, H' is higher.

The significance of the interactions of grazing with age and with culture to H', then, can be explained by their effects on $H'(D)$ and $H_D'(S)$. Since H' is the sum of $H'(D)$ and $H_D'(S)$, the ANOVA results suggest that there is some correlation between these two components and that the relationship is affected by grazing. A correlation between $H'(D)$ and $H_D'(S)$ is predictable from the previously mentioned asymmetry in species distribution; a grazing effect on this correlation might be expected then from the effect of grazers on the relative frequency of blue-greens.

Linear correlations between the two diversity components confirm this intuitive explanation (Table 11). $H'(D)$ and $H_D'(S)$ are weakly positively correlated in grazed communities while they are more strongly negatively correlated in ungrazed. These differences happen because the grazed communities have higher proportions of green algae. In the grazed communities, highest $H'(D)$ values tend to occur at 60 days when the frequency of green algae was approximately 40% of the total (Table 10). In the ungrazed communities, the proportion of greens is already low (22%) by 40 days. Thus the highest $H'(D)$ values are found at a time when blue-greens are dominant. Since the green subcommunity is more diverse, the grazed communities had higher values

TABLE 11. Linear correlations between H′(D) and $H'_D(S)$ for both grazed and ungrazed treatments at 40 and 60 days.

	Grazed	Ungrazed
40 Days	0.157	-0.709
60 Days	0.412	-0.606

for $H'_D(S)$ when H′(D) values were also high.

This unexpected result suggests a dilemma in equating age with successional state. Instead, we might define successional state by the relative frequency of blue-greens and compare grazed and ungrazed communities based on that criterion. Data in this study are insufficient for such comparisons, but consideration of the data for the 20 day old Series II communities is helpful. These data were not used in the previous analyses because there are no corresponding data for Series I.

The diversity values at 20 days (Figure 4) suggest that the peak diversity in the ungrazed system comes much earlier than in the grazed system. This early peak in H′ depends on the high value of H′(D) (Figure 2). As blue-greens increase in relative frequency, H′(D) drops but $H'_D(S)$ increases. The net effect is that H′ does not change much between 20 and 40 days. Eventually, greens become relatively rare so that both H′(D) and $H'_D(S)$ decrease, thus lowering overall diversity. The same pattern exists in the grazed communities except that the initial phase of green algae dominance is prolonged. Thus $H'_D(S)$ makes a greater contribution to H′ in the early stages; later

$H'(D)$ becomes more important while $H'_D(S)$ decreases. I infer a similar pattern in the Series I cultures, although less intense grazing in the early stages may have allowed H' to reach higher levels in the Series I cultures. The H' values for grazed and ungrazed cultures may not be very different in that case.

Thus grazing may increase or decrease diversity. The outcome depends on the age of the community as well as the intensity of grazing at the time of sampling.

Mechanisms

The pattern observed here fits a model of non-selective grazing delaying the exclusion of green algae by blue-green algae. However, the same pattern could be produced by several other mechanisms.

First, the possibility of selective grazing must be considered. Chydorids are predominantly bottom-feeders and gather algae, bacteria and detritus by scraping (Fryer 1969). They are generally regarded as generalists but are probably somewhat size-selective (Neill 1975). Although there is evidence that zooplankton reject noxious blue-greens in laboratory studies, in natural situations blue-greens are eaten (see review by Porter 1977). More probably algae are rejected because they are too large to be handled or because they are sheathed or enclosed in a gelatinous matrix (McNaught et al. 1980). The second most abundant grazer in this system was an ostracod species. Little is known about feeding preferences of ostracods. In one study, ostracods chose some blue-greens over others but generally preferred greens such as <u>Ankistrodesmus</u> or <u>Scenedesmus</u> (Mills and Wyatt 1974). The greater frequency of blue-greens in the ungrazed cultures suggests that they may be eaten preferentially. This seems unlikely given the studies on feeding previously cited, but it should be pointed out that even large filamentous forms such as the Rivulareaceae start out small and they may be more susceptible to grazing at this stage. This is also suggested by the decreased diversity of both greens and blue-greens at 40 days in Series II. Thus it seems likely that grazers did not selectively graze some species but they might have eaten smaller cells. Blue-greens, then, are just as likely to have been eaten when small but may escape predation once they achieve some size.

A second explanation is that the grazers are non-selective but that some green algae survive gut passage; some species with gelatinous matrices are known to do this (Porter 1975) but species of this type are rare in these communities. Some of the species with spines (Scenedesmus quadricauda) or tough cell walls (Cosmarium sp) might be more resistant to grazing than species such as Ankistrodesmus. However, it seems unlikely that all the green algae are more resistant to grazing than the blue-greens, particularly since two of the blue-green species are sheathed.

The third possibility is that the grazers are regenerating nutrients necessary for the persistence of green algae. The growth rates of green algae and blue-green algae are optimal at different N:P ratios (Rhee and Gotham 1980), and this has been suggested as an important determinant of dominance during succession (Tilman 1982, 1983). Microcrustaceans are known to be a significant source of both nitrogen and phosphorus in lakes (Lehman 1980). More importantly, they excrete nutrients in a form immediately usable by algae (Lehman and Scavia 1982). Obviously this is not the only source of nutrients given the bacterial and protozoan community in both systems. Possibly the microcrustaceans change the ratio of nutrients in a way favorable to green algae. Thus, nutrient regeneration may slow the rate of succession by prolonging the period of favorable growth for green algae. If so, microcrustaceans do not supply enough nitrogen to prolong it indefinitely.

All three of these mechanisms have been implicated in models of succession in communities of planktonic algae (O'Brien 1974; DePinto et al 1976; Nilssen 1978). Although the role of selective grazing and gut passage have received more attention than has nutrient regeneration in field and laboratory studies (Porter 1977; McCauley and Briand 1978; Lynch and Shapiro 1981; Crumpton and Wetzel 1982), Tilman (1983) has hypothesized that increased nitrogen recycling by zooplankton was responsible for a decrease in blue-green algae in Lake Trummen.

The conditions of growth in these cultures are probably much more extreme than in most natural situations. Natural systems will have some allochthonous input of nutrients while the laboratory systems were closed. Therefore the complete absence of grazers in a pond or lake might not produce such a rapid succession to blue-green dominance. It is also unlikely that natural algal communities experience grazing pressure as intense as that in these cultures. However, Porter (1973) noted that differences in timing and intensity of grazing affected the response of the algal community of a temperate pond.

Intense grazing pressure in the early spring ultimately reduced diversity by removing species while moderate grazing reduced the dominance of highly edible species and increased diversity. A similar pattern is seen here with moderate grazing increasing diversity while early intense grazing reduced it.

The applicability of these results to other systems depends partly on the mechanism involved. If regeneration of nutrients is the main effect of grazers, then these results should apply to most aquatic systems. However, the effect of predation may be to increase the rate of succession (Sousa 1980; Day and Osman 1981). In these cases, the role of the predator was to remove the early dominant and create more opportunities for the establishment of late successional species. Snails grazing on epilithic algae alter the relative frequencies of algal types by viable gut passage and highly localized nutrient recycling (Cuker 1983). This system is similar to terrestrial plant communities where nutrients are localized. Certainly, the patchiness created by deposits of dung or urine should increase overall diversity. Again, the temporal as well as the spatial scale used will affect the observed relationship.

Any seasonal or successional community may show a similar response to predation, particularly if the predator is also seasonal (Porter 1973; Thiery 1981). One advantage of microcosms such as these is that ecological events occur over a relatively short time span, whereas some other communities change very little in the life-span of the researcher. Long-lived organisms may appear to be in equilibrium with their predators when in fact the change is simply too slow to be seen. Thus, seasonal and successional variations in predators and their effects on the community are more easily detected in microcosms.

In summary, grazing by microcrustaceans in freshwater microcosms increased the diversity of the algal community at some stages in succession but reduced it at others. The mortality due to grazing is only one aspect of this interaction as microcrustaceans may also alter the competitive interactions by changing the nutrient ratios. The intensity and timing of grazing are also influential. Early, intense grazing appears to lower diversity relative to the effects of moderate grazing.

CHAPTER FOUR

DISTURBANCE IN SUCCESSIONAL ALGAL COMMUNITIES

Introduction

Theories concerning the role of disturbance in determining community structure are based on two different paradigms of community structure. The intermediate disturbance hypothesis was empirically derived for sessile communities where competition for space was clearly important (Levin and Paine 1974; Horn 1975; Connell 1978; see also analysis by Tilman 1982, Chap. 8). The mechanism proposed is that disturbance disrupts competitive exclusion and thereby leads to increased diversity. Furthermore, intermediate levels of disturbance will maintain the highest diversity since only the fastest growing species will survive at high levels of disturbance.

The other school of thought relies on evolutionary arguments (Loucks 1970; Denslow 1980). Here the assumption is that communities are made up of species adapted to various successional phases and that the life-history strategies have been determined by the history of disturbance in the community. Diversity is predicted to be highest at the historical rate of disturbance.

One problem with disturbance theory is a lack of consensus on the definition of disturbance. Some definitions are all-encompassing. Levin and Paine (1975) described disturbances as "...extinctions due to natural catastrophe, competition, or predation-related agents." For a computer simulation model of disturbance in competing populations, Huston (1979) defined disturbance as a reduction in the population size of all species in the system. This definition is nonselective in that no species is more susceptible than any other. In practice, disturbance must be defined with respect to the system of interest although this makes comparisons between systems difficult. In this paper, disturbance is considered to be an extrinsic factor that potentially confers an equal probability of mortality on all individuals.

The alteration of the physical environment by disturbance must also be considered. It is difficult to think of a naturally occurring disturbance that does not alter the environmental conditions of the community. Species diversity may be increased by the addition of new habitats. While this argument fits the evolutionary theory quite well, it could also be viewed as a mechanism for reducing competition. In competition theory terms, disturbance changes the competitive coefficients while it also reduces the number of competitors.

Most field case studies, field manipulations and laboratory experiments support the predictions of the disturbance hypothesis but the results may be affected by seasonality of recruitment, predation and other factors. Disturbance increases the diversity of patches of sessile organisms in the intertidal zone by removing the competitive dominant, Mytilus californianus (Paine and Levin 1981); however, diversity of organisms that live in these mussel beds increases as the beds age and become more complex structurally (Suchanek 1979). Algal succession on boulders was disrupted by overturning of boulders and greater diversity resulted (Sousa 1979b), but timing of the disturbance affected the outcome because recruitment was seasonal. Robles (1982) found that disturbance resulting from wave scouring removed the grazers on ephemeral algae and that the release from grazing pressure resulted in increased algal diversity. However, fouling communities subjected to periodic biomass removal by scraping showed no change in diversity (Mook 1981) apparently because the communities were already subjected to intensive predation and recruitment was low.

Studies of disturbance in nonsessile communities also show increased diversity with disturbance. The number of protozoan species colonizing artificial sponges increased after squeezing regardless of the length of time they had been immersed in a lake (Cairns and Yongue 1971). Both greater numbers of algal species and their higher evenness were maintained in gnotobiotic systems that were disturbed by removal of part of the culture and replacement with fresh culture medium (Robinson and Sandgren 1983). In both these studies, competition was presumably the primary factor determining the structure of the undisturbed community.

This study is concerned with small freshwater algal communities in which the importance of competition to community structure is less obvious. Most of the work on diversity of algal communities involves field studies of lacustrine systems or controlled laboratory studies of artificially assembled groups of algae. Diversity and species composition in natural algal communities is primarily determined by seasonality (Lund 1965; Moss 1973; Reynolds 1973), grazing (Porter

1973; McCauley and Briand 1979; Crumpton and Wetzel 1982; DeCosta et al 1983) and competition for nutrients (Tilman, Kilham and Kilham 1982).

These factors are not mutually exclusive, however; seasonality is a comprehensive notion that may include changes in temperature, pH, grazer abundances and nutrient levels; moreover, nutrient levels may be affected by the abundance of grazers (Axler et al. 1981). Furthermore, laboratory studies have shown that competitive interactions cannot be completely described by competition for a single nutrient. Tilman (1982) argues that many species can coexist in a heterogeneous environment at equilibrium if each species is limited by a different ratio of nutrients. Diversity in algal communities, then, is poorly modelled as a simple function of Lotka-Volterra competitive interactions.

This is a study of the effects of exogenous abiotic disturbance on the diversity of successional algal communities. Microcrustacean grazers are present in this system and have been shown to affect diversity by decreasing the rate of succession in laboratory studies (Chapter 3). Possible interactions between this endogenous biotic disturbance and the experimental abiotic disturbance must also be considered. The null hypothesis that disturbance does not affect diversity or species composition is tested.

Methods

Experimental Methods

Thirty algal cultures were established outdoors in early June 1981 and again in 1982. Sterilized wide-mouth 600ml jars (17cm in height) were placed in a 20 X 42 X 96 cm wooden box in Eugene, Oregon (44°N, 123°W, 109 m elevation). This box held a total of 36 jars. The box was oriented with its longest dimension on an east-west axis. A fence (approximately 2 m high) on the south side of the box shielded it from direct sunlight. A black plastic canopy 65 cm above the box also provided some shade and kept out the rain. A wire screen over the top of the box kept out large insects, leaves and animals. Each jar contained six grains of rice and 400 ml of distilled water. Twenty ml of well-stirred inoculum was added to each jar. The inoculum was taken from a shallow outdoor concrete tank that has standing water all year. Some of the sediments were included in the inoculum.

Algal diversity was measured by estimating the Shannon-Wiener index,

$$H' = -\sum^{S} p_i \ln p_i,$$

where p_i = relative frequency of species i, and S= number of species in sample. Mean numbers of species are also included for descriptive purposes but are not tested statistically. The rationale for this procedure has been discussed elsewhere (Moss 1973; Chapter 3, this dissertation).

The cultures were allowed to grow for 21 days. Then H′ was determined for each community from a 4 ml sample. Algal diversity was determined by counting approximately 1000 individuals (cells, coenobia, filaments) at 160X magnification. Identification to species was made whenever possible according to the taxonomic classification of Edmondson (1959) and Prescott (1954). By repeated sampling of six communities, this method was found to have, at worst, a 5% error rate in communities up to three months of age. That is, the mean plus or minus 5% of the mean gives the range of values expected. At the same time, protozoa and metazoa were identified but numbers were not counted.

Communities were ranked by diversity and the lowest and highest three were excluded from the experiment. In 1981, the remaining 24 were divided into 6 ranked groups and one jar from each group was randomly assigned to each of four treatments. Thus the initial means and variances were as similar as possible, and any possible effects owing to position in the box were distributed among treatments. In 1982, only three treatments were used, each with eight replicates. The fourth treatment from 1981 was not used in the following statistical analyses.

Disturbance was defined as a 50% reduction in the populations of all species. This reduction was effected by shaking each jar thoroughly for approximately 60 seconds and then pouring half the culture into another jar. This portion was then filtered using Whatman No. 1 paper and returned to the original jar. The filter paper retained all the algal cells but did allow some of the very small flagellated protozoa through. Three frequencies of disturbance were used: low (disturbance frequency, f, equal to 0), medium ($f=0.056$ days^{-1}) and high ($f=0.111$ days^{-1}).

The grains of rice broke down at different rates in the jars. To minimize the loss of nutrients resulting from the loss of partially decomposed rice during a disturbance episode, rice was added to maintain four grains in each jar until mid-August in 1981. In 1982, the rice broke down very quickly so that very few whole grains were left by mid-July. Since rice grains were only lost during the first disturbance, one grain was added to the medium and high disturbance jars after the initial disturbance episode but no more food was added after that. No rice was added to the undisturbed jars since the only loss of nutrients was from sampling and therefore small.

The first disturbance episode in the high disturbance communities was on July 10 in 1981 and on July 13 in 1982. The medium disturbance treatment was initiated two days later in both years. All communities were sampled every 18 days, 9 days after the most recent disturbance. A 4 ml sample was taken from each jar by withdrawing small aliquots from 10 points on the bottom of the jar. Preliminary sampling had shown that very few algal cells were in suspension or on the sides during the first few months. After disturbance treatments began, three samples were taken, the last one in early September. Only the sample taken before disturbance (initial sample) and the final sample are used in analyses. Samples were counted on the same day that they were collected and then preserved in 4% formalin for use in subsequent analyses.

The disturbance treatment defined above was chosen so as to minimize changes in the culture medium. By returning the same medium to the jar, any changes from algal extracellular products were retained. However, the nutrients in the system increasingly become tied up in the biomass. Removing 50% of the biomass therefore must remove a substantial portion of the nutrients as well. Also, it was difficult to obviate differences in nutrient levels, especially between years. To assess the importance of the kind of disturbance to the outcome of the experiment, in 1982 an alternative medium disturbance treatment was applied to the remaining 6 jars. Again, jars were shaken and 50% of the culture was removed. An equivalent amount of a mixture of distilled water and tap water was added. The conductivity of the water was 20^{-6}mhos per cm (the average conductivity of the undisturbed jars). Two grains of rice were added after the second disturbance (on the 54th day). This treatment will subsequently be referred to as disturbance-substitution.

The experiments described so far deal only with relatively young communities. If stability increases with age (Odum 1969), older algal communities should be less affected by disturbance. This hypothesis was tested in 1982 only. The communities used were cultures from the 1981 study which had been left outdoors over the winter. Thus, they were 12 months old at the beginning of the 1982 experimental period. The sides of all jars were scraped with a rubber spatula to remove the algal growth that had developed over winter. The diversities of these communities were measured in late May and early June (mean $H'= 1.406$, s.e.= 0.0945). These older communities had higher errors in measuring H' than the younger ones. This was especially true for communities with numerous filamentous blue-greens. These species tended to form tangled clumps and were less likely to be randomly located within a jar. In the worst case, diversities differed 20% between two samples. Generally, the error was within 10%. Eighteen jars were assigned to three different disturbance treatments (6 jars per treatment) so that between treatment variance was minimized as described previously. The three treatments were low disturbance (undisturbed), disturbed ($f=0.07$ days^{-1}) and disturbance-substitution ($f=0.07$ days^{-1}). The only change in procedure was that vacuum filtration with Whatman No. 42 paper was used.

Experimental Rationale and Design

The system used in this experiment was controlled only for physical differences in volume and substrate. My objective was to reduce variation resulting from physical abiotic differences in the habitat but to preserve most of the biotic variability. While better replicability could have been achieved by other methods, biological realism was deemed more important for this study.

The experimental design was a factorial model with fixed disturbance effects and a random year effect. However, the interaction of the microcrustacean grazers with the disturbance effect could not be predicted before the experiment was run. Therefore, grazer density was treated as an independent variable in preliminary analysis and subsequent tests depended on the results of this analysis.

Animal Community, Physical Data and Colonization

The number of animal species (excluding microcrustaceans) declined over time in all treatments (Table 1, complete species list in Appendix A). A diverse assemblage of large ciliates and small flagellated forms developed in the first three weeks but declined rapidly during the summer. By fall, the animal community consisted primarily of _Difflugia_ sp., _Cinetochilum_ _margaritaceum_, peritrichs and a few small ciliates and flagellates. Two rotifer species and a gastrotrich were found in the initial and final samples. Nematodes and oligochaetes were seen occasionally. It is possible that some of the rotifers and larger ciliates grazed on the algae, but no evidence of this was ever found. Therefore, only grazing by microcrustaceans will be considered.

In the younger communities, the microcrustaceans were primarily cladocerans (Chydoridae) but cyclopoid copepods and ostracods were also found. Copepods and ostracods were dominant in the one year old communities; cladocera were found in only one of these jars.

TABLE 1. Mean and standard error of number of animal species in cultures (excluding microcrustaceans) at beginning and end of study under three frequencies of disturbance.

Year	Initial	Final		
		Low	Medium	High
1981	10.02 (.62)	6.29 (2.01)	6.29 (1.33)	4.86 (1.17)
1982	5.04 (.62)	4.00 (.60)	2.13 (.35)	2.38 (.65)

Temperature and pH were monitored in both years; conductivity was measured at the end of 1982 only. Six aquarium thermometers were placed in different jars so that all areas of the box were represented. Temperatures were monitored at irregular intervals, on different days and on the same day at different times. These temperatures were correlated with the air temperature data from the National Weather Service at the Eugene airport (R^2=0.916). So, in 1982, temperatures were checked only on very hot days to determine whether there were within box variations in temperature. pH was measured with pH hydrion paper which had a resolution of 0.5 units.

Temperatures were similar between years except in June (Table 2). Temperatures within the box varied by 1°C at most. Cultures near the sides of the box tended to warm faster and cool slower than those in the middle. The communities tended to be acidic (pH 4.8-5.3) but did not vary between treatments. The one year old communities were near neutral (6.7-7.4) at the beginning of the summer but declined to around 5.3 by fall.

Conductivity was higher in the medium and high disturbance treatments but the disturbance-substitution treatment was not different from the undisturbed (Table 3). The 15-month-old jars showed little between treatment variation. The higher conductivity in the two 3-month-old disturbance treatments may be due to the shaking, but if so, the same phenomenon should be seen in the late successional communities.

Colonization was monitored by placing traps at various places in the box. The traps were jars in which algae had been grown for the pre-

TABLE 2. Mean monthly temperatures, °C.

Year	June 10-30	July 1-31	August 1-31
1981	18.1	18.2	20.1
1982	15.3	18.0	19.2

TABLE 3. Conductivity (10^{-6} mhos per cm) of all treatments, 1982 (mean and S.E.).

Age	Treatment: Undisturbed	Treatment: Disturbed		Treatment: Disturbed with substitution
3 mos.	20.0 (1.0)	Medium:	41.1 (10.7)	20.0 (0.7)
		High :	38.4(2.2)	
15 mos.	25.2 (3.3)		22.3 (4.4)	18.3 (1.5)

vious nine months. The medium was filtered using Whatman No. 1 paper to remove most of the biomass, diluted with an equivalent amount of distilled water and then autoclaved to kill any remaining organisms. Two grains of rice were added. Samples were taken periodically and the species identified. Two jars were used in 1981, 4 in 1982.

Colonizing species were similar in both years (Table 4). The small number of traps gives only a minimal sample of the potential colonizers as the between jar differences within a year attest. *Scenedesmus* spp. have been found in the air in the Eugene area during the summer months (Sheridan 1963), but between year variations are cer-

TABLE 4. Number of occurrences of colonizing species in traps.

Species	1981 (2 traps)	1982 (4 traps)
Chlorella sp.	2	4
Phormidium sp.	1	1
Small coccoid green	2	1
Mougeotiopsis sp.		1
Diatom		1
Sphaerocystis sp.	1	
Unidentified greens	1	
Unidentified blue-greens		2

tainly possible. Eight of the chlorophytes in this study belong to genera which have been found in air samples (Coleman 1983), so they are potential colonists. Nevertheless, I conclude from the data that the diversity of colonizers was low during this study.

Experimental Analysis

Composition of Algal Communities

Differences in the species composition of the communities were analyzed by a method known as k-means clustering that is based on the relative frequencies of the species in the communities. K-means clustering is a nonhierarchical method in which all the data are first grouped in one cluster and then divided into a specified number of groups (Anderberg 1973). The center of each cluster is a vector of the means of each species. Group membership is determined by calculating the Euclidean distance of the community from the center of a

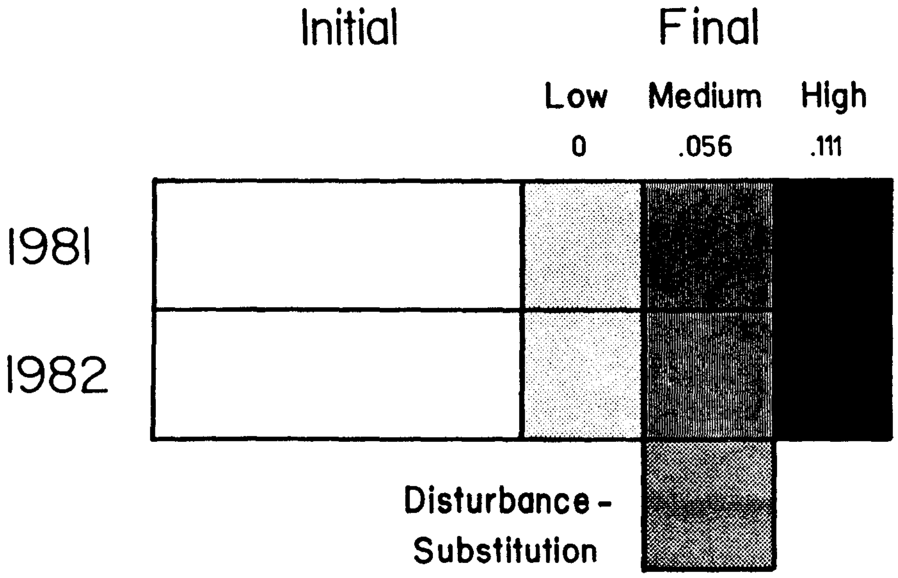


FIGURE 1. Factors considered: initial and final samples and low, medium and high disturbances in both years, plus disturbance-substitution in 1982. If these treatments were the sole determinants of species composition, then cluster analysis of the communities should produce 9 distinct clusters. Years are sorted on the ordinate, treatments are arranged by increasing age and disturbance frequency. Open bars are initial sample communities, shaded bars are final. Patterns represent the disturbance frequency indicated.

cluster. Several passes are made through the data, reallocating communities to clusters and recalculating the centers of each cluster. Computation stops when each case is in the cluster whose center is closest. Since there are nine possible combinations of factors (Figure 1), nine clusters were specified for the early successional communities.

The species composition of the 15-month-old communities was tested by k-means clustering with four clusters specified (initial and final samples with three treatments).

In all, 18 algal species were found, most of them Chlorophyta (Table 5). The number of species increased during the summer but varied little between treatments (Table 6). There were more species in the initial sample of 1982, but these differences disappeared by fall.

The major pattern in species composition is the decline in the relative frequency of Scenedesmus spp. (Figure 2). The concomitant increase in other species is particularly evident in those clusters with the highest average disturbance (clusters 7,8,9) where Ankistrodesmus or Phormidium is the dominant species. The 21 day old communities tend to form two distinct year groups (clusters 1 and 2) but there is less distinction between years among the fall communities. Cluster 9 is almost entirely composed of high disturbance communities from 1981, but the high disturbance communities from 1982 do not form a distinct group. The disturbance-substitution treatment does not appear to differ much from the other disturbance treatment as it is represented in clusters with medium and high disturbance communities from both years (clusters 4,5,6,8 and 9).

Only the initial and final samples were used in this analysis. The data from interim samples (not shown) show that the changes in the relative frequencies of species were monotonic.

A comparison of the species found in the colonization jars and the species in these communities suggests that invasions by new species are relatively rare. The only event of this sort was the

TABLE 5. Major algal species (>5% of total numbers at any time). Other species are listed in Appendix B.

Division Chlorophyta	Division Chrysophyta
Scenedesmus quadricauda	Diatoms (Naviculaceae)
Pediastrum boryanum	
Cosmarium sp.	Division Cyanophyta
Ankistrodesmus falcatus	
Small coccoid green	Phormidium sp. 1
Microspora amoena	Phormidium sp. 2
Oedogonium sp.	Nostocacean sp.
Chlorella sp.	Calothrix sp.
Gloeocystis sp.	Gloeotrichia sp.

TABLE 6. Number of algal species in each treatment at initial and final sampling dates. Means are of the number of species in a culture averaged over the treatment, totals are number of species found in all cultures in a given treatment.

Early successional communities

		Initial	Final			
			Low	Medium	High	Substitution
1981	Mean:	5.4	9.3	10.7	10.2	
	Total:	8	12	12	12	
1982	Mean:	7.9	8.9	9.4	9.9	9.2
	Total:	14	13	13	14	13

Late successional communities

		Initial	Final		
			No	Disturbance	Substitution
1982	Mean:	12.7	8.3	8.8	10.3
	Total:	18	12	12	13

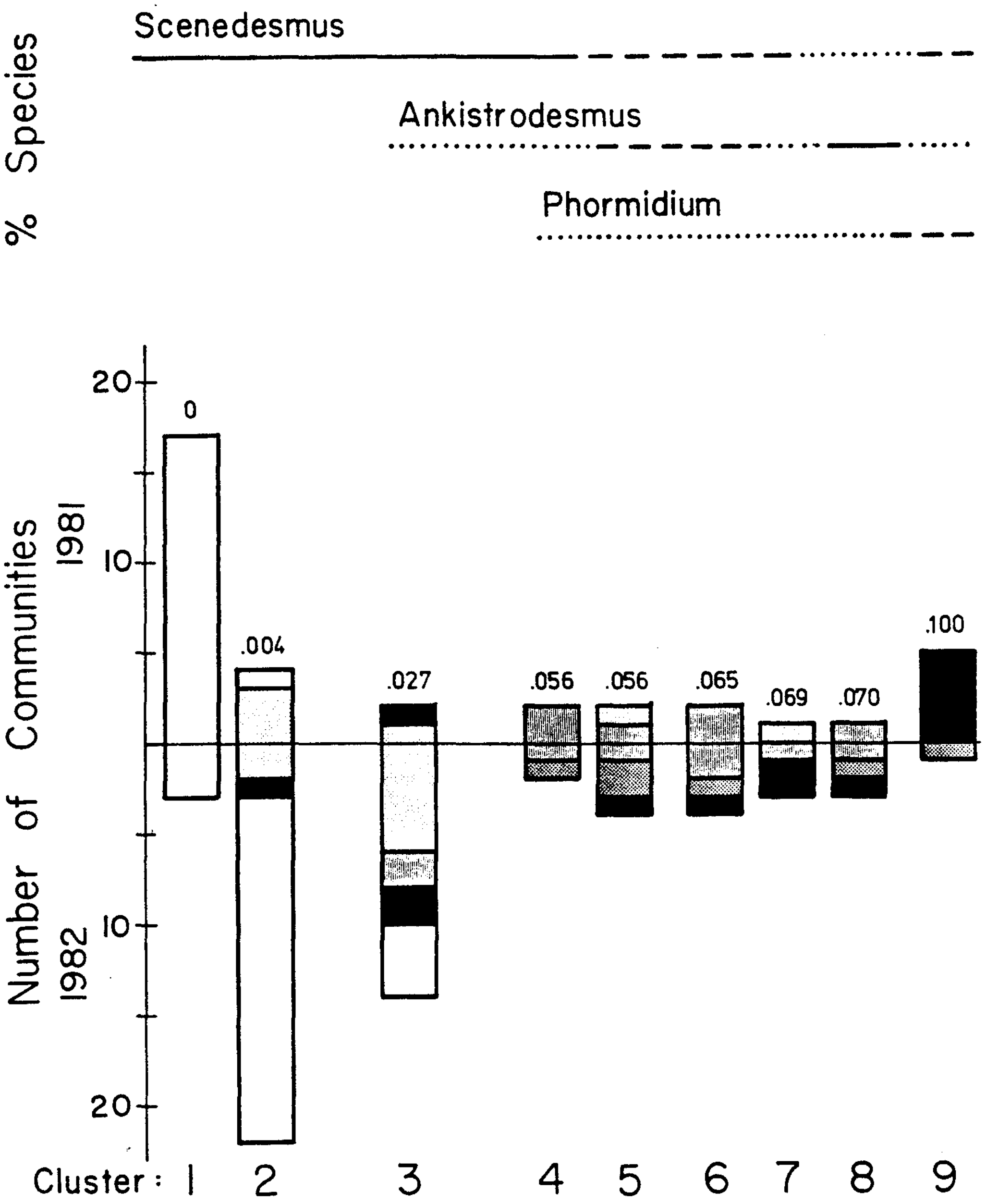


FIGURE 2. Cluster analysis of early successional communities (both years) shows that the youngest communities (open bars) tend to be different in different years and also from later communities (shaded bars). Clusters are arranged in order of increasing average disturbance frequency (shown above each cluster). Average relative frequency of the three dominant species in each cluster are shown (solid line, rel. freq. > 50%; dashed line, 25% < rel. freq. < 50%; dotted line, 10% <rel. freq.< 25%). Shading indicates treatment as in Fig. 1.

development of a high relative frequency (31%) of _Trochisia pachyderma_ in one jar in 1981.

The 12- to 15-month-old communities show no patterns except for a slight tendency of the spring communities to be grouped together (Figure 3). The initial and final samples of seven (39%) of these communities are in the same clusters, whereas only two (4%) occurred together in the early successional communities. This indicates that late successional communities are more constant in species composition than are early successional communities. Since this could be due to the difference in the number of clusters specified, the clustering program was rerun on the early successional communities specifying only 4 clusters. The value for 5 pairs found together (10%) is still lower than that for the older communities.

Thus, the characteristic change in species composition is the successional replacement of _Scenedesmus_ by _Ankistrodesmus_ or _Phormidium_. Most of this occurs in the first three months and appears to be irreversible, at least under the conditions of this experiment. By the beginning of the second year, species composition is relatively stable.

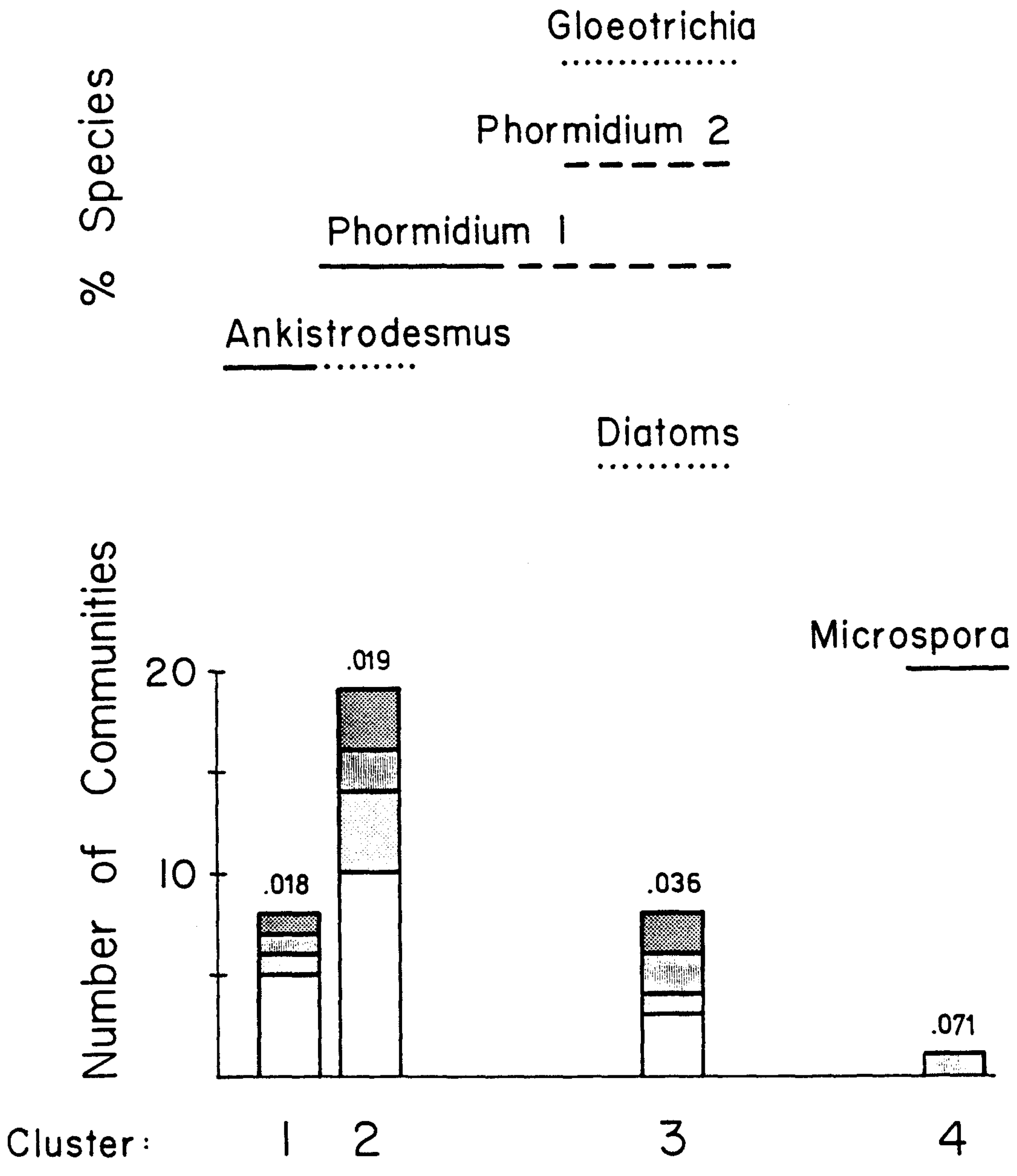


FIGURE 3. Cluster analysis of late successional communities shows little variation due to any of the factors. Shading indicates treatment (as in Figure 1) except that here "medium" disturbance frequency is 0.071 days^{-1}.

Diversity and Disturbance

The average H′ of the initial communities (before disturbance) was 0.6053 in 1981, 0.9514 in 1982. These means are significantly different ($t=8.72$, $P<0.001$). So, the effect of the experimental disturbance on diversity of early successional communities was determined by a mixed model analysis of variance with a fixed disturbance effect and a random effect of the two years. The replacement-disturbance treatment was compared to the other 1982 communities using pairwise comparisons of mean diversity. The older communities were analyzed by one-way analysis of variance with three treatments.

Early successional communities

Disturbance treatment affected H′ but there were no differences between years (Table 7). The mean H′ (1.477, s.e.=0.107) of the disturbance-substitution treatment was significantly different from the undisturbed treatment ($t= 4.22$, $P= 0.0012$) but not from either of the other disturbance treatments.

H′ is predicted to decrease with increased productivity (Tilman 1982). Therefore, to the extent that conductivity measures productivity, a similar relationship should be found. Both conductivity and H′ increased with disturbance, but within a treatment they were not correlated. It is impossible to say whether this shows that diversity and productivity are uncorrelated, or that conductivity is a poor measure of productivity. However, the disturbance-substitution treatment results show that it is not necessary that conductivity increase

TABLE 7. Mixed-model analysis of variance of effects of disturbance (fixed effect) and year (random effect) on H′. Maximum likelihood estimates of the parameters of the model are computed. The significance of each effect is tested by setting the specified effect to zero and reestimating the parameters. The difference between the maximum likelihood for this submodel and that for the overall model is a test of the significance of the effect (Dixon 1981).

Effects	df	Likelihood Ratio, χ^2	
Disturbance	2	10.433	P= 0.005
Year	1	0.000	ns
Disturbance X Year	1	0.000	ns

Disturbance treatment:	Mean	s.e.	n
None	1.0652	0.0635	14
Medium	1.2898	0.0568	14
High	1.4161	0.0720	14

for diversity to increase. Thus, the increased conductivity in the two disturbance treatments is unlikely to have caused the increased diversity.

Late Successional Communities

Although there appears to be a slight increase in diversity in the disturbance-substitution treatment, the ANOVA results were not significant for any of the diversity measures (Table 8). The high variability within treatments and the low sample size make detection of differences unlikely. From the cluster analysis of species compo-

TABLE 8. Mean diversities and standard errors of late successional communities. The treatments are not significantly different by analysis of variance.

Treatment	H'	$H'(D)$	$H'_D(S)$
No disturbance	1.0435 (.175)	0.5876 (.080)	0.4559 (.113)
Disturbance	1.1283 (.166)	0.6171 (.092)	0.5112 (.104)
Disturbance-substitution	1.3475 (.211)	0.6331 (.109)	0.7144 (.156)

TABLE 9. Community characteristics after 15 months.

	>70% Greens	30%<Greens<70%	Greens<30%
H'	0.940 (0.13)	1.642 (0.21)	1.222 (0.13)
$H'(D)$	0.517 (0.07)	0.852 (0.11)	0.515 (0.06)
$H'_D(S)$	0.423 (0.09)	0.790 (0.16)	0.706 (0.13)
Density of grazers	1.040 (0.38)	0.432 (0.29)	0.103 (0.03)
1981 disturbance frequency	0.022 (0.01)	0.035 (0.03)	0.099 (0.01)
Conductivity	23.11 (3.09)	16.50 (1.50)	24.20 (3.51)

sition, three different late successional stages are present: green-dominated, blue-green dominated and a mixture of these two. I classified the communities into three groups by algal composition (Table 9) and compared some characteristics. One surprising result of this classification is that the groups seem to differ in disturbance history (the frequency of disturbance experienced during early successional stages in 1981) and in grazer densities. Furthermore, these two variables are inversely related (not tested statistically as results suggest the test).

Thus, disturbance events early in succession are more important determinants of later community structure than are later disturbance events. This might not have been true if the experiment had been more carefully designed so that only communities of one successional stage had been used. For example, if changes in dominance are considered, only three changes between the initial and final samples occurred. All of these occurred in the disturbance treatment, and the change was from green to blue-green.

Grazer Densities

The number of microcrustaceans was difficult to determine without destructive sampling of the community. Therefore, densities were estimated from 1ml of the preserved samples taken for algal counts. A 1ml aliquot of well-stirred sample was placed in a Sedgewick-Rafter cell and the cladocera, copepods and ostracods in ten transects were counted. The accuracy of this method was determined by a more intensive count of the 1982 communities after the end of the experimental period. Each community was concentrated by filtering through nylon mesh (90μm opening) until approximately 20ml of the culture remained. These were preserved in 4% formalin. Thirty transects were counted on a Sedgewick-Rafter cell, and from these counts the density of crustaceans in the entire culture was estimated.

Copepods were overrepresented in the counts made on the small samples so only cladocera and ostracods were used. The density estimates from the whole culture were correlated with the counts from samples. The correlation is adequate but not very high ($R^2=.64$) so the counts must be used with caution.

Microcrustaceans from the first sample taken after disturbance and from the final sample were counted and then averaged to give an index of grazer density for each community.

The grazer density in each treatment was highly variable (Figure 4). Since homoscedasticity of variances could not be assumed, the nonparametric Kruskal-Wallis test was used to test the null hypothesis of no differences in the grazing intensity in the 6 groups. There were significant differences (Table 10), and analysis of ranks (Lehmann 1975, p. 238) showed that high and medium disturbance treatments varied between years but the undisturbed treatments did not. The disturbance-substitution treatment was not different from any other treatment.

The between year differences in the numbers of microcrustaceans may be due to differences in the inoculum. But since there were equivalent numbers in the undisturbed communities from both years,

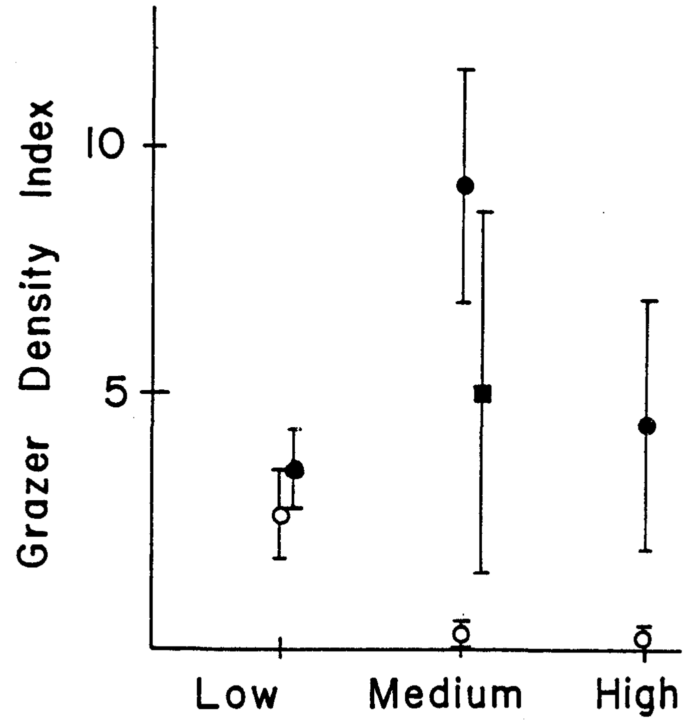


FIGURE 4. Means and standard errors of grazer density indices show extreme variations between years in some treatments. ○ 1981, ● 1982, ■ disturbance-substitution 1982.

TABLE 10. Kruskal-Wallis analysis of grazer density indices in early successional communities.

Group		n	Rank sum
1	1981, low disturbance	6	156.5
2	1981, medium disturbance	6	68.0
3	1981, high disturbance	6	53.5
4	1982, low disturbance	8	240.0
5	1982, medium disturbance	8	307.5
6	1982, substitution	6	147.5
7	1982, high disturbance	8	203.0

Kruskal-Wallis test statistic= 22.417, P= 0.001 (χ^2, 6 df)

Analysis of ranks: 3 2 1 6 7 4 5

this explanation seems unlikely. Another possibility is that the much warmer temperatures in late June of 1982 caused more rapid development, so that by the time disturbance manipulations were begun in July large populations of reproducing adults were already established. With generation times on the order of several days (Hrbacek 1977), it is unlikely that they would then be driven to extinction at either of the disturbance rates used in this study.

The variation in grazer density and in conductivity suggests that disturbance may be altering the physical environment. It is not hard to imagine that the numbers of grazers would be reduced by disturbance, but why should they increase? Disturbance may have increased the food supply by reducing large inedible particles to smaller manageable proportions. At the same time, the increased surface area would facilitate microbial activity and the increased remineralization would have made more nutrients available for the algae. Thus, higher algal productivity and an increased non-algal food supply would have allowed greater densities of grazers to persist.

Grazing and Diversity

The laboratory studies of grazing (Chapter 3) suggested that algal diversity declined with increasing grazer densities. This relationship was tested in these communities by linear regressions. In undisturbed communities, regressions of H' (Figure 5), $H'(D)$ and $H'_D(S)$ on grazing intensity showed significant negative relationships (Table 11). In the medium and high disturbance communities, similar regressions were not significant. However, H' was negatively correlated

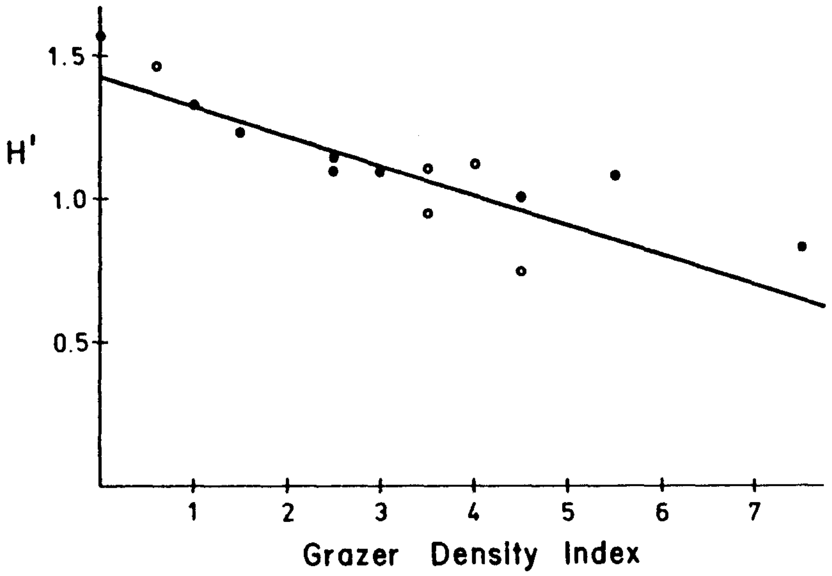


FIGURE 5. Diversity decreases with increased grazer density index in the undisturbed early successional communities (○ =1981, ● =1982).

TABLE 11. Regressions of diversity indices on grazer density indices in early successional communities show variability between treatments (12 df for all regressions except disturbance-substitution treatment which has 4).

Disturbance		r	Regression equation
None	H´	-.837 ***	Y=1.425-0.092X
	H´(D)	-.636 **	Y=0.296-0.039X
	H´(S)	-.740 **	Y=1.064-0.055X
Medium	H´	.145 ns	
	H´(D)	-.325 ns	
	H´(S)	.357 ns	
Substitution			
	H´	-.821 *	Y=1.6127-0.028X
	H´(D)	-.687 ns	
	H´(S)	-.023 ns	
High	H´	-.430 ns	
	H´(D)	-.504 ns	
	H´(S)	-.023 ns	

*** $P<=0.001$, ** $P<=0.01$, * $P<=0.05$, ns $P> 0.05$

with grazing intensity in the disturbance-substitution treatment.

From the results of the regression in undisturbed communities, one would predict that diversity should be lowered in the disturbed jars with very high grazer densities. This was not the case. These results indicate that disturbance uncouples the relationship between grazer density and H'. This may be due to an increase in food availability resulting from the disturbance process (as discussed above). Thus, the negative relationship was maintained by the disturbance-substitution treatment where one-half of the usable food supply was removed and replaced with inedible rice grains. However, it should be noted that the high $H'(D)$ in this treatment is due to an increase in the relative frequency of diatoms as well as blue-greens. Thus, the underlying mechanisms by which diversity is increased may be different in the two treatments.

Grazing, Disturbance and Diversity

Although H' was not different between years, the subcomponents may behave differently. Variation in grazer densities can produce differences in $H'(D)$ and $H'_D(S)$ (Chapter 3). Since the grazer density indices were significantly lower in the 1981 medium and high treatments, between year comparisons of $H'(D)$ and $H'_D(S)$ within the two disturbance treatments were made by t-tests of the means.

Pairwise between year comparisons of mean diversity within treatments found significant differences in $H'(D)$ in both the medium and high disturbance treatments (Figure 6a) and for $H'_D(S)$ in the high disturbance only (Figure 6b). Thus, the increased diversity at high

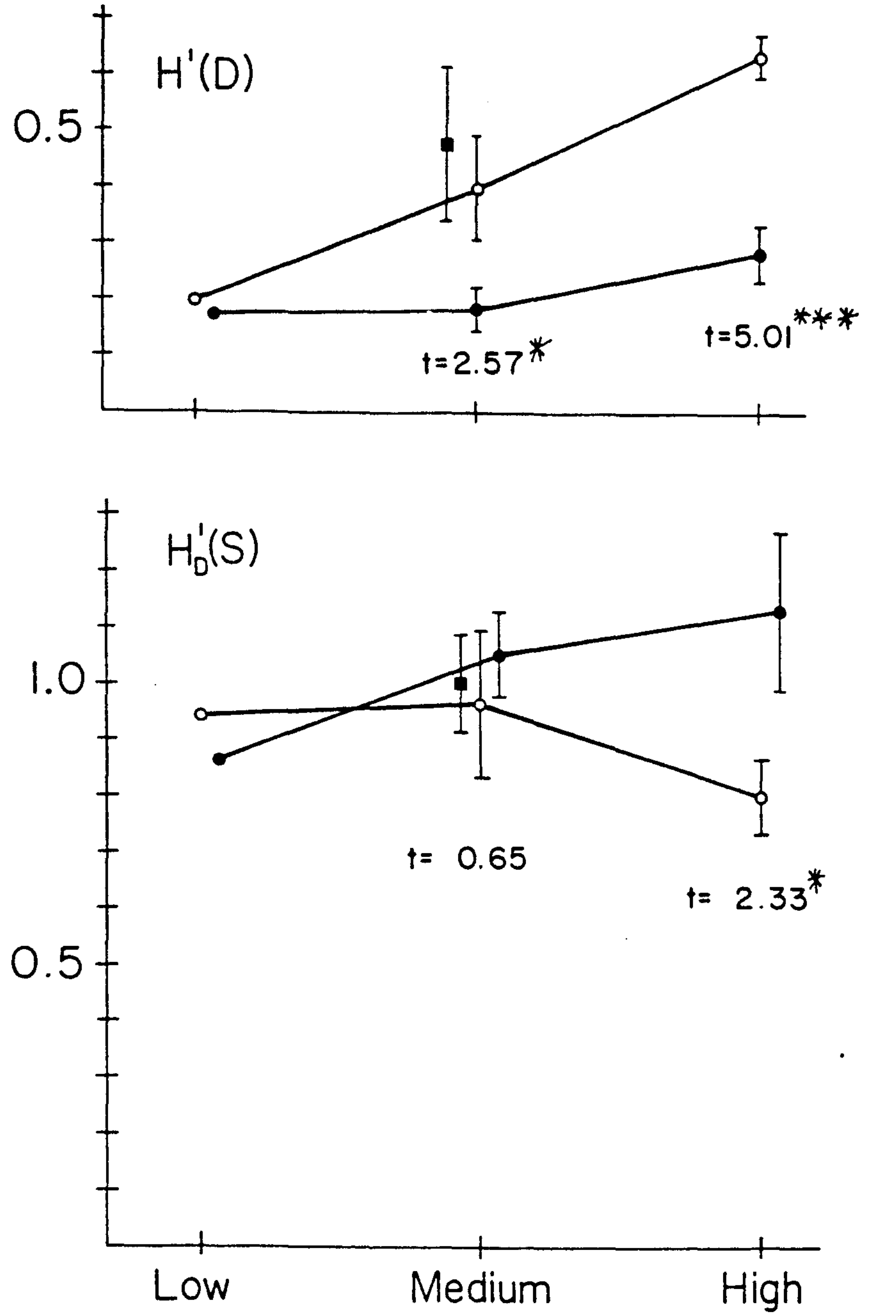


FIGURE 6. Within treatment comparisons of $H'(D)$ and $H'_D(S)$ between different years (which were shown to have different grazer density indices) reveal significant differences for $H'(D)$ (a), but only at high disturbances for $H'_D(S)$ (b). Statistics for undisturbed and disturbance-substitution treatments are shown but not tested. (o =1981, ● =1982, ■ =disturbance-substitution)

disturbance frequency in 1982 was mostly attributable to $H'(S)$, while in 1981 $H'(D)$ was higher.

The increase in $H'(D)$ in 1981 was caused by the increase in the relative frequency of *Phormidium*. I hypothesized that the extinction of grazers in some jars in 1981 caused the increase of this blue-green species. The medium and high disturbance communities from both years were divided into two groups, those without grazers (grazer density = 0) and those with grazers (grazer density > 0). The mean relative frequency of blue-greens in the first group was 34.1% ($n=9$), in the second 6.0% ($n=19$). After arcsine transformation of the data, these two percentages were significantly different ($t=5.98$, $P<0.001$).

While this does not prove that extinction of grazers led to increased blue-green dominance, coupled with the laboratory studies, it strongly suggests such a relationship.

Discussion

Disturbance affected diversity in these algal communities despite considerable "noise" from grazer activities, differences in physical variables and, probably, considerable within culture differences due to varying growth rates of the species. In fact, I shall argue that this variability accounts for the robustness of the disturbance hypothesis. First, three assertions based on the results of these experiments are made. Then a model of succession in the algal community is used to argue these assertions. Finally, the generality of the model will be discussed.

The most important points to be drawn from this study are

(1) Diversity may be increased by a variety of mechanisms; in fact, there is no evidence for the disruption of competitive exclusion by disturbance in this system.

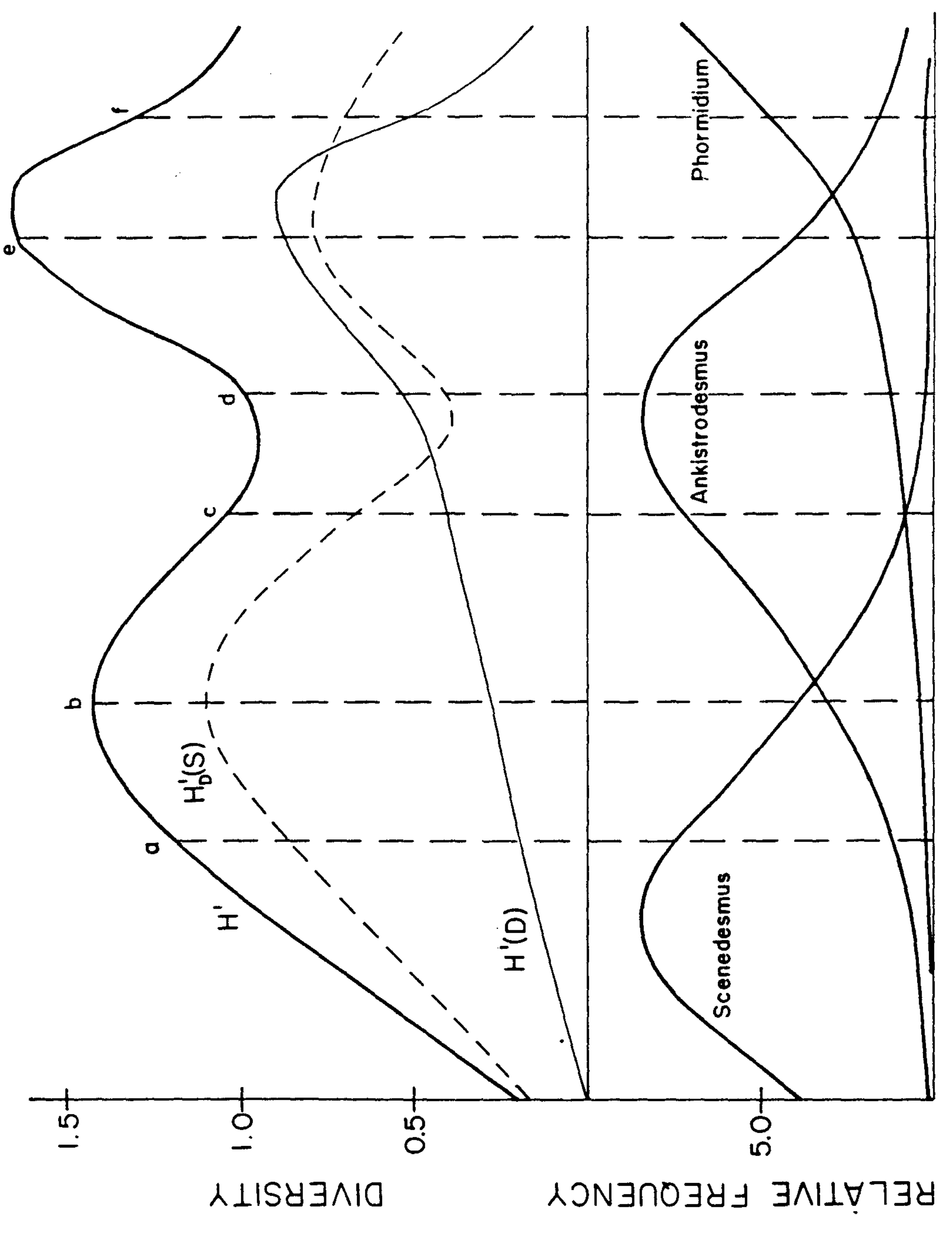
(2) The apparent increase in H′ depends on the timing of the sampling. If I had sampled later, I might have drawn the conclusion that disturbance lowered H′.

(3) Disturbance has a greater effect on early successional communities than on late ones.

The long-term (15 month) trend is a change in dominance from greens to blue-greens (Figure 7). Within these two groups, a succession of species can be seen. Thus the initial green phase is characterized by a large population of Scenedesmus which peaks in the first few weeks. It is slowly replaced by other greens, primarily Ankistrodesmus. By the end of the first 90 days, Scenedesmus is still dominant but declining (Figure 2). By the end of the first year, it is rare in all communities. This change appears to be unidirectional as Scenedesmus never again reached great densities. This first state then must be considered transient or unstable.

Disturbance appears to hasten the succession process in these microcosms, particularly in the first three months. Diversity increased as changes in dominance occurred, and since that change was accelerated by disturbance the peak diversity occurred earlier (point b in Figure 7). This suggests that, had I sampled at a later date (or disturbed at greater frequency), the disturbed communities would be dominated by Ankistrodesmus (point c in Figure 7) while the undis-

FIGURE 7. Model of relationship of H´ and succession in this algal community shows that fluctuations of H´ occur as relative abundances of species rise and fall. The abscissa represents time. Only the three dominant species are shown, but the values of the diversity indices were taken from the data using all the species. Thus the value for H´(S) is higher in the green phase because there are more green algae species in this system than blue-greens.


DIVERSITY
1.5
1.0
0.5
RELATIVE FREQUENCY
5.0
H'
H'D(S)
H'(D)
a
b
c
d
e
f
Scenedesmus
Ankistrodesmus
Phormidium

turbed would be at the transition point (b). The results would have indicated that disturbance reduced diversity.

The older communities are in one of two states, green-dominated (primarily Ankistrodesmus although Microspora has reached very high densities in a few communities) or blue-green dominated (two species of Phormidium and two Rivulareacean species). It is possible to change directly from the Scenedesmus phase to the blue-green phase and it seems quite likely that this happens if grazers are driven to extinction (presumably as a result of the exogenous disturbance regime). This happened in five high disturbance communities in 1981 and one substitution-disturbance in 1982 (Figure 2, cluster 9). In all of these communities, the microcrustacean grazer community had never developed (index of grazer density = 0).

This model assumes coexistence of species with changes in dominance accounting for changes in diversity (or evenness). In fact, extinctions of species were very rare in these jars. Most species persisted albeit in low numbers, the exception being Pediastrum boryanum which was never found in the older communities.

Once a community reaches the Ankistrodesmus phase, it may remain there indefinitely. One key to the stability of this phase may be the density of grazers. Although a correlation was found between blue-green abundance and low grazing intensity in the early successional communities, it was obscured by high variance and small sample size in late successional communities (Table 9). Laboratory studies (unpublished data) suggest that removing grazers from the older communities leads to increased numbers of blue-greens, but the process is very slow and highly variable. The mechanism that underlies this process is not clear from this study but the most likely explanation is that microcrustaceans are regenerating nutrients required by green algae (see discussion in Chapter 3). Microcrustaceans are important nutrient recyclers in natural systems (Barlow and Bishop 1963; Axler et al. 1981). They may also play a similar role in these systems, particularly in the first few months. Once the community is established, however, other recyclers may become increasingly important.

The possibility that competition is important in structuring this community is not excluded by this model, but the response to disturbance does not support it. The arguments of traditional competition theory predict that disturbance would slow down the rate of displacement of Scenedesmus by Ankistrodesmus, but in fact the opposite occurs. However, such models assume constant competition coefficients and constant environmental conditions; neither can be assumed here. A more likely explanation is that conditions in the culture are changing to favor Ankistrodesmus. These include changes in nutrients and the accumulation of the extracellular products of algae, protozoa and bacteria. Both growth-inhibiting and growth-promoting substances may be produced by green and blue-green algae (Lefevre 1964; Wolfe and Rice 1979). Thus the reductions in numbers from disturbance would be beneficial to the growth rate of Ankistrodesmus but not Scenedesmus. Disturbance merely widens the gap between the two species, as Ankistrodesmus can recover quickly after disturbance but Scenedesmus can not. This scenario is consistent with the facilitation model proposed by Connell and Slatyer (1977).

However, this sequence of species is also consistent with a model of succession proposed by Tilman (1982) in which dominance changes as nutrient ratios change, particularly if disturbance increases the supply rate of resources. *Scenedesmus* and *Ankistrodesmus* have similar nutrient requirements (e.g., Rhee and Gotham 1980) and thus could coexist only within a narrow range of nutrient ratios.

It is impossible to distinguish between the models with these data. Indeed, both could be valid at the same time or at different times during succession. A similar observation has been made about temperate forest succession by Christensen and Peet (1981) who observed that the successional sequence of pines to hardwood forest was determined by several different mechanisms. Succession in this community was episodic, the episodes correlated with changes in resource availability. Furthermore, they suggest that the sequence of dominant species in these forests might be affected by disturbance in the pine stands. This model for algae could be applied to the forest succession or to any episodic successional community. Thus the effects of disturbance in terrestrial communities are seen as patches of differing successional state.

A "successional patchwork" also describes the effects of disturbance on the intertidal landscape (Paine and Levin 1981). In this case, competition is clearly the determinant of community structure in the absence of disturbance. However, Tilman (1982) points out that competition for space in the intertidal zone should not be expected to pertain to terrestrial communities where space also means nutrients, water and other variables.

So, a variety of mechanisms may underly successional processes, and one explanation of the increase in diversity by disturbance is that disturbance initiates succession. Inasmuch as the evolutionary model allows for many different mechanisms, it is the more general and hence better paradigm for the disturbance-diversity phenomenon; the intermediate disturbance hypothesis is a special case of the evolutionary model. Adoption of this paradigm reconciles the findings of Paine and Levin (1981) and Suchanek (1979): the sessile community described by the former authors includes species which have evolved in a perturbed environment, while the community of organisms living in the mussel beds have evolved to exploit the increased complexity of an undisturbed community.

The relationship between disturbance and diversity appears to be far more complex than the intermediate disturbance hypothesis predicts. The scale at which the community is analyzed, the timing of the observation and the successional state of the community determine the relationship.

CHAPTER 5

CONCLUSIONS AND SYNTHESIS

To return to the motivating questions set down in Chapter 1, I deal with each separately and in the order given.

The Importance of Competition

Two points of view were identified amongst the proponents of disturbance theory (Chapter 4): the evolutionary paradigm and the competition paradigm. The evidence presented in all of my studies suggests that only the evolutionary paradigm is sufficiently general. While competition is certainly the most important factor in some communities, it is not so in all of them. However, the competition paradigm is most often cited as the explanation of the relationship between disturbance and diversity. Why? I suggest these three reasons:

(1) A widely-accepted mathematical model is already available (Lotka-Volterra equations and variations) that facilitates analysis dealing in these terms.

(2) Many of the authors are population biologists who tend to think in the short-term (i.e., practitioners of the "bottom-up" approach).

(3) A wide-spread belief, almost faith, exists in the importance of competition as the basis of species competition. This may partly

be attributable to the concepts of niche breadth and limiting similarity of species as developed by MacArthur and Levin (1964, 1967). Although these two authors admitted the role of environmental uncertainty in their models, the focus tended to be primarily on the competitive interactions of species in stable environments.

I do not mean to imply that individual populations are not important in the study of community behavior. Denslow (1978) developed her evolutionary model of disturbance by examining the life-history strategies of various species along a disturbance gradient. However, the generality of disturbance theory does not require that competition be shown to be important. It does require that there be heterogeneity within the system.

The Equivalency of Disturbances

Many authors use disturbance to include a broad spectrum of biotic and abiotic phenomena. They include predation, fire or the physical disturbance used in this study. Many *a priori* reasons exist to suggest that biotic and abiotic disturbances should have different effects on the community. However, this dichotomous classification is probably too simple as adaptation to frequent predictable abiotic disturbances may resemble adaptations to predation. Some differences that might be predicted are

(1) Predation tends to be continuous whereas abiotic disturbances are discrete phenomena. However, predation pressure varies seasonally and storms may occur so often as to seem continuous.

(2) Both may have secondary effects but not necessarily the same

ones. For example, grazers may regenerate nutrients and so may physical disturbance but the ratios and kinds of nutrients may not be the same. Also, certain kinds of disturbance may remove nutrients (erosion of soil, for example).

(3) Feedback mechanisms in many predator-prey systems that limit the predators' ability to reduce prey numbers. Usually, no such mechanism exists for abiotic disturbances. However, some communities have evolved with a particular disturbance (fire in certain forests, for example). In these situations, some species have developed resistance to the disturbance or may even depend on the disturbance in some way (e.g., pines which require heat from fire to open cones for seed dispersal).

(4) Finally, an abiotic disturbance is likely to affect both the predator and the prey in a system. Thus, the effects of abiotic disturbance are likely to be more complex and more unpredictable in outcome than are the effects of predation. Biotic and abiotic disturbances, when they occur in the same system, are operating at different scales.

The results of the microcosm studies confirm some of these intuitive notions. The overall effect of grazing was to slow the rate of succession while the physical disturbance (Chapter 4) accelerated it. In those instances where the exogenous disturbance led to extinction of grazers, discontinuities in the normal successional pattern were seen. Menge (1983) has looked at the interaction of predators and disturbance in the intertidal and suggests that the effects of predation vary along an environmental stability gradient. In forest communities, plants which have animal-dispersed seeds are more common in low disturbance regimes (Denslow 1978). These studies suggest that the effects of disturbance on the plant community will partially depend on the role of animals in the system and how they are affected by exogenous disturbance.

The Information Content of H'

H' is a measure of the information content of the system (Pielou 1977). We might ask just what sort of information it conveys.

As a measure of species diversity, H' has value only in a relative sense. That is, given two communities from similar environments, we might ask which is the more diverse. In the past, diversity was equated with stability and thus appeared to be a vital statistic of community health. Although this idea has been discredited (Goodman 1975), it will not go away (see discussion by Allen and Starr 1982, pages 184-208), probably because it is intuitively appealing. I suspect that the notion that higher diversity is "good" stems from the same human aesthetic that prompts us to decorate our walls. In any event, diversity remains an active area of investigation.

The hierarchical treatment of H' offers some hope that diversity can be used as a diagnostic tool to evaluate community processes. Assuming that different taxonomic levels respond to different magnitudes and types of disturbance (Chapter 1), then by partitioning diversity hierarchically we can evaluate the effect of disturbance on the system. At the very least, this method could be used early in a community study to generate hypotheses for more in depth testing.

Another possible use of hierarchical diversity analysis is in monitoring and predicting the response of a community to perturbation. For example, the effects of pollutants in a stream might be assessed by monitoring the changes in the algal population (e.g., Patrick 1949). If small variations in within-genera diversity are the norm, then the appearance of sudden changes at higher taxonomic levels signal a significant change in conditions. However, we must know something about the "normal" state of the system before this technique will be useful.

Synthesis

This study encompasses the population biology approach to communities as well as the ecosystem approach (as distinguished by McIntosh 1981). Despite my criticisms of the former, both have validity and fit together to give a more complete picture than does either one alone.

The selection pressures on life-history strategies of a population are a function of the successional stage of the community (MacArthur and Wilson 1968). An extension of this model predicts that late successional species should have different strategies from early ones (Pianka 1970). For example, species that are characteristic of late successional prairie communities show reduced interspecific competition (Parrish and Bazzaz 1982). The role of r, K and a in determining the community's response to disturbance suggests that the mechanism by which diversity is increased may vary successionally.

The question of how disturbance affects diversity, then, is really a question about succession. Namely: how does diversity vary with succession? Traditional community ecologists have long recognized that areas of transition between different communities (ecotones) were areas of high diversity. To the extent that the communities are part of a successional continuum (in the sense that a disturbance creates patches of different successional state), the ecotones are products of disturbance. Thus, the old school of community ecology avoided this "noise" introduced by disturbance and concentrated on the apparent steady-state. The current interest in disturbance is simply the recognition that climax communities are relatively rare and most communities are in a state of transition.

These arguments rest on the assumption that succession is episodic; that is, succession is characterized by periods of stable species composition followed by periods of transition. This scenario certainly applies to many algal (Moss 1973; this study) and forest communities (Christensen and Peet 1981). To some extent, the episodic nature may be caused by exogenous disturbance. Although biotic interactions within a state may drive the system, a large-scale disturbance may set the successional process in motion. The creation of an even-aged community at this stage means that senescence is likely to be synchronized. The adaptation of different taxa to conditions that vary successionally assures the appearance of episodes over time.

If succession is not episodic, then the role of exogenous disturbance is better described by looking at individual populations. The non-episodic model suggests that diversity varies little with successional state. Exogenous disturbance may increase diversity, but the effect will depend strongly on the relative values of r, K and a of the individual populations.

It is possible that even if succession is truly episodic, the world may look more like the alternative model. The different successional stages will only be clearly visible if a permanent quadrat can be followed through time or if the history of a place is well enough known to determine the scale and timing of disturbance events. Otherwise, it is quite likely that a particular community consists of variously aged patches, and the failure to recognize this may give a false impression of the underlying processes.

In the absence of exogenous disturbances, the episodic nature of succession may disappear as small-scale phenomena become more important. In terrestrial communities, these may be the formation of patches resulting from deaths of plants from predation or old age. In aquatic communities, the seasonal variability of nutrients and grazers may produce short-term changes in species composition.

Disturbance, in the non-ecological sense of the word, implies disorder and disruption. Paradoxically, the results of this study suggest that disturbance sets in motion an orderly and somewhat predictable successional sequence. Whether this is regarded as "noise" or not depends on one's view of communities. If the norm is an unchanging set of species then disturbance deserves its name. On the other hand, if communities are dynamic and always changing, then perhaps "disturbance" is a misnomer and some less suggestive term such as "biomass reduction" is more appropriate.

APPENDIX A

PERCENT OCCURRENCES OF ANIMALS (EXCLUDING CRUSTACEA)

The percentage of jars in which species were found in the initial and final samples are given below. The disturbance treatment which was not included in the 1981 analysis (see Chapter 4) was used in this survey; the disturbance-substitution treatment of 1982 was not included here. Thus, the total number of jars surveyed at each time in both years was 24.

Species names are given whenever possible. Most of the unidentified species were only found at one time period or in a few jars, and then in small numbers. The only abundant unidentified ciliate (Ciliate 15) that was both persistent and abundant was too nondescript to be identified with any certainty. It was small (less than 30 µm) and looked most like *Chilodonella* although no tubular gullet could be seen. However, I relied only on characteristics that could be discerned without staining so this limited my ability to make fine distinctions.

Species	% Occurrence Initial 1981	 1982	 Final 1981	 1982
CILIATA				
Order Holotrichida				
Suborder Gymnostomina				
Tribe Prostomata				
Family Holophryidae				
Urotricha sp.	12.5	4.2		
Lacrymaria olor		11.5		
Plagiocampa sp.	58.3		8.3	
Tribe Hypostomata				
Family Chlamydodontidae				
Chilodonella uncinata	12.5		4.2	

Suborder Trichostomina				
Families:				
Paramecidae				
Paramecium bursaria	4.2			
Colpodidae				
Colpoda sp.				5.6
Suborder Hymenostomina				
Families:				
Frontoniidae				
Cinetochilum margaritaceum	91.7	11.5	54.2	5.6
Pleuronematidae				
Cyclidium glaucoma	79.2	30.8	4.2	
Order Spirotrichida				
Suborder Heterotrichina				
Families:				
Spirostomidae				
Spirostomum sp.	4.2			
Stentoridae				
Stentor sp.		7.7		
Suborder Oligotrichina				
Family Halteriidae				
Halteria grandinella		19.2		
Suborder Hypotrichina				
Families:				
Oxytrichidae				
Oxytrichia sp.	25.0	26.9		
Stylonychia sp.		3.8		
Euplotidae				
Euplotes sp.	4.2	19.2		11.1
Aspidiscidae				
Aspidisca costata	33.3	7.7	16.7	16.7
Unidentified species (30-100um)				
Ciliate 8	12.5			
Ciliate 15	75.0	11.5	58.3	16.7
Ciliate 21		7.7		

Ciliate 23		7.7		
Ciliate 25			8.3	
Ciliate 30		23.1		
Ciliate 31				11.1
Order Peritricha				
Family Vorticellidae				
Unidentified spp. (sessile)	95.8	57.7	50.0	44.4
Opisthonecta sp. (motile)	37.5	19.2	16.7	

FLAGELLATA (All unpigmented flagellated forms are included here. Species nomenclature follows Edmondson (1959), but otherwise this class was created for my own convenience.)

Order Euglenales				
Family Euglenaceae				
Astasia sp.	4.2	4.2		
Peranema tricophorum		4.2	8.4	4.2
Peranema sp.	8.4			
Order Cryptomonadales				
Family Cryptomonadaceae				
Chilomonas paramaecium	8.4	100.0	4.2	
Unidentified flagellates (10-30 μm)				
Flagellate 1	100.0		100.0	
Flagellate 2	8.4			
Flagellate 3	45.8		20.5	
Flagellate 4	8.4			
Flagellate 6	12.5			
Flagellate 7	12.5			
Flagellate 8	54.1	33.3	4.2	8.4
Flagellate 10			45.8	

LOBOSA

Order Amoebaea				
Family Chaosidae				
Amoeba 1	87.5	45.8	58.3	4.2
Order Testacealobosa				
Family Difflugiidae				
Difflugia oblonga	8.4	12.5		41.7

HELIOZOA				
Unknown 1	75.0		45.8	
Unknown 2			21.0	
GASTROTRICHA	29.2	12.5	21.0	29.2
ROTIFERA				
Rotifer 1	41.7		21.0	25.2
Rotifer 2		21.0	37.8	37.8
OLIGOCHAETA*				4.2
NEMATA*	4.2		4.2	

* These were actually more common than these data indicate. These counts are from the small subsamples used to count algae. When counting microcrustacea (see Chapter 4), I noticed far more oligochaetes. I would guess that by September, at least 33% of the jars had worms in them.

APPENDIX B

RARE AND UNCOMMON ALGAL SPECIES

The following categories of rare (found in less than 25% of the jars and never exceeded 5% relative frequency) and uncommon (never exceeded 5% relative frequency but found in more than 25% of the jars) algae were used in analyzing diversities in the disturbance study.

1. Clumped forms of green algae: In nearly all the jars, irregular clumps of algae were found. The number of cells in the clumps ranged from 3 to approximately 15. Color varied from pale green to very dark green and cell sizes (between clumps) were from 5 um to 10 um. Although these clumps were treated as a single species, they probably were not.

2. Irregular branched algae: These relatively large (branches spanning 20-40 μm) algae were found near the end of the summer in most jars. Again, possibly more than one species was involved.

3. Euglena sp., Phacus sp.: Occasionally (in less than 25% of the cultures), one or two individuals were found early in the summer. A greater variety of species was found in 1981 than in 1982.

4. Kirchneriella sp.: One or two colonies were found in 3 cultures in 1981 only.

5. Staurastrum spp., Tetraedron sp.: Occasionally, one or two individuals were found in early summer.

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