THE EFFECTS OF GRAZING BY SNAILS ON COMMUNITY STRUCTURE OF PERIPHYTON IN LABORATORY STREAMS

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CHAPTER I

INTRODUCTION

Periphyton or benthic algae contribute significantly to total primary production in many aquatic systems. Piecyznska (1968) found the contribution to be about 75% in the littoral zone of lakes, and Wetzel (1963) reported that periphyton were the most important producers in Borax Lake, California. Since streams contain no true phytoplankton community (Reid, 1965), periphyton and macrophytes are the most important producers in streams.

Artificial substrata have been used frequently to study taxonomy and standing crop of periphyton (Cooke, 1956; Sladeckova, 1962; Wetzel, 1964), but rarely to measure periphyton production. Kevern, Wilhm, and Van Dyne (1966) measured the rate of biomass accumulation on plexiglass plates in a series of exposures of increasing duration. They developed a discontinuous, linear regression model to separate the colonization and exponential growth phases of the periphyton growth curve. They concluded that the slope of the exponential phase approximated the production rate of the periphyton.

Many investigators have related chlorophyll concentration to production and/or standing crop. According to McConnell and Sigler (1959) production and biomass may be approximated from chlorophyll concentration. Relationships between chlorophyll content and

photosynthetic ability were described by Fleischer (1935), Manning and Juday (1941), Blaauw-Jansen, Komen, and Thomas (1950), Edmondson (1955), Ryther (1956), and Waters (1961). Yount (1956) used the rate of accumulation of chlorophyll on glass slides to estimate production in a large Florida spring. Phytopigment absorbancy was related to ash-free weight by Grzenda and Brehmer (1960). Although values relating chlorophyll concentration, production, and standing crop of algae have been determined, inconsistency of results has revealed difficulties and faults in the chlorophyll method of measuring these parameters.

While one approach in the study of communities stresses biomass and production, another emphasizes community structure. Community structure may be described by mathematical expressions called diversity indices. These expressions permit summarization of large amounts of information about numbers and kinds of organisms (Patten, 1962). Several indices have been proposed to describe community structure (Simpson, 1949; Margalef, 1951; Patten, 1962; Menhinick, 1964). Hairston and Beyers (1954) evaluated two diversity indices while analyzing populations of soil arthropods. Menhinick (1964) suggested an index to describe a community of field insects. Wilhm and Dorris (1966) used diversity indices to evaluate water quality. Kullberg (1968) used the dominance diversity approach to relate periphyton diversity to water temperature and velocity in thermal effluents. The relationship between production, chlorophyll concentration, and diversity in periphyton has not been thoroughly investigated.

Knowledge of the effects of consumers on biomass accumulation, chlorophyll concentration, and diversity of primary producers is

important to understanding primary production. The effects of grazing on species composition, vigor, and yield in terrestrial ecosystems have been studied extensively (Smith, 1940; Daubenmire, 1940; Costello and Turner, 1941; Canfield, 1944; Tomanek and Albertson, 1953; Johnson, 1953; Johnson, 1956; Hazell, 1967). Aquatic grazing, however, has received less attention. Fleming (1939) studied grazing by zooplankters on diatom populations. Taub and Dollar (1964) and Ryther (1954) investigated inhibitory effects of phytoplankton on planktonic grazers. Grazing rates of zooplankters were studied by Fuller (1937), Gauld (1951), and Ryther (1954). Slobodkin (1959) studied the effects of predation upon grazing of daphnids. Beyers (1963) recorded effects of grazing by snails on nighttime respiration and net photosynthesis in microcosms, and Dickman (1968) studied the effects of grazing by tadpoles on species diversity and standing crop of periphyton in a shallow pond.

In order to study effects of grazing on production, chlorophyll concentration, and species diversity of periphyton, it is necessary to control environmental factors such as light, current, and temperature. This control is possible in laboratory ecosystems called microcosms. Use of microcosms also enables replication and measurement of precision. Although microcosms cannot duplicate natural ecosystems, striking similarity of processes occurring in microcosms and the natural environment were demonstrated by Odum and Hoskin (1957), Beyers (1965), Kevern and Ball (1965), and Kevern et al. (1966).

Stream microcosms were used by Odum and Hoskin (1957) to study periphyton communities colonizing the inside of a condenser. McIntire et al. (1964) used six laboratory streams to study primary

production and community respiration in simple communities under differing environmental conditions. McIntire and Phinney (1965) related illumination intensity to primary production and community metabolism in laboratory streams. Kevern and Ball (1965) studied the effects of light, temperature, and chelate concentration on net production in laboratory streams. The effects of current on primary production were determined by McIntire (1966). Davis and Warren (1966) studied trophic relations, and McIntire (1968) studied structural characteristics of periphyton communities in laboratory streams.

The objectives of the present study were (1) to use a mathematical model to describe periphyton growth under grazing stress and (2) to determine the effects of grazing on biomass accumulation, chlorophyll *a* concentration, and species diversity of periphyton colonizing laboratory streams.

CHAPTER II

MATERIALS AND METHODS

Four laboratory streams were constructed of marine plywood and housed in an enclosure covered with black plastic. Each stream was coated with white, nontoxic, marine enamel and measured 2.4 x 0.15 x 0.07 m (Fig. 1). Glass microscope slides with total exposed area of 19.0 cm^2 lined the bottoms. Illumination of 250 ft-c was provided by 40 Sylvania Gro-lux fluorescent bulbs suspended 41 cm above the stream surface. Lights were controlled by individual rheostats and activated by 120-volt transformers. Photoperiod extended from 0600 to 1800 hours. Heat was removed by an exhaust fan near the top of the enclosure. Water temperature varied between 30°and 34°C. Water flowed from the stream outlets into two 23-gallon plastic buckets and was then pumped by Little Giant Submersible Pumps back to the inlets. Polyethylene flow valves maintained the current at 8 cm/sec.

The streams and reservoirs were filled with natural stream water on 15 March 1969. The water was filtered and 120 ppm nitrates and 20 ppm phosphates in carrier compounds $Ca(NO_3)_2 \cdot 4H_2O$ and $NaHPO_4 \cdot 7H_2O$ were added. These concentrations allowed the highest net productivity in a study of algal mat communities in microcosms (Wilhm and Long, 1969). Although most natural waters contain less phosphate, higher values have been reported in nature (Eley, 1969). To assure

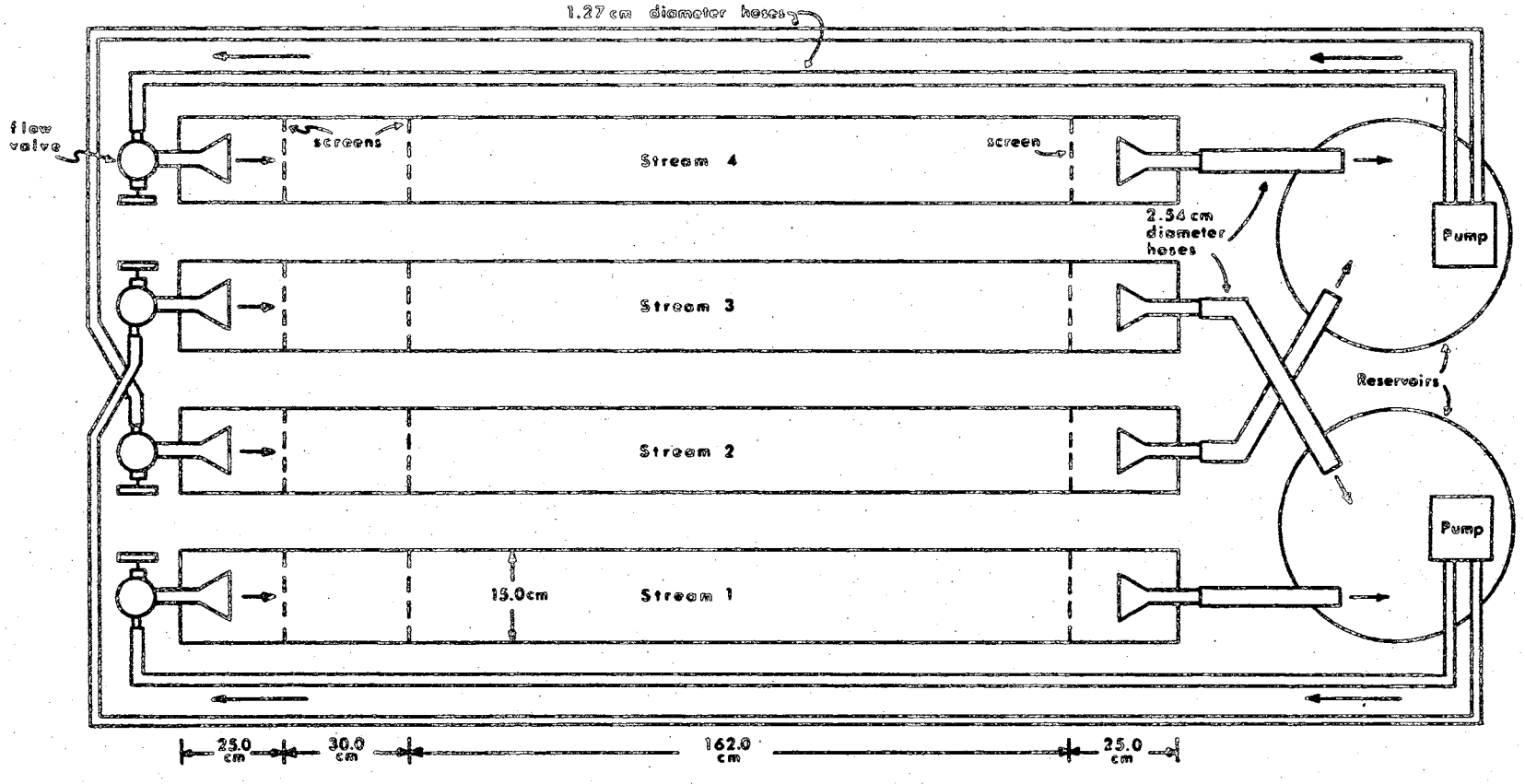

Figure 1. Four Laboratory Streams Used to Study Effects of Grazing on Community Structure of Periphyton.

colonization of similar communities until introduction of grazers, the outflow tubes were adjusted so that complete mixing occurred among all streams and reservoirs.

On 24 March snails were placed in the streams in densities of zero and 0.012 snails/cm^2, as suggested from a pilot study. Forty Physa gyrina averaging 0.13 g each were placed in streams one and three and water from streams one and three was separated from streams two and four. Plastic screens near the stream ends confined the grazers to the units. Streams one and three are identified as Tg (treatment with grazing) and streams two and four as Tng (treatment with nongrazing).

A one-way classification analysis with two treatments and two replications with three subsamples each was used to determine the effect of snails on accumulation, chlorophyll a, and species diversity of periphyton colonizing the streams. Nine slides were removed from each stream on day 4, 8, 14, 21, 28, 36, 44, 53, 65, 79, and 92 and three slides were analyzed for each variable for each time period. Slides were numbered and then designated by a table of random numbers.

Periphyton was scraped from the slides and oven dry weight and ash-free weight were determined gravimetrically using a temperature of 103°C for drying and 525°C for muffling. Chlorophyll a concentration was measured by scraping the periphyton into large test tubes and extracting the pigment in 90% acetone in the dark for 72 hours. The samples were centrifuged for 3 minutes and the absorbancy of the supernatant fluid was read at 430 and 665 mμ on a Bausch & Lomb Spectronic 20 Colorimeter. Chlorophyll a concentration was calculated according to Odum, McConnell, and Abbott (1958). Periphyton for

species diversity was scraped into 4% formalin, mixed in a Sorvall Omni-mix, and filtered through a 0.45 μ Millipore filter. The filter was placed on a clean microscope slide and allowed to dry for 10 minutes at 100°C. Four drops cedar oil were immediately applied, clearing the filter instantly, and a cover slip was added. Absence or presence of algal genera was recorded in 30 random fields per slide and results were converted to cells/cm^2 (McNabb, 1960). Species diversity of periphyton was determined for each slide using the formula,

$$\bar{d} = -\sum_{i}^{s} (n_i/n)\log_2(n_i/n),$$

where n = total number of individuals, n_i = number of individuals in the "i"th genus, and s = number of genera (Patten, 1962).

CHAPTER III

RESULTS AND DISCUSSION

Algae Present and Physical Appearance

Six algal genera developed in the laboratory streams (Table I). The sparsity of taxa was evidently caused by the high temperature of the streams. Inverse relationship between species numbers and temperature was reported by Kullberg (1968).

The most common genera, Scenedesmus, Senechocystis, and Lyngbya, were present throughout the study. Oocystis was first observed day 8, Gloeotrichia day 36, and Cylindrospermum appeared in Tng day 36 and in Tg day 65. No diatoms were observed throughout the study.

A green mat developed by day 5 on the bottom under both treatments. The mat ascended the sides of the streams as time progressed. The mat was greener in Tg than in Tng throughout the study. By day 20 the algae appeared greenish-brown under both treatments. On day 22 Tng was brown. By day 28 the algae was orange-green under both treatments. The water in Tg was always clear, but Tng was slightly turbid from day 20 to day 65.

Oven-dry Weight and Ash-free Weight

Oven-dry weight did not appear to be affected by grazing on most sampling dates. Oven-dry weight was significantly higher in Tng than

TABLE I

TEMPORAL VARIATION IN ALGAL CELL NUMBERS PER SQUARE CENTIMETER IN LABORATORY STREAMS WITH GRAZING (Tg) AND NONGRAZING (Tng) CONDITIONS

Genus	Treatment											
Scenedesmus	Tg	185	3346	15382	44545	23601	38732	52987	58463	39984	35176	45237
	Tng	192	4304	13477	34178	56037	40390	31715	38044	33430	54072	44734
Senechocystis	Tg	113	2572	22672	19546	7208	11150	15037	7346	3138	3896	4404
	Tng	113	2572	16778	13625	19736	16232	9480	4226	2464	3757	2580
Lyngbya	Tg	91	1989	9379	9504	6327	14806	35477	44723	43780	60545	63420
	Tng	89	1926	8817	6759	26739	18302	15019	18287	38034	51102	34667
Oocystis	Tg		791	2238	3810	1614	2010	3576	13024	12762	20362	19631
	Tng		880	2811	3012	2671	2430	1830	8225	14387	21371	13150
Cylindrospermum	Tg									376	6838	13326
	Tng						995	4551	2715	3444	5526	9425
Gloeotrichia	Tg						6569	10328	10938	8684	7239	7160
	Tng						3310	5712	6388	4398	2927	5261

in Tg only on days 28 and 36 but was similar under both treatments on other days (Table II). The significant differences were revealed in the Analysis of Variance (AOV) of the oven-dry weight responses. Oven-dry weight increased abruptly in both Tg and Tng and leveled off around 50 g/m^2 on day 21 (Fig. 2). A maximum of 76.8 g/m^2 occurred in both Tg and Tng on day 92. These maxima correspond to McIntire's (1966) maximum of 94 g/m^2 on day 65 in laboratory streams and Wilhm and Long's (1969) value of 84.9 g/m^2 on day 110 in battery-jar microcosms.

Fluctuations in ash-free weight followed the same general trends as changes in oven-dry weight (Fig. 2). The AOV of the ash-free weight responses showed Tng to be significantly higher than Tg only on day 44 (Table II). No significant differences were found between Tg and Tng on any other sampling dates. Maximum values of ash-free weight were 66.1 g/m^2 in Tg and 57.0 g/m^2 in Tng, both on day 92. McIntire (1966) reported a maximum of 73.2 g/m^2 on day 36 in a stream microcosm. Beyers (1963) reported severe overgrazing by snails in aquaria in which 1000 cm^2 were subjected to 20 g of large Marisa. In the present study 5000 cm^2 were subjected to 5.2 g of small Physa. Dickman (1968) reported significant reduction in periphyton standing crop caused by tadpole grazing in a shallow pond.

No significant difference in mean ash-free percentage of oven-dry weight was found between Tg and Tng (Table III). Under both treatments the ash-free percentage was extremely low on day 4 and fluctuated around 60% during the remainder of the study except for an increase after day 65 (Fig. 3). The means were 62.17% in Tg and 58.52% in Tng. Comparable data reported from laboratory streams are in Table IV.

TABLE II

MEAN VALUES OF OVEN-DRY WEIGHT, ASH-FREE WEIGHT, CHLOROPHYLL *a* CONCENTRATION, PIGMENT DIVERSITY, AND SPECIES DIVERSITY IN LABORATORY STREAMS WITH GRAZING (Tg) AND NONGRAZING (Tng) CONDITIONS

Day	Dry Weight (g/m^2)		Ash-Free Weight (g/m^2)		Chlorophyll *a* (g/m^2)		Pigment Diversity (D_{450}/D_{665})		Species Diversity ($\bar{d}$)	
	Tg	Tng	Tg	Tng	Tg	Tng	Tg	Tng	Tg	Tng
4	0.7	0.4	0.1	0.2	0.00	0.00	2.1	2.0	1.04	1.03
8	6.2	6.8	5.1	5.3	0.02	0.02	2.4	2.5	1.20	1.20
14	37.1	35.7	18.0	18.3	0.04	0.03	2.8	2.8	1.11	1.08
21	44.7	49.2	30.7	25.0	0.03	0.03	3.2	3.2	1.07	1.06
28	39.7 *	51.9	23.5	27.1	0.03	0.03	3.3	3.8	1.05	1.13
36	38.9 **	62.2	28.4	37.8	0.05 **	0.03	3.8	3.3	1.27	1.18
44	49.3	58.1	24.7 *	35.7	0.07 **	0.04	3.1	3.9	1.23	1.48
53	46.0	57.9	30.8	34.1	0.12 **	0.05	3.1	3.1	1.30	1.37
65	70.7	63.8	43.9	29.7	0.13 **	0.05	2.8	3.4	1.32	1.31
79	73.4	70.9	52.7	48.5	0.12 **	0.05	2.7 *	3.7	1.28	1.31
92	76.9	76.9	66.1	57.0	0.12 **	0.08	2.8	3.1	1.41	1.32

One asterisk (*) between two values indicates difference significant at 95% level. Two asterisks (**) indicate difference significant at 99% level.

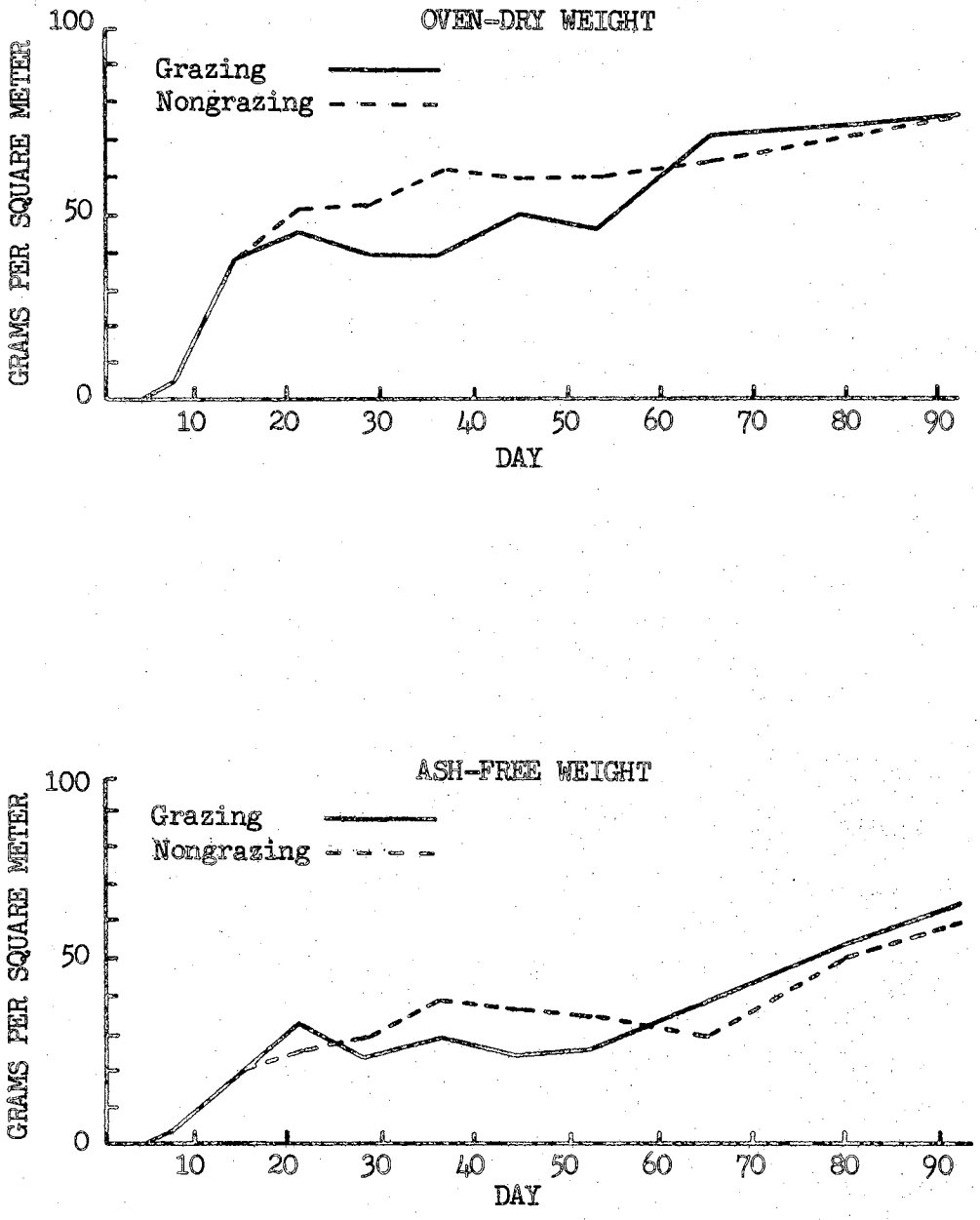

Figure 2. Temporal Variation in Oven-dry Weight and Ash-free Weight in Laboratory Streams.

McIntire et al. (1964) and McIntire (1966) stated that young communities, dominated by green algae, usually contain a higher ash-free percentage than older communities dominated by diatoms and blue-greens. No such relationship was evident in the present study. Wide fluctuations in ash-free percentage occurred and no clear trends in algal dominance were apparent. The greens and blue-greens were similar in abundance under both treatments (Fig. 4).

TABLE III

"t" VALUES OBTAINED FOR CERTAIN PARAMETERS TO TEST DIFFERENCES BETWEEN GRAZING AND NONGRAZING CONDITIONS

Parameter	t		
	Calculated	Tabulated 95% level	99% level
Ash-free Percentage of Oven-dry Weight	0.54	2.23	3.17
Chlorophyll a Percentage of Ash-free Weight	0.95	2.23	3.17
Chlorophyll a Percentage of Oven-dry Weight	1.29	2.23	3.17
$\frac{\text{mg Ash-free Weight}}{\mu\text{g Chlorophyll a}}$	1.17	2.23	3.17
$\frac{\text{mg Oven-dry Weight}}{\mu\text{g Chlorophyll a}}$	11.50*	2.23	3.17

* = significant at the 99% level.

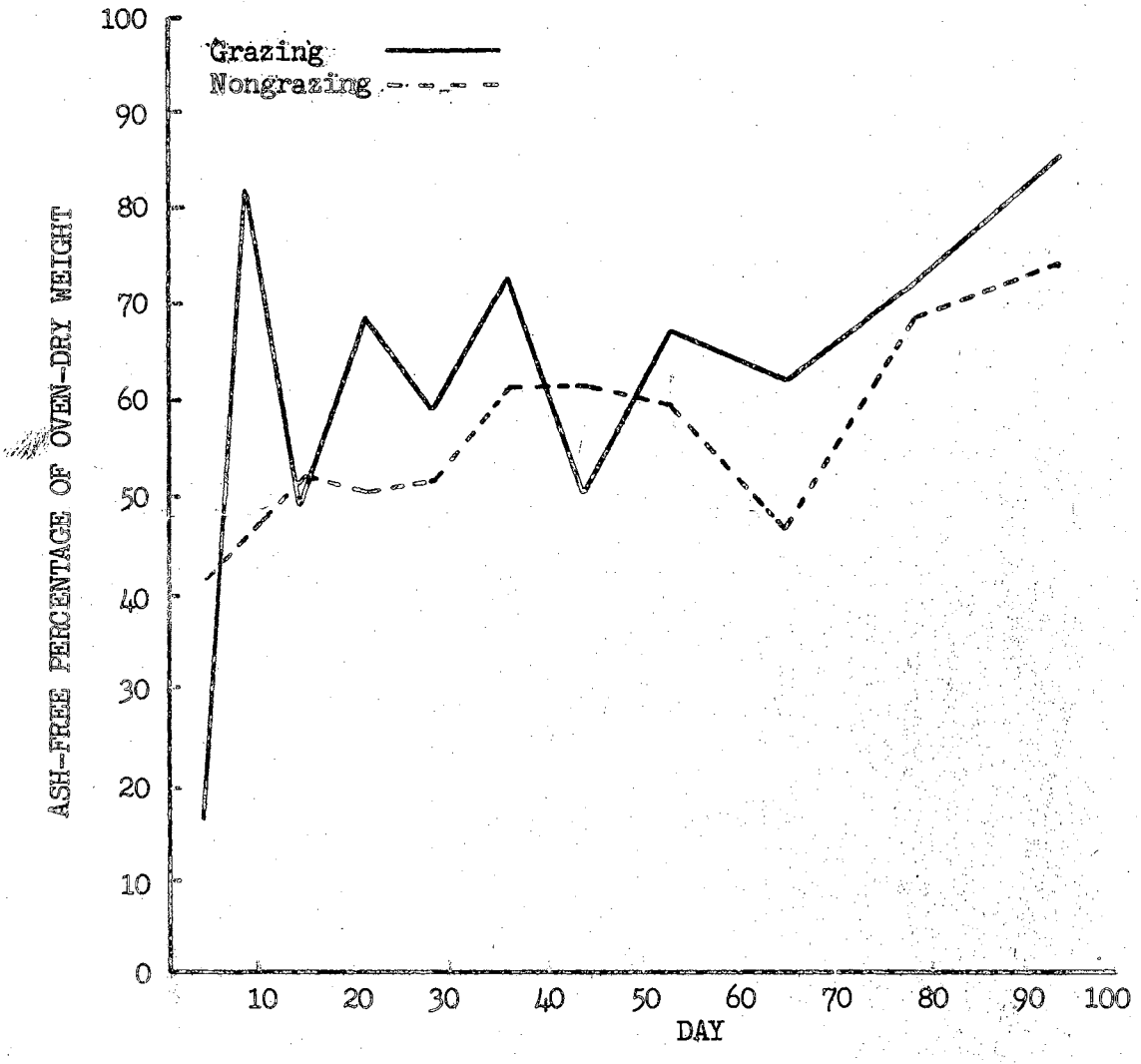

Figure 3. Temporal Variation in Ash-free Percentage of Oven-dry Weight in Laboratory Streams.

TABLE IV

MEAN ASH-FREE PERCENTAGES OF OVEN-DRY WEIGHT
REPORTED FROM LABORATORY STREAM STUDIES

Dominant Algal Type	Ash-Free Weight (%)	Reference
none (Tg)	62.6	Present Study
none (Tng)	58.5	"
greens	43.0	McIntire et al. (1964)
diatoms	36.0	"
not reported	50.0	McIntire (1966)
greens	56.0	McIntire (1968)
diatoms and blue-greens	53.0	"
"	44.0	"
"	42.0	"

Tg = grazing; Tng = no grazing

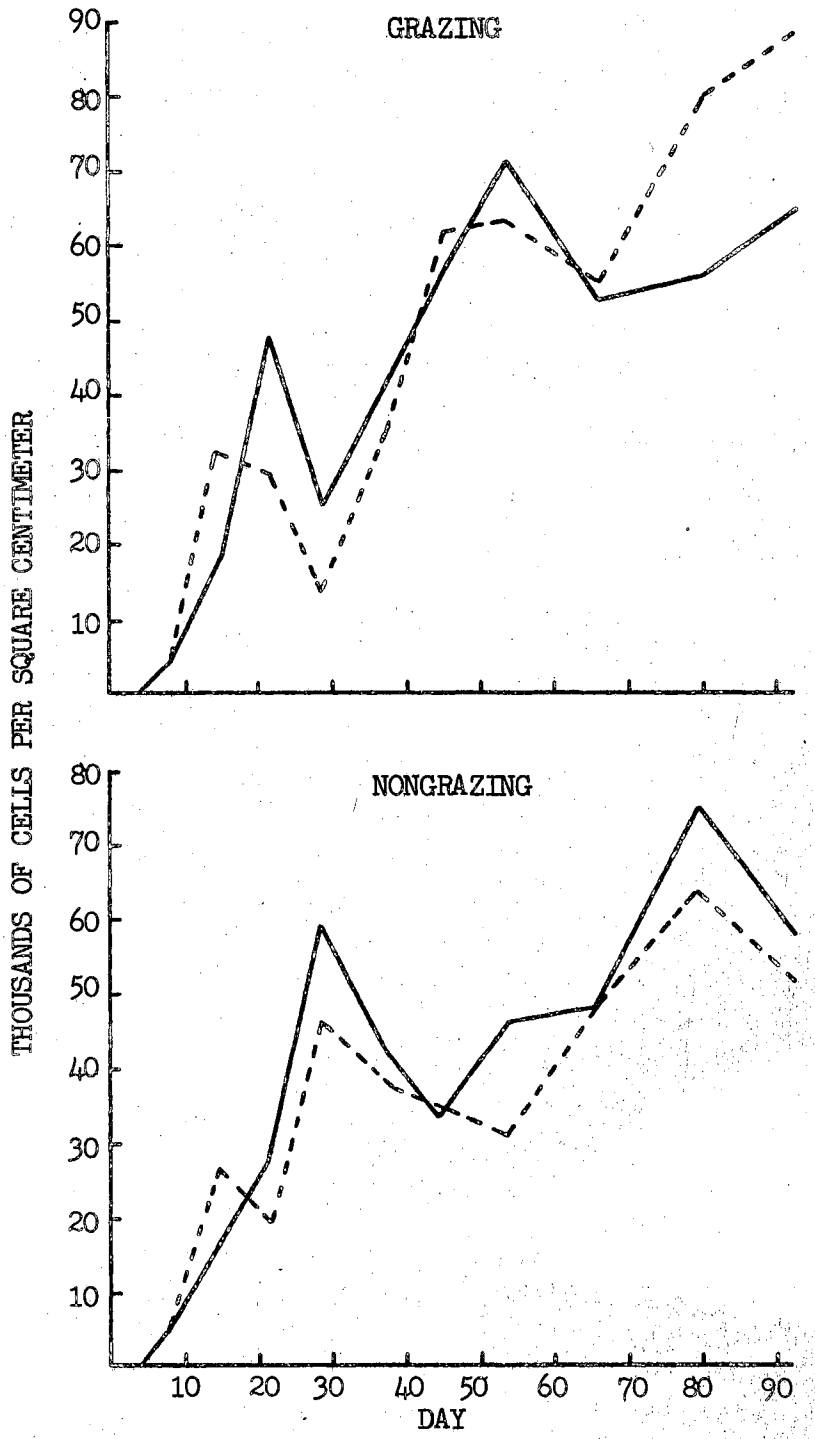

Figure 4. Temporal Variation in Abundance of Greens and Blue-greens Under Grazing and Nongrazing Conditions.
Greens ——————
Blue-greens - - - -

Kevern et al. (1966) studied the accumulation of biomass on plexiglass plates and recognized two linear components in the periphyton growth curve, a colonization and lag phase and an acceleration phase. They considered the instantaneous growth rate, the slope of the regression during the acceleration phase, to be a satisfactory estimate of periphyton production. They found agreement between estimates of daily net production as estimated by instantaneous growth rate and by diurnal oxygen curves. Two linear components were not recognized in the present study (Fig. 2). Due to the high temperature and fertilization in the streams, the colonization and lag phase ended before the first samples were taken and therefore was not recognized. Kevern et al. (1966) stated that an asymptotic phase of growth, characterized by fluctuations in standing crop due primarily to sloughing, follows the acceleration phase. Since sloughing was not observed in the present study, it was assumed that the asymptotic phase was not reached. Only the acceleration phase, therefore, was recognized and the instantaneous rate of accumulation was determined from the entire growth curve. The growth rates in Tg were 0.769 g/m^2 per day for oven-dry weight and 0.583 g/m^2 per day for ash-free weight. In Tng the rates were 0.603 g/m^2 per day for oven-dry weight and 0.512 g/m^2 per day for ash-free weight. These results are compared to those of other investigators in Table V.

Assumption that the instantaneous growth rate of periphyton is an estimate of its production requires two conditions: (1) accumulation of periphyton is large relative to accumulation of other materials, and (2) a one-one relationship exists between periphyton accumulation and production. The laboratory stream enclosure precluded

TABLE V

INSTANTANEOUS RATES OF ACCUMULATION OF OVEN-DRY WEIGHT AND ASH-FREE WEIGHT IN LABORATORY STUDIES

Microcosm Type	Treatment	Oven-dry Weight g/m^2 per day	Ash-free Weight g/m^2 per day	Reference
stream	grazing	0.769	0.583	Present study
"	nongrazing	0.603	0.512	"
battery-jar	low nutrient level	0.140		Wilhm and Long (1969)
"	med. nutrient level	0.400		"
"	high nutrient level	0.750		"
stream	none		0.510	Kevern et al. (1966)

allochthonous material from entering the streams. It was assumed, therefore, that the material accumulating on the slides was primarily periphyton. Close agreement between estimates of daily net production of periphyton as estimated by the instantaneous growth rate and by diurnal oxygen curves was found by Kevern et al. (1966) and Wilhm and Long (1969).

Grazing had no effect on net production in the present study as measured by the method of Kevern et al. (1966). In a pilot study, however, in which four levels of grazing were tested, a clearly negative correlation between grazing intensity and periphyton production was observed. The levels were zero, 0.0053, 0.0107, and 0.0160 snails/cm^2, and the respective instantaneous growth rates were 0.813, 0.247, 0.150, and 0.100 g/m^2 per day. The pilot study differed from the present study by having the water constantly circulate among all four treatments, so that any effects of the snails on the water chemistry was felt in all treatments and the only difference among treatments was the number of snails present. In the present study Tg and Tng were completely separated and the increased availability of nutrients probably caused by the grazers (Macfadyen, 1961; Brock, 1967) was present only in Tg. The effects of grazing on periphyton standing crop and, therefore, production were compounded with the effects of the increased nutrient supply.

Chlorophyll a and Pigment Diversity

Chlorophyll a increased abruptly in Tg through day 53 except for a slight reduction between days 4 and 21 (Fig. 5). In Tng chlorophyll a increased sharply through day 14, increased slightly through day 79,

and increased abruptly between days 79 and 92. The maxima were 0.13 g/m^2 in Tg on day 65 and 0.08 g/m^2 in Tng on day 92. Both values correspond to maxima reported in other stream microcosms. McIntire et al. (1964) found maxima of 0.14 and 0.07 g/m^2 and Odum and Hoskin (1957) reported maximum values of 0.10 and 0.03 g/m^2. The AOV for chlorophyll a concentration revealed that Tg and Tng were significantly different from each other on day 36 and on all subsequent dates (Table II). Positive correlation between chlorophyll a concentration and number of planktonic grazers was found by Spangler (1969).

Chlorophyll a concentration was highly correlated with ash-free weight and oven-dry weight in both Tg and Tng. Correlation coefficients (r) in Tg were 0.85 for ash-free weight and 0.86 for oven-dry weight. In Tng r was 0.88 for ash-free weight and 0.86 for oven-dry weight. Wilhm and Long (1969) obtained correlation coefficients of 0.88, 0.91, and 0.93 between chlorophyll concentration and oven-dry weight in communities subjected to three nutrient levels.

Relationships between chlorophyll a concentration and ash-free weight were calculated by dividing ash-free weight by chlorophyll a concentration. The ratios obtained were 0.47 mg ash-free weight per µg chlorophyll a in Tg and 0.72 mg ash-free weight per µg chlorophyll a in in Tng. These values were not significantly different (Table III). The results are somewhat higher than those calculated from McIntire (1968): 0.22, 0.27, and 0.32 and McIntire (1966): 0.20. Such discrepencies among similar studies emphasize the inconsistent relationship between chlorophyll a concentration and standing crop. The daily percentage of chlorophyll a in ash-free weight ranged from 0.085% to

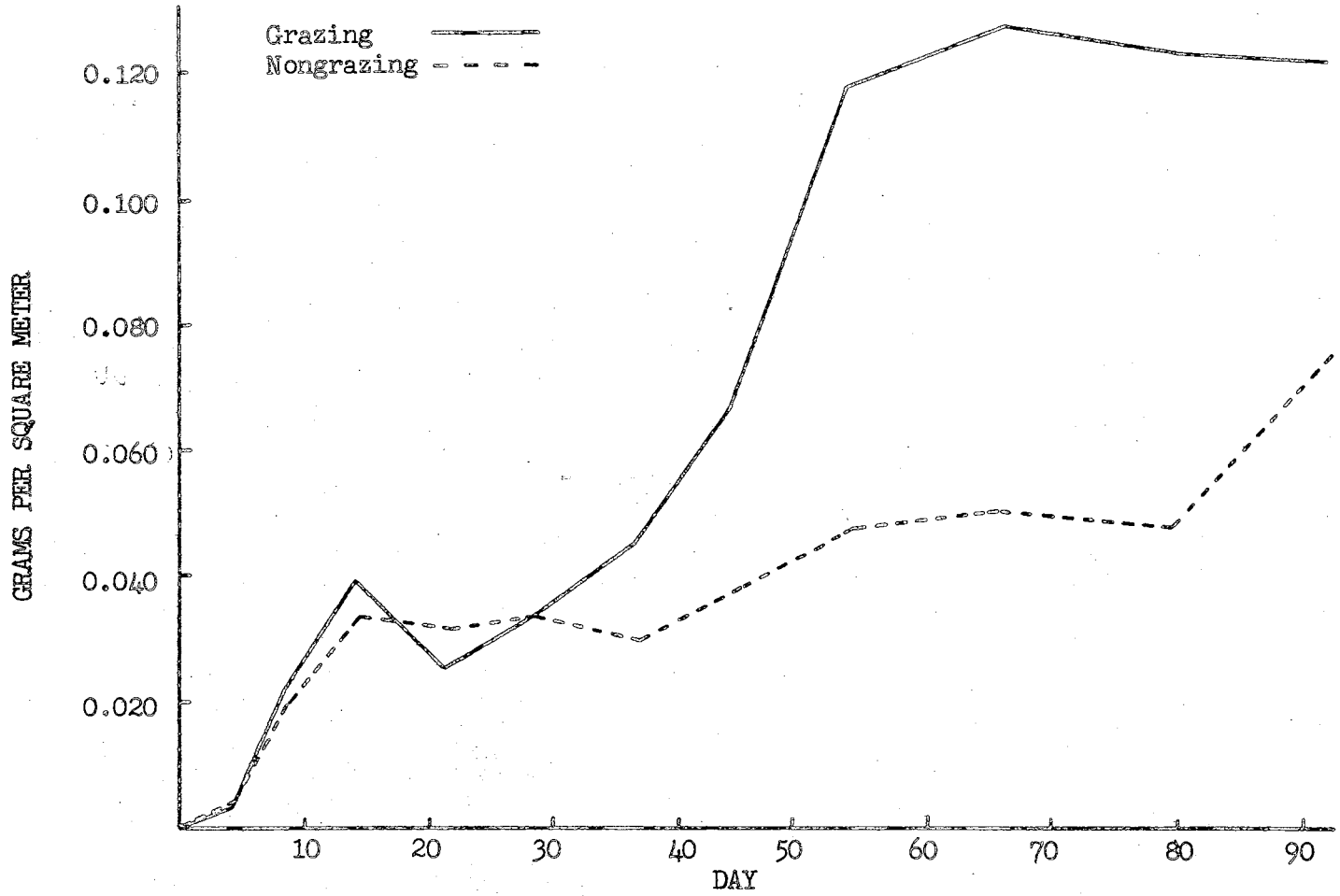

Figure 5. Temporal Variation in Chlorophyll a Concentration in Laboratory Streams.

1.080% in Tg and from 0.080% to 0.910% in Tng. These values correspond to a range of from 0.4% to 2.0% obtained by McIntire and Phinney (1965).

Relationships between chlorophyll a and oven-dry weight were also calculated. The ratios obtained were 0.77 mg oven-dry weight per μg chlorophyll a in Tg and 1.23 mg oven-dry weight per μg chlorophyll a in Tng. The significant difference between these values (Table III) is due to the significantly higher chlorophyll a content in Tg. These results compare to ratios of 0.65, 0.56, and 0.49 calculated from McIntire (1968) and 0.38 calculated from McIntire (1966).

Instantaneous rates of chlorophyll a accumulation were calculated following the method of Kevern et al. (1966) for dry weight accumulation. Use of chlorophyll instead of oven-dry weight eliminates inclusion of consumer biomass. The rates were 0.0015 g/m^2 per day in Tg and 0.0006 g/m^2 per day in Tng. Similar rates of 0.00046, 0.00213, and 0.00414 g/m^2 per day were reported in microcosms subjected to low, medium, and high nutrient levels, respectively (Wilhm and Long, 1969).

Pigment diversity or the ratio of optical density readings of 90% acetone extracts at 430 mμ and 665 mμ (D_{430}/D_{665}) has been related to maturity and species composition in algal communities (Margalef, 1963). Since yellow pigments absorb heavily in the 430 mμ region and green pigments in the 665 mμ region, the ratio is essentially a "yellow/green" index. In the present study, pigment diversity in Tg increased from a minimum of 2.1 on day 4 to a maximum of 3.8 on day 36 and then leveled off around 2.3 (Fig. 6). Similar trends were reported by Cooke (1967) and Wilhm and Long (1969) in microcosms. In Tng pigment diversity increased from a minimum of 1.9

on day 4 to a maximum of 3.8 on day 28 and then fluctuated around 3.3. Until day 79 pigment diversity in Tg and Tng were not significantly different. On day 79 the index was significantly higher in Tng (Table II).

Kingsbury (1956) and Odum and Hoskin (1957) reported that aging and cessation of growth in a culture was accompanied by a change in overall pigment from green to yellow, causing an increase in pigment diversity over time. Margalef (1963) stated that young, growing populations are characterized by low pigment diversity and old populations normally have higher indices.

Fogg (1965) stated that deficiency of nutrients may be one of the most important factors causing cessation of growth in algal populations. The importance of animal grazers in promoting nutrient cycling was emphasized by Macfadyen (1961) and Brock (1967). Brock stated that organic carbon which enters bacteria is locked in them and is released only if animal grazers are available. The snails, by recycling nutrients, inhibited cessation of growth, increased chlorophyll a concentration, and lowered pigment diversity. Action of the grazers caused the community to maintain a relatively low level of maturity. Dickman (1968) reported a similar effect of grazing by tadpoles in a shallow pond.

Species Diversity

Many diversity indices have been proposed to describe community structure. A comparison of six indices applied to thirteen different habitats (Wilhm, 1969) revealed the superiority of Patten's (1962)

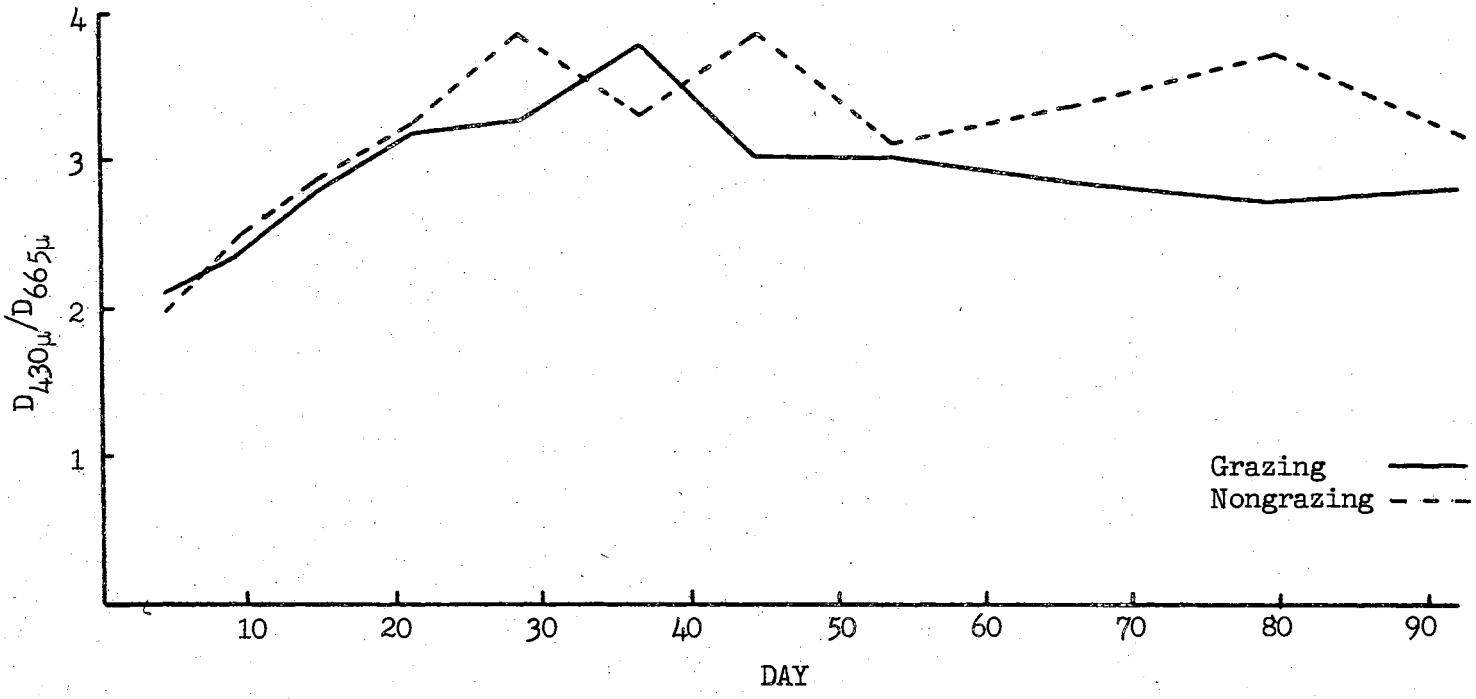

Figure 6. Temporal Variation in Pigment Diversity in Laboratory Streams.

diversity index,

$$\bar{d} = -\sum_{i}^{s} (n_i/n)\log_2(n_i/n).$$

Wilhm stated that as sample size increases, values of $\bar{d}$ increase rapidly at first and then level off. He found that $\bar{d}$ had the lowest coefficient of variation in the asymptotic region of the diversity curve and had the highest correlation with number of species. He emphasized that $\bar{d}$ expressed the relative importance of the various species and was not just a relationship between number of species and individuals.

A general increase in species diversity ($\bar{d}$) over time was observed under both treatments (Fig. 7). In Tg diversity increased from a minimum of 1.04 on day 4 to a maximum of 1.41 on day 92. Diversity in Tng increased from a minimum of 1.03 on day 4 to a peak of 1.48 on day 44 and then decreased slightly to 1.32 on day 92. Margalef (1968) stated that species diversity usually increases as succession proceeds. The AOV for $\bar{d}$ revealed no significant differences between Tg and Tng throughout the study (Table II). Dickman (1968) found that tadpole grazing reduced the diversity of periphyton and thus caused the community to approach a much lower level of maturity. Significant effects of terrestrial grazers on species composition were reported by Tomanek and Albertson (1953) and Hazell (1967), but diversity indices were not calculated.

Margalef (1968) stated that during community succession positive correlation exists between species diversity and pigment diversity. This trend was not observed in Tg. Correlation coefficients (r) between species diversity and pigment diversity were 0.17 in Tg and 0.54 in Tng.

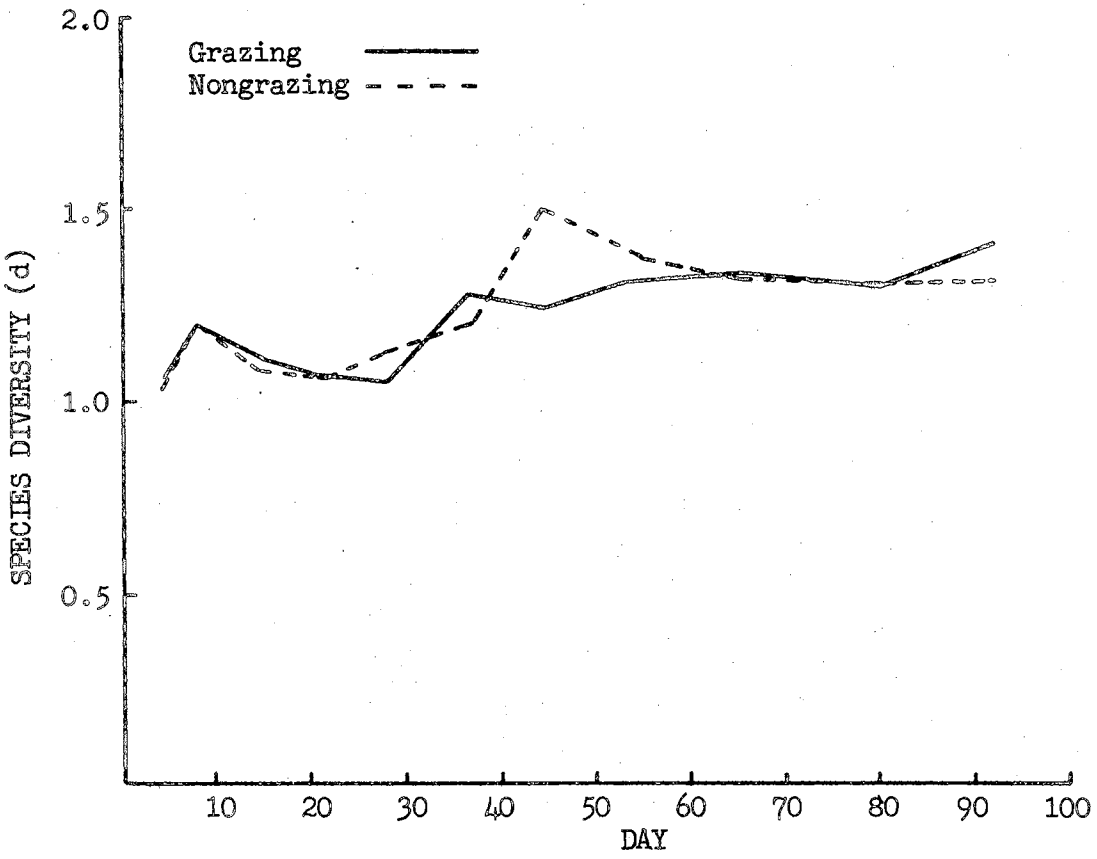

Figure 7. Temporal Variation in Species Diversity in Laboratory Streams.

CHAPTER IV

SUMMARY

1. The effects of grazing by snails on community structure of periphyton were determined in laboratory streams from 15 March 1969 through 15 June 1969. Oven-dry weight, ash-free weight, chlorophyll a concentration, pigment diversity, and species diversity were measured from periphyton accumulation on glass microscope slides sampled over increasing exposure periods.
2. Oven-dry weight was significantly higher in Tng (treatment with nongrazing) than in Tg (treatment with grazing) on days 28 and 36 but no significant difference was observed on other observation dates. A maximum of 76.8 g/m^2 was reached by both Tg and Tng on day 92. Instantaneous rates of accumulation of oven-dry weight were 0.769 g/m^2 per day in Tg and 0.603 g/m^2 per day in Tng.
3. Ash-free weight in Tng was significantly greater than in Tg only on day 44. Maxima were 66.1 g/m^2 in Tg and 57.0 g/m^2 in Tng, both on day 92. Instantaneous rates of accumulation of ash-free weight were 0.583 g/m^2 per day in Tg and 0.512 g/m^2 per day in Tng. No significant difference in mean ash-free percentage of oven-dry weight existed between Tg and Tng. The means were 62.17% in Tg and 58.52% in Tng.

4. Chlorophyll a concentration was significantly higher in Tg than in Tng from day 36 through day 92. Maxima of 0.13 g/m^2 in Tg and 0.08 g/m^2 in Tng were observed. Instantaneous rates of accumulation of chlorophyll a were 0.0015 g/m^2 per day in Tg and 0.0006 g/m^2 per day in Tng.
5. Correlation coefficients between chlorophyll a concentration and oven-dry weight were 0.86 in Tg and 0.86 in Tng. Correlation coefficients between chlorophyll a concentration and ash-free weight were 0.85 in Tg and 0.88 in Tng. The ratios of chlorophyll a to standing crop were 0.77 mg oven-dry weight per μg chlorophyll a in Tg and 1.23 oven-dry weight per μg chlorophyll a in Tng and 0.47 mg ash-free weight per μg chlorophyll a in Tg and 0.72 mg ash-free weight per μg chlorophyll a in Tng.
6. Pigment diversity was significantly higher in Tng on day 79. In Tg pigment diversity increased initially, decreased slightly, and leveled off. Minimum and maximum values were 2.1 and 3.8 in Tg and 1.9 and 3.8 in Tng.
7. Species diversity in Tg and Tng were never significantly different. General increase was observed under both treatments. Minimum and maximum values were 1.04 and 1.41 in Tg and 1.03 and 1.48 in Tng.

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