

NARALA, CHANNA REDDI. Seasonal Changes in Lotic Phytoplankton and Their Successional Responses to Experimental Temperatures. (1973) Directed by: Dr. Paul E. Lutz

An investigation was made of algae collected on glass slides from polluted waters of an urban creek in Greensboro, North Carolina. Observations were made on the successional properties of these planktonic algal communities in relation to changes in temperature under in vitro conditions. Experimental thermal conditions at $15^{\circ}, 20^{\circ}, 25^{\circ}$, and $30^{\circ} \mathrm{C}$ were used. Constant photoperiods of 11 hours duration were maintained for the cultures at the temperature conditions.

Highest colonization of algae took place in May and the least in January. Nitzschia, Navicula, and Stigeoclonium were the algae most frequently found. Diatoms colonized the slides in all the collections with a statistically significant increase in numbers in May. Green and bluegreen algae were predominant in the summer with the former showing a statistically significant increase in numbers in August. In the laboratory cultures, green algae successfully competed with blue-green algae at $15^{\circ}$ and $20^{\circ} \mathrm{C}$, but lost this competitive advantage to blue-green algae at $25^{\circ}$ and $30^{\circ} \mathrm{C}$. When green and red algae appeared in the microcosm at $20^{\circ} \mathrm{C}$, the responses of the two were similar in that both of them co-existed within a heterogeneous community. Diatoms showed fluctuating trends at all four thermal conditions. Successional changes were very rapid in laboratory cultures, and climax communities were established in 3 to 4 weeks time. The responses of phytoplankton at different thermal conditions indicated the crucial role of temperature in determining the fate of organisms involved in the process of succession.

## SEASONAL CHANGES IN LOTIC PHYTOPLANKTON AND

 'THEIR SUCCESSIONAL RESPONSES TO EXPERIMENTAL
TEMPERATURES
by
Channa Reddi Narala

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This thesis has been approved by the following committee of the Faculty of the Graduate School at the University of North Carolina at Greensboro.


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## INTRODUCTION

The changes in species diversity, a consequence of the study of both quantitative and qualitative characters of the constituent organisms, is one of the means for evaluating the degree of change taking place in a community under different environmental conditions over a period of time. It can be used not only in comparing the organisms in the ecosystem but also in obtaining a clue as to the nature and patterns of succession within a community.

The addition of chemical pollutants to a water system changes its chemistry and of exents great effect on a stream community by limiting the number of species. Brinley and Katzin (1942) argued that the density of planktonic algae may be temporarily reduced in a system receiving large amounts of sewage. Yet, one might generally conclude that in organically enriched waters, there may be a reduction in the total number of species. Those species with wide tolerance ranges are likely to grow in large numbers thereby increasing total production (Blum 1956).

Owing to the instability caused both by seasonal variations and by pollutants, the concept of "climax" may not be totally applicable to a running water system (Hynes 1972). Margalef (1963) argued that the ecosystem "cannot build history" in an unstable environment. This would mean that a progressive and directional change can only be expected in a system which is undisturbed. However, Eddy (1925) established that succession does take place in running waters with the initial stage being dominated by unicellular algae. Patrick et al. (1954) and Yount (1956)
observed that many species might colonize initially, but their number decreases as the total population increases. Blum (1956) attributed the success of the pioneering unicellular algae to their having more resistant developmental stages than the filamentous types.

Current is, perhaps, one of the most important factors in running waters. Many species grow dominantly at different current speeds, showing a kind of "innate current demand." Ruttner (1960) hypothesized that current makes water "physiologically richer" by supplying fresh material to the surface of aquatic organisms. Commenting on this hypothesis, Whitford (1960) added that a swift current brings water with a high concentration of diffusing material closer to the cell surface, thereby reducing the diffusion distance between the two and producing a steep diffusion gradient. Butcher's (1932) observations revealed that fast moving waters allow only those organisms having efficient devices for attachment to establish; where the current is slow, an increase in number of organisms not endowed with such devices will often be encountered. Flushing action of the current will reduce the phytoplankton crop (Williams 1964).

Odum (1969) proposed a model of succession showing how ecosystems tend to evolve toward a stable state, maintaining overall homeostasis at maturity with a large organic structure. Beyers (1962, 1963), Margalef (1963), and Cooke (1967) used laboratory microecosystems since these were found more suitable for investigating the relationship between the structure and function of the ecosystem during succession. The time for development is also shorter, and succession is not interrupted by seasonal variations.

The development of an ecosystem is influenced not only by the physical environment that surrounds the system but also by the tolerance capacity of its organisms to variations in the habitat. Environmental variations can limit the growth of organisms and their success in life by upsetting their metabolic rates at different intensities (Reid 1961). Observations on green and blue-green algae reaching their maximum development in summer indicated the possible role of temperature in shaping the development of an ecosystem by creating diminishing response of organisms with respect to growth rate, reproduction, etc. when it is not maintained at the optimum level. Alexander (1970) suggested that in vivo the optimum is determined by many environmental factors; however, mainly one factor such as temperature or light plays a prominant role in in vitro cultures.

Of the many factors that might influence the tolerance of an organism, the most important are the capacity of the organism to endure an environmental variable, the age of the organism, and also duration of exposure time to the variable. While many species with similar tolerance ranges can live in harmony, at least some of them cannot establish in the community because of several interactions taking place among them. Therefore, tolerance is governed to a large extent by the interactions inside the system. The number of organisms dwindles when the intensity of the factor exceeds or falls short of the optimum. Such a change in a community is a must because the populations of which the community is composed are never static in themselves.

Eddy (1925) made observations on fresh-water algal succession in streams. Margalef $(1963)$, Beyers $(1962,1963)$, and Cooke (1967) studied
patterns of succession by working with aquatic laboratory microecosystems. However, very little attention has been given to the successional characteristics of planktonic algal communities in relation to controlled temperature. I, therefore, studied the periodicity of planktonic algal groups in a lotic, polluted, water system, identified the algae resistant to pollution, and studied the successional properties of these algal populations under controlled conditions of temperature in the laboratory.

## MATERIALS AND METHODS

HABITAT: This study was conducted on Cedar Creek in Greensboro, Guilford County, North Carolina. Originating as a small spring near Walker Avenue, the creek flowed about 100 m before joining a storm sewer at the junction of South Cedar Street and McGee Street on the eastern side of Greensboro College. The stream received surface runoff from many drains along its course; it flowed northwest about 1.9 km ending as a tributary of Buffalo Creek near the intersection of Battleground Avenue and Benjamin Parkway near the Mitchell Water Plant. Figure 1 diagrams the creek, the surrounding area, and the study area.

The creek was relatively shallow, about $5 \mathbf{- 2 0} \mathrm{~cm}$ deep in riffles. The bed was mostly gravel and sand. The land on either side was covered with grasses and shaded by trees at some places. The sampling station, as indicated in Figure 1, was located in open sunlight about halfway between its source and mouth.

Preliminary chemical analysis of the creek water was made using a kit supplied by LaMotte Chemical Company. This study revealed relatively high concentrations of silicates ( 15 ppm ), phosphates ( 0.90 ppm ), nitrates ( 1.82 ppm ), and chlorides ( 65 ppm ), suggestive of a good natural environment for planktonic algae to grow. pH values were found to vary from 6.6 to 6.8 .

SAMPLING PROCEDURE: Clean microscopic glass slides of $2.5 \times 7.5$ cm size were arranged horizontally in a metal rack and suspended from an iron stake driven into the middle of the creek bed. The rack was oriented

Figure 1. Diagram of Cedar Creek and the surrounding area with the study area marked.
*Study Area

1. Cedar Creek
2. McGee Street
3. S. Cedar Street
4. N. Cedar Street
5. Friendly Avenue
6. S. Mendenhall Street
7. N. Mendenhall Street
8. W. Smith Street
9. Battleground Avenue
10. Benjamin Parkway

parallel with the direction of the current, and about 10 cm below the surface of the water. The slide technique was adopted because it was the most frequently used method, useful not only in collecting algae but also in identification of the attached algae. The slides were exposed in the creek water only for seven days so that the growth on them represented very young stages of algae. Extensive growths of algae occurred on the slides left for two weeks or more in the creek which caused difficulty in the ennumeration process.

METHODS OF STUDY: Eight collections of phytoplankton were made at monthly intervals from November, 1972 to August, 1973. Each collection of slides occurred after seven days of exposure in the creek water. The ambient temperature of the creek water was recorded at each time of collection. The slides were brought to the laboratory suspended in natural water with minimum agitation. Direct counts of algae on each slide were made before incubation. One slide was kept in each of four 8 oz glass jars filled with natural creek water as media for incubation. The slides were incubated under experimental conditions in incubators supplied by Precision Scientific Company with constant temperature maintained at $15^{\circ}, 20^{\circ}, 25^{\circ}$, and $30^{\circ} \mathrm{C}$. The cultures were subjected to a daily light cycle of 11 hours provided by two, 15 -watt, cool white, fluorescent bulbs and controlled by separate automatic time switches. Except for small amounts of creek water used to replace that which had evaporated, no further additions were made to the system in the glass jars.

Both quantitative and qualitative estimates of the phytoplankton were made from the slides by the differential count method. A kind of
grid system was followed in counting the cells by using a Whipple micrometer with which the microscope had been calibrated to read $0.16 \mathrm{~mm}^{2}$ area in each microscopic field. Algae were counted in ten microscopic fields selected at random from each slide. Average numbers of individuals per $\mathrm{mm}^{2}$ were computed from the actual counts. Each filament of a multicellular alga was counted as a single individual (cell). All counts were determined in situ on the glass slides. Changes in appearance, size and shape, distinctive features of small and large forms, estimates of individuals in the communities, and sequential developmental phases were noted. Identification of the phytoplankton to genus only was attempted. The mean and standard error of the mean were computed for each experimental group, and t-values were obtained to assess statistical differences between means.

## RESULTS

SEASONAL VARIATION: The results indicated marked seasonal variation in numbers of phytoplankton as shown in Figure 2. Direct counts of algae made on 0 day of incubation revealed that the early stages of succession in the natural habitat were dominated by diatoms, although green and blue-green algae were also observed as developing filaments. Temperature seemed to be a factor of paramount importance in controlling the populations both in the natural habitat and in laboratory studies. A drop in natural temperature, for example in January, caused green algae almost to disappear from the stream water (Figure 3), although some of them appeared in the laboratory after incubation at higher temperatures. On the other hand, diatoms were less affected by temperature than green or blue-green algae suggesting their capability to tolerate a wide range of temperatures. In general, the number of phytoplankton increased with the onset of warm vernal weather and reached a peak in May.

Among the algae found in the periphyton complex of the natural habitat, diatoms were predominantly represented by Nitzschia, Surirella, Diatoma, and Navicula; Caloneis, Cocconeis, and Achnanthes were found occasionally. Fragilaria and Pinnularia took part in succession later after incubation. Green algae had many genera among which Stigeoclonium, Oedogonium, Cladophora, Microspora, Mougeotia, and Ulothrix colonized the slides. Chlorococcum, Pediastrum, Gongrosira, Rhizoclonium, Tribonema, and Chaetophora appeared after incubation. Red algae did not colonize the slides in nature, but their representative, Batrachospermum, was

Figure 2. Seasonal variation in numbers of algae collected from Cedar Creek from November, 1972 through August, 1973.


Figure 3. Numerical abundance of diatoms, green algae and bluegreen algae collected in 1972-73 from Cedar Creek.

found in later counts. Anabaena, Oscillatoria, and Phormidium were the pioneering blue-green algae in different seasons. Nodularia was recorded in weekly counts in June after incubation.

Figure 2 depicts seasonal variation of phytoplankton from November 1972 to August 1973. The general trend in the occurrence of algae was toward a numerical increase with increase in natural temperatures with the lowest number in January and highest in May. Statistical analysis of successive samples of phytoplankton revealed a dramatic increase in the numbers of plankton resulting in a major peak in May with an estimated average of 113 individuals per $\mathrm{mm}^{2}$. The elevated counts for May were statistically significant from the samples taken earlier or later in the year. By June, their numbers fell to a level slightly higher than in April. Thereafter, a progressive increase in numbers took place in the summer with green algae dominating.

Diatoms comprised the largest and most prevalent single group of algae at every collection as illustrated in Figure 3. Even though the number of diatoms decreased in January, this fact indicates that the development of diatoms continued even at low temperatures. During the May peak, Surirella was the most numerous diatom superceding Nitzschia and Diatoma; Nitzschia became predominant again in the late summer. A sharp decline in numbers of green and blue-green algae took place in May when diatoms were at their largest numbers. Numbers of green algae increased progressively from June through August with a statistically significant increase from July to August. The most prominant genera of green algae in the summer were Stigeoclonium, Cladophora, Ulothrix, and Microspora. The pattern of distribution of blue-green algae looked rather
deceptive since their numbers increased in January and April collections but not in the summer. The frequency of occurrence as well as number of individuals counted before incubation showed that Nitzschia, Surirella, Stigeoclonium, and Cladophora were some of the genera of algae thriving best in this aquatic habitat.

INCUBATION: The main advantage of the microcosm method of studying succession used in this study is in that the experiments can be controlled. It is an unnatural system in which neither export nor import of materials takes place. One would, therefore, predict changes in the community in terms of relative abundance of individuals, not in the composition of species. But the possibility that new genera of algae might be encountered during succession is always there since only about $0.5 \%$ of the total area of a slide was studied in counting the cells.

The responses of phytoplankton on which were imposed experimental conditions clearly indicated that irrespective of the nature of seasons in which collections were made, temperature was involved in determining the subsequent rates of development of algal communities. With the advent of time the communities were dominated by a mat of green algae and finally by blue-green algae depending on the temperature used and the duration of incubation. Successional events were observed to be taking place rapidly resulting in a large structure at maturity of climax communities. As succession proceeded the slides appeared less green to the unaided eye; the slides were dominated by diatoms and blue-green algae except at $20^{\circ} \mathrm{C}$ when green and red algae were found to flourish. Clumping of diatoms and other algae was the general rule at maturity thus making the counts more difficult. Gas bubbles were seen evolving from
the cultures; these probably represented gaseous oxygen produced by photosynthesis. Two other impressive phenomena were 1) the arrival in later stages of succession of the largest genus of diatoms, Pinnularia, and 2) increasing amount of detritus on the slides some days after incubation. Diatoms, in general, were found to co-exist with green, red, and bluegreen algae, but the main interactions took place between green and blue-green algae. Also, red and blue-green algae never occurred together at any temperature so that only one of these two ever occurred with diatoms or green algae. There were many kinds of fluctuations in numbers of diatoms indicating that they thrive in a wide range of temperatures and period of incubation. Blue-green algae were found to be tolerant of both low and high temperatures while green algae favored temperatures at $20^{\circ} \mathrm{C}$ as optimum. A similar pattern of change was evident in all the eight readings taken during the study period.

Figures 4 and 5 illustrate responses of phytoplankton to $15^{\circ} \mathrm{C}$ incubation. These graphs are representative of the general responses that occurred in all collections. When green and blue-green algae occurred together, it was the green algae that gained the competitive advantage over blue-green algae (Figure 4). In the absence of green algae, however, blue-green algae maintained themselves till they showed a tendency toward reaching a climax stage in 21 days of incubation (Figure 5). The data also suggest that no definitive conclusion could be drawn in regard to the response of diatoms at $15^{\circ} \mathrm{C}$. The high percentage of blue-green algae throughout the period of incubation (Figure 5) was suggestive of their capacity to tolerate low temperatures which is also a unique character for them in the natural habitat.

Figure 4. A sample collection showing the interactive effects between green and blue-green algae during incubation. This algae collection was made in May, 1973 and incubated at $15^{\circ} \mathrm{C}$ for 28 days.


Figure 5. Average numbers of algae collected in January, 1973 and incubated at $15^{\circ} \mathrm{C}$ showing that in the absence of green algae, numbers of blue-green algae increased rapidly.

TNC $=$ too numerous to count


Green algae succeeded in competing with blue-green algae both at $15^{\circ}$ and $20^{\circ} \mathrm{C}$ showing their highest response at $20^{\circ} \mathrm{C}$. Figure 6 represents the data from one collection incubated at $20^{\circ} \mathrm{C}$; other collections produced similar results. At this temperature diatoms showed a corresponding numerical decrease when green algae were at the peak of their development. The small number of blue-green algae encountered in the first two weeks of incubation was overrun by massive growth of green filaments which reached a number too numerous to count after 21 days.

One of the most interesting features of this study was the observation that in the absence of blue-green algae competing with green algae, red algae alone seem to challenge the existence of green algae when incubated at $20^{\circ} \mathrm{C}$. Batrachospermum, a genus of red algae, made its startling appearance 7 days after incubation in May (Figure 7). It demonstrated its reproductive potential by multiplying to high levels within 14 days of incubation. The interplay between red and green algae seemed to be quite positive or neutral since both of them flourished together thereafter, showing similar responses to $20^{\circ} \mathrm{C}$ incubation. In contrast blue-green algae were always superceded by green algae at this temperature.

Figure 8 shows that green algae could tolerate temperatures up to $25^{\circ} \mathrm{C}$ but that their development took place in the absence of blue-green algae. In this May collection, only diatoms had colonized the slides. Green algae appeared 14 days after incubation and reached a number too numerous to count within a week. The response of diatoms was similar to that at $20^{\circ} \mathrm{C}$ in that they showed a corresponding decrease in numbers with increase in numbers of green algae. A temperature of $25^{\circ} \mathrm{C}$ was found more

Figure 6. Phytoplankton populations from a collection in May, 1973 and incubated at $20^{\circ} \mathrm{C}$ showing the interactive effects between green and blue-green algae.

TNC $=$ too numerous to count


Figure 7. Average numbers of algae from a collection in May, 1973 and incubated at $20^{\circ} \mathrm{C}$ showing similar responses of red and green algae.

TNC $=$ too numerous to count

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Figure 8. A collection of phytoplankton in May, 1973 and incubated at $25^{\circ} \mathrm{C}$ showing that green algae could thrive at temperatures of $25^{\circ} \mathrm{C}$.

TNC $=$ too numerous to count

favorable to blue-green algae than green algae (Figure 9). In the initial collection in mid-May, both green and blue-green algae were seen to colonize the slides along with a correspondingly high number of diatoms. Green algae were more responsive than blue-green algae in the first week of incubation, but thereafter the latter showed a dramatic boost ultimately reaching a climax stage after 21 days. Diatoms fluctuated in numbers with a minimum occurring at seven days and maximum at 21 days of incubation. Their cell number was low when blue-greens had their maximum response.

Figure 10 illustrates the relative responses of green and bluealgae and diatoms collected in November to $30^{\circ} \mathrm{C}$ incubation. As at $25^{\circ} \mathrm{C}$, blue-greens had an established supremacy over green algae at this temperature. Interestingly, the rapid increase of blue-green algae after 14 days of incubation occurred simultaneously with the diatom bloom. Diatoms showed a logistical growth curve over time without any fluctuating trends. Although the responses of green algae were greater than bluegreen algae in the first and second week after incubation, blue-greens showed a faster response afterwards completely eliminating the greens.

Figure 11 shows the responses of the algal groups to the four thermal conditions after 7 days incubation. Average numbers of algae per $\mathrm{mm}^{2}$ were calculated out of the total number of algae counted during the entire period of study at 7 days of incubation. While calculating the averages, the number of green algae recorded as too numerous to count at $20^{\circ} \mathrm{C}$ incubation in April and May was arbitrarily fixed at 1000 individuals per $\mathrm{mm}^{2}$. It is very clear from the graph that the responses of red and green algae were faster at $20^{\circ} \mathrm{C}$ than at other thermal environments. The

Figure 9. A collection of algae in May, 1973 and incubated at $25^{\circ} \mathrm{C}$ in which green algae did not compete very successfully with the blue-green algae.

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Figure 10. Average numbers of phytoplankton from a collection in November, 1972 and incubated at $30^{\circ} \mathrm{C}$ showing interaction between green and blue-green algae.

TNC $=$ too numerous to count


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34
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Figure 11. Combined mean responses of phytoplankton groups collected from November, 1972 to August, 1973 to the four thermal conditions after 7 days incubation.

responses of diatoms and blue-green algae were minimal at this temperature, but these were more responsive than the former two divisions at $30^{\circ} \mathrm{C}$. Whenever the number of an algal division was at its maximum at a particular temperature, numbers of other divisions showed a corresponding decrease. This may not have applied to red algae because they showed similar responses to $20^{\circ} \mathrm{C}$ which was most favorable for green algae to survive.

From the results presented replacement of one community by another was mainly due to changes induced by temperature. The appearance of increasing numbers of algal divisions after incubation was due to alteration of the habitat by temperature to be more conducive for proliferation of those forms arriving late.

## DISCUSSION

An unstable environment and rapid changes in component organisms of a flowing water system make it somewhat difficult to define the planktonic community. Variations in environmental factors upset the ecological conditions causing populations of algae vary in the same season of occurrence. A distinct association of planktonic groups cannot, therefore, be found in streams.

Two things that need to be discussed in this study are 1) seasonal occurrence of phytoplankton in the natural habitat as related to physical and nutritional factors, and 2) successional properties of these algae under controlled conditions in the laboratory as determined by their tolerance to temperature and the consequent changes in the community over time. The two situations are totally different since in the former case, the fate of organisms is determined by a complex of factors as light, temperature, current, turbidity, and nutrient regeneration. In the latter case temperature is probably most important in determining the degree of variability in the community structure.

The first part of investigation dealt with collection of data about the types of algae, their numerical abundance, and periodicity in the natural habitat. Some algae were seen flourishing as mere "opportunists" when conditions were more conducive for their existence, but the ecological requirements for many of them seemed to be a group of several factors of which temperature is important (Brinley and Katzin 1942). This assumption does not, however, agree with Pearsall's (1922) findings
that the composition and distribution of phytoplankton are largely influenced by dissolved chemical nutrients. Also, plankton diatoms occur in waters rich in nitrate and silica content, and blue-green algae occur abundantly in waters having abundant organic matter. In my study, the habitat contained relatively high concentrations of nitrates, silicates, phosphates, and chlorides indicating loading of pollution. Diatoms were collected in all seasons of study although their diversity was low. Blue-green algae were present in all but two collections.

Floods brought abundant quantities of nitrates and silicates and controlled diatom periodicity by providing nutrients required for their growth in winter (Pearsall 1923) and spring (Butcher 1932). According to Butcher (1932) maximum colonization takes place in May. The period of least colonization is winter when plankton have slower growth rates. In this study the occurrence of smaller quantities of plankton in January (Figure 3) could be due to heavy rains washing off the biota and impeding colonization on the smooth surface of the glass slides. Rising temperatures and optimal light favored maximum colonization in May.

Though floods bring higher nitrate and silicate content to produce greater quantities of diatoms, another limiting factor in this creek seemed to be the current which had its physical effect on the distribution and variety of the algae. A flushing effect of the current reduced phytoplankton standing crop in November, January, and April resulting in lowered total primary productivity. The swift action of floods may reduce or eradicate the stream biota (Williams 1964). Whitford (1960) reported that a strong current favors growth chiefly among others of forms like Stigeoclonium, Oedogonium, Cladophora, Rhizoclonium, Mougeotia, Fragilaria,

Cocconeis, and Achnanthes. Blum (1956) found that Ulothrix, Stigeoclonium, and Diatoma were characteristic of riffles. My observations coincided with their findings since the same genera were collected by me under similar conditions. Blue-green algae were common in all seasons except in November and April. Distribution of green algae was a bit different since they appeared in November and April collections and reached maximum development through August. Diatoms thrived under varied conditions of temperature with an irregular pattern of distribution characteristic of polluted waters. Riley (1946) correlated the variation in the distribution of phytoplankton from one month to next month partly to factors like depth of water, temperature, and dissolved nutrients. Diatoms showed no definite pattern of distribution and blue-green algae depended upon a rich food supply consisting of organic matter. Green algae fell intermediate in the category in regard to their occurrence and needs.

The increase in numbers of algae as a consequence of a water system receiving organic matter had been emphasized by some workers (Brinley and Katzin 1942, Lackey 1942, Butcher 1947, and Patrick et al. 1954). In an environment whose supporting capacity is increased by loading of pollution, the inhabitants will have different rates of multiplication. This results in a decrease of diversity (Margalef 1963). The occurrence of less diverse genera with more individuals of each points to the fact that the stream was affected by pollution. Pollution eliminated more sensitive species to favor more tolerant ones (Patrick et al. 1954). The total elimination of desmids in the creek was another point of interest since these were the algae which could not tolerate the polluted habitat. As a consequence of low diversity of forms, competition was minimized and
the most tolerant forms spread out in the habitat. Butcher's (1947) observation that Nitzschia and Stigeoclonium were most resistant to pollution provides a satisfactory evidence to my recording of the same algae frequently in the creek water.

In connection with the successional properties of the laboratory cultures, two explanations are possible. First, the pioneering algae alone brought about the sequence of changes by depleting or altering the concentration of nutrients as they make the habitat more favorable for those arriving late in succession. Secondly, replacement of one community by another took place because of changes induced by temperature. Both these assumptions may be true since in either case the succeeding community gained the ecological advantage. It should also be remembered that the nutritional requirements of the community might be a function of temperature. When the organisms were subjected to temperature, their success in succession was determined mainly by their capacity to tolerate the variable and overcome the environmental resistance and their ability to proliferate in the modified habitat. Interactions between the organisms and the physical environment lead to establishment of a self-replicating, stable, climax community. While temperature perhaps controlled the composition of phytoplankton, the communities themselves determined the direction of succession (Odum 1971).

Turnover of algal populations was so rapid that climax communities of one or other type were established within 3 to 4 weeks of incubation except in the collection of mid-May incubated at $15^{\circ} \mathrm{C}$. Here populations did not show any tendency toward reaching a stabilized state even after 28 days of incubation (Figure 4). Variability in temperature seemed to
be very important ecologically. Aquatic organisms have a more narrow limit of tolerance to temperature than land animals (Odum 1971). It is obvious from the graphs (Figures $4-10$ ) that some organisms failed to develop at a particular temperature while others proliferated tremendously and established themselves into climax communities in a short time. This could mean that temperature is the major limiting factor controlling the density of phytoplankton populations. When temperature exceeded the optimum, the algal divisions failed to develop at different thermal conditions because of vigorous competition of one population with the other at temperatures most favorable to them. Figure 11 illustrates how one community showed its maximum response at a particular condition while the response of others was either low or absent. Red and green algae had their maximum development at $20^{\circ} \mathrm{C}$. The response of blue-green algae was faster at $25^{\circ}$ and $30^{\circ} \mathrm{C}$ but not at $20^{\circ} \mathrm{C}$. Diatoms were tolerant of the entire range from $15^{\circ}$ to $30^{\circ} \mathrm{C}$. All these features indicate that temperature was a critical determinant of the very existence of algal divisions. Higher temperatures showed a negative effect on green algae probably by increasing respiration and using up the body energy. The higher the temperature, the greater will be the flow of energy (Margalef 1963). The molecular mechanism underlying the response of organisms to temperature might include a number of enzymic changes also (Somero 1969). Once the community approaches integration of a balanced ecosystem, its respiration will be less affected by temperature (Beyers 1962).

Figures 9 and 10 show that the population size depended not only on the temperature used but also on the intrinsic rate of increase of the algal divisions as determined by the interactions among communities. At
$25^{\circ}$ and $30^{\circ} \mathrm{C}$, blue-green algae increased in numbers at the expense of green algae which became rare (Figure 9) or were excluded (Figure 10). The fact explains that blue-greens gained a competitive advantage over green algae at that temperature. Conversely, green algae had this advantage over blue-greens at $15^{\circ} \mathrm{C}$ (Figure 4), and $20^{\circ} \mathrm{C}$ (Figure 6). When both green and blue-green algae were introduced into the environment at $20^{\circ} \mathrm{C}$ (Figure 6), they were initially scarce at 7 days incubation. The combined population increased in the second week and showed a tendency toward saturation of the environment. Green algae began to increase their reproductive potential at day 14 while the number of blue-green algae dwindled to zero. It was at this stage that the mechanism of competition operated on these competing populations.

Physiologically dissimilar organisms residing in identical environments but having different growth rates cannot co-exist; the one multiplying faster causes displacement of the other whose reproductive potential is low (Gause 1934, Alexander 1970). Increase in abundance of one population must result in decrease in numbers of the competing population (MacArthur and Connell 1966). However, two competing populations can co-exist if each of them required a different resource or have a common resource in abundance and if the tolerance ranges of the two are similar. In this study I was not concerned with competition among different species but rather among algal divisions. This concept can justifiably be used because the algal divisions are defined in terms of major physiological capabilities. One division with one set of physiological capabilities had a competitive advantage over another algal division with a different set of physiological capabilities. In Figure 7, red algae appeared at 7 days
incubation and co-existed with green algae thereafter. This interplay between the two divisions could be either positive or neutral since neither of the two populations imposed deleterious effects on the survival of the other. The two divisions also had similar growth rates and degree of thermal tolerance, and their capacity to convert nutrients and synthesize and store food reserves must have been identical. All these factors seemed to have played a role in the appearance of a heterogeneous community in the culture. Grenney and his co-workers (1973) pointed out that co-existence is made possible between two communities because one of the competitors utilizes the substitute nutrient source out of the excreted metabolites of the other. Cooke (1967) explained the possible role of inhibitors in laboratory microecosystems. According to his results, changes in community structure during succession may be regulated by secretion of metabolic inhibitors which regulate the ecosystem as it ages.

Mention was made in the results sections about the clumping behavior of planktonic groups during incubation. Clumping should naturally occur with decreasing abundance, but this inverse relationship provided no validation in my experiments because diatoms were the organisms which of ten showed clumping and yet were too numerous. Hairston (1959) explained this phenomenon by suggesting that in succession, the degree of success of abundant species may not be uniform, and so they show clumped arrangement "but to a lesser degree than the rare species." Rapid and erratic changes in the populations with time offered a picture of instability of plankton groups, but the feature of fundamental importance to succession was found to be the interplay of communities affecting one another in response to
temperature variable. More tolerant organisms often replaced less tolerant ones suggesting that succession, in a general sense, is an evolutionary process of communities.

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[^0]:    TNC $=$ too numerous to count

