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The Effects of Succession on Niche Breadth and Overlap in a Hot Spring Algal Community

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ABSTRACT.—An experimental approach was used to evaluate the effect of interspecific competition on succession in a hot spring algal community in Yellowstone National Park, Wyoming. The algae in the spring were sampled at ten, 10-m intervals along a thermal gradient from 57.2 C to 45.7 C. Percent frequency of each algal species in each sample was determined using standard microscopic techniques. Following the initial sampling, algae were removed from the hot spring substrate by sweeping. Successional buildup of the algae community was then monitored by sampling at the same 10-m intervals at 1, 3, 5 and 7 wk after the disturbance. Distributions of the 14 major species along the thermal and temporal gradients were analyzed using stepwise multiple regression techniques. The niche breadth of each species and the interspecific overlaps were also analyzed along the temporal gradient. The major algal species were distributed differently with respect to the thermal gradient, and the distributions of the species along the thermal gradient changed significantly from the initial sampling to the 7th wk after removal, After removal, niche breadths and inter- specific overlaps increased until about the 3rd wk. However, from the 3rd wk to the 7th wk, mean niche breadth and overlap decreased to a point similar to those of the predisturbance community. These patterns are consistent with the hypothesis that significant competition for space occurs following the establishment of an algal mat.

INTRODUCTION

Succession is a widely studied concept of ecology, especially in "higher plant" communities (Payette, 1988; White, 1979). In those communities successional changes generally require decades, which has been a disadvantage in studying the full process at a single site (McIntosh, 1980). As a result, much of our knowledge must be inferred from multisite comparisons (McIntosh, 1980) or abstract models (Connell and Slayter, 1977).

A hot spring algal community offers an unusual opportunity to study succession because of the high reproductive rates of the algae. Thus, large quantities of data can be obtained in a relatively short time. The hot spring algal community is also unusual because of the degree of uniformity of biotic and abiotic factors and the lack of grazers that act as predators on some members of the community.

Algal succession in hot springs has been studied previously. A chance discovery, in Yellowstone National Park, of a hot spring algal mat broken up by a hail storm led to the Brock and Brock (1969) study of the recovery rate of one species at three temperatures for 3 wk. Also in Yellowstone National Park, Fraleigh and Wiegert (1975) diverted a stream over a constructed board substrate for 37 days to determine the biomass increase and chlorophyll/carotenoid ratio change, species diversity and percent volumes of three species during successional development at 43 C. Horizontal succession was studied in six thermal springs in Montana in which algae were sampled in the temperature gradient from 52–58 C downstream to about 35 C (Kullberg, 1968, 1971). Although bacteria can live in the temperature range encountered in this study, the blue-green algae (Cyanophyta) are the only algae. Diatoms (Bacilliariophyceae) do not occur in the hot spring at temperatures above 42–45 C, and green algae (Chlorophyta) do not occur at temperatures above 40–42 C (Kullberg, 1968, 1971). Likewise, grazing invertebrates are not found at the temperatures encountered in this stream.

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Since only blue-green algae occurred in the stream we studied, any allelopathic effects of one species on another would be restricted to those between organisms of similar taxa. Whereas one population of plants can produce toxins that can alter the course of succession in communities of significantly different taxa, the similar toxins of the algae in the hot spring will likely have a reduced effect (Rice, 1984). Also, the rapidly flowing water in the hot spring may minimize the build-up of any potential allelopathic toxins.

The fact that the system studied here is controlled, and the study highly repeatable and freer than most from allogenic and autogenic effects, provides us with an unusual opportunity to study the role of environmental exploitation and interspecific competition in structuring a hot spring community. The results obtained in this study should contribute significantly to our understanding of the effects of these factors during succession of algae.

The information presented in this paper is an elaboration of the original study by Kullberg (1982). In that study, changes in relative frequencies and relative volumes along the thermal gradient were reported for the temporal successional stages. In this paper, we analyze the distributions of the algal species as well as changes in niche breadths and interspecific niche overlaps.

METHODS

Based on knowledge gained from previous studies of hot springs, we chose this spring for the temperature range, constant flow, water velocity, dissolved substances, sufficient light, a properly confining channel, and the number of species present (Kullberg, 1968, 1971). Other hot springs were unsatisfactory because they: (1) were intermittent in flow; (2) were too hot from the point of emission from the ground until they flowed into a cold stream; (3) had water flowing slowly in a thin, wide sheet over the sinter which could have allowed the wind and clouds to alter temperature too much; (4) had a very high concentration of dissolved substances; (5) had a pH too high or too low or (6) they were too shaded.

The unnamed spring used in this study is located at the eastern base of Twin Buttes in the Lower Geyser Basin of Yellowstone National Park. This spring flowed into the effluent of another hot spring and then into Fairy Creek. The spring flowed in a channel that varied in width from ca. 0.2–1.0 m, and at a depth of 0.04–0.25 m. The substrate consisted of calcareous sinter. The spring erupted at 80 C, the temperature recorded throughout the summer of the study and during summers of a previous study.

Although the spring erupted at 80 C, and although one species was known to exist from 73.5 C downstream to about 60 C, the first point of sampling was chosen at 57.2 C where four species were known to exist. This temperature was chosen as the first point of sampling because the objective of the study was to observe the interactions among species during the succession process. Ten sampling intervals, 10 m apart, were designated along the stream beginning at 57.2 C and ending downstream at 45.7 C. This temperature range was chosen because no invertebrates or other algal taxa were represented. Thus, effects of grazing and competition from more variant algae on algal succession could be ignored. Beginning at 57.2 C, stakes were driven into the sinter at the stream's edge at 10-m intervals so the same sampling intervals could be used each time.

The algae lived as long streamers trailing in the water, as loose flocculent-like masses growing attached to the shore but suspended in the water, as gelatinous mats, as vertical columns attached to the substrate, etc., and as many combinations of these growth forms. Because the life forms were so different in the continuum, no sampling device could be used to sample these variations. Therefore, several grab samples were arbitrarily chosen at each sampling interval to obtain representative diversity at that point in the stream. Care was always taken to record the temperature.

Following the initial sampling, the stream substrate in the sampling area was swept clean of algae using a broom. Beginning at the lower reaches of the stream, 3–4-m sections of algae were moved back downstream. This was repeated by progressing upstream and again moving 3–4-m sections downstream until reaching the approximate 60 C point in the stream. Then the entire process was repeated several times until all visible algae were removed. The algae were resampled at the swept sites at intervals of 1 wk, 3 wk, 5 wk and 7 wk after removal.

For microscopic examination, an arbitrarily chosen clump of the preserved algae was taken from a vial, teased apart on the microscope slide and squashed with a cover glass. Teasing apart the algal strands on the microscope slide did not homogenize the algal community. However, any potential bias should have been minimized by the large number of samples examined.

In counting, a mechanical stage was used. After the algae in an area of 13 × 39 μm in the microscope field were counted, the stage was moved to another arbitrarily chosen position and counted again. This was repeated until the algae in 50 similar-sized fields were counted. Another slide was prepared of algae from a different arbitrarily selected portion of the same vial, and the process repeated again. A mean of 678.6 algae were counted in 100 microscope fields from each 10-m sampling interval for each of the five sampling periods. Regardless of their life forms or the number of cells, the algae were always counted as individuals. Thus, a one-celled individual received the same numerical value as a 20-celled filament. The volumetric importance of each species was dealt with in the original paper (Kullberg, 1982).

Distributions of the 14 most abundant algae along temporal and thermal gradients were analyzed using stepwise multiple regression techniques (Neter and Wasserman, 1974). The dependent variable in each regression model was the number of individual algae counted for each species at each location during each successional sere. The independent variables of the regression models included both a linear and a quadratic temperature component, four indicator variables representing the five sampling events, and terms representing the interactions between the temperature components and the sampling events.

Indicator variables (Neter and Wasserman, 1974) aided the analysis in the following way. Since indicator variables take on values of only 0 or 1, the inclusion of an indicator variable as a main effect in a regression model yields two regression models with identical slopes but significantly different Y intercepts. For example, if the relationship between the number of individuals of species A, temperature and sere were being studied the indicator variable would be assigned a value of 0 representing the first sampling event and a value of 1 representing the second sampling event. The regression model would be given as follows:

$$Y = b_0 + b_1 T + b_2 S$$

where Y equals the number of algae, T represents the temperature along the thermal gradient and S is the indicator variable representing the first (S = 0) and second sampling events (S = 1). If S = 0, the model becomes:

$$Y = b_0 + b_1 T.$$

On the other hand, if S = 1, the model becomes:

$$Y = (b_0 + b_2) + b_1 T$$

where $(b_0 + b_2)$ represents the new intercept. Since five sampling events were examined, only four indicator variables were required to distinguish between the sampling events. The four indicator variables representing the five sampling events were also used in interaction

terms with both the linear and quadratic temperature variables. In this case the inclusion of the indicator variable in the model modified the slope of the equation. Thus, the indicator variables made it possible to identify significant differences in the distribution of each algal species with respect to temperature and seral stage.

Pairwise Spearman rank correlations were used to analyze the co-occurrences of the 23 algal species during the study. For each of the five sampling events, number of individuals for each algal species along the thermal gradient was correlated with the number of individuals of each other algal species. Thus, each sampling event is represented by a 23 × 23 matrix of correlation coefficients. Since repeated pairwise correlations using the same data can significantly change the probability of committing a type 1 error (Brownlee, 1965), the matrices were summarized in the following way: each significant ($P < 0.05$) correlation was represented by $+1$ or -1 indicating significant positive and negative correlations, respectively. Nonsignificant correlations were represented by 0. The five matrices were then summed to produce a matrix with values ranging from -5 to $+5$. A value of $+5$ indicates that during each sampling event the distributions of the two species indicated were positively related.

Pianka's modification of the MacArthur-Levins (1967) overlap formula (Pianka, 1975) was used to estimate thermal pairwise niche overlaps among the 23 species of algae during each sampling event. Similarly, niche breadth was estimated (MacArthur, 1972) for each species in each seral stage. The distribution of the niche breadth and niche overlap parameters was analyzed using nonparametric schematic plots (Tukey, 1977). These plots indicate the quartiles, means and pseudo-standard deviations for the distribution of values during each successional stage.

RESULTS

The amount of variance explained by each regression model varied from a low of 5.6% for *Phormidium subtruncatum* with only 15 individuals counted to 82% for *Synechococcus lividus* with 15,755 individuals counted (Table 1). The signs of the coefficients for the temperature variable indicate that *Synechococcus lividus*, *Mastigocladus laminosus* and *Phormidium laminosum* were all positively associated with increasing temperature while the remaining species were negatively associated with temperature or showed no relationship with temperature.

The species distribution changed during the study. As shown by the indicator variables for the sampling events, the abundance of many species changed significantly. Relative to the first sampling event, *Synechococcus lividus* and *Phormidium laminosum* were significantly less abundant at the 3- and 7-wk visits. Both *Oscillatoria geminata* v. *tenella* f. *breve* and *O. geminata* v. *tenella* showed significant increases at 7 wk and were higher in the predisturbance community relative to the 1st wk.

Across all sampling sessions, no species pair exhibited both positive and negative correlations. The results of the correlation analysis (Table 2) indicate that *Synechococcus lividus* and *Mastigocladus laminosus* were most often positively associated with one another and negatively associated with virtually all other species. The only other species that were always negatively associated were *Phormidium laminosum* and *Chroococcus minor*. In the regression analysis, *Chroococcus minor* showed no significant temperature or temporal effects. The remaining species showed either no relationship with one another, a value of $+1$, or relationships which varied week by week. The strongest positive relationship occurred between two closely related forms, *Oscillatoria geminata* v. *tenella* and *O. geminata* v. *tenella* f. *minor,* and two unrelated forms, *Phormidium angustissimum* and *O. limosa*. The strongest negative relationships occurred between *Synechococcus lividus* and *P. angustissimum* and between *S.*

lividus and *O. geminata* v. *tenella* f. *minor*. *Synechococcus lividus* showed a positive relationship with temperature while both *P. angustissimum* and *O. geminata* v. *tenella* f. *minor* were negatively associated with temperature.

Between the 1st and 3rd wk of the study, mean niche overlap increased (Fig. 1). However, from the 3rd wk to the 7th, the distribution of the mean niche overlap values shifted consistently to smaller values and approached those of the predisturbance community. In fact, more than 75% of the mean niche overlap values for the predisturbance stage were smaller than the mean or median of the 3rd-wk values. Thus, as the algal community proceeded through the successional stages, mean niche overlap decreased. As with the niche overlap values described above, mean niche breadths during the 1st wk were considerably smaller than during the 3rd wk. Also, from the 3rd wk to the 7th, mean niche breadth values decreased consistently and approached those of the predisturbance community.

<div align="center">DISCUSSION</div>

Because of the rapid growth rates of algae species, it is clear that the sampling done during the 1st wk after removal probably did not reveal a true "pioneer" community. Also, since the removal consisted of simply sweeping the algal mat downstream, a complete removal was probably not effected. Thus, remnants of the predisturbance community probably contributed significantly to the succession. In spite of these problems, the data obtained in this study provide an opportunity to investigate community dynamics under relatively controlled conditions.

The ambient temperatures present in the sampled hot spring permitted only certain blue-green algae to inhabit the stream. Thus, during the succession process only certain blue-green algae were capable of invading the community after the disturbance. The invading species may have been remnants of the initial predisturbance community, or may represent true "r-strategist" pioneer species rather than "K-strategist" equilibrium species. In this study, the evidence suggests that the initial postdisturbance colonizer was *Synechococcus lividus*, the dominant species in the predisturbance community (Kullberg, 1982). This species comprised 75.8% of the algae in the predisturbance community, and 98.8% of the algae during the 1st wk after disturbance.

A number of hypotheses have been offered to explain patterns observed during succession. Connell and Slayter (1977) used three models to explain the development of communities: the facilitation model, the tolerance model and the inhibition model. In each model the early occupants modify the environment so that it becomes less suitable for subsequent recruitment of other species. Research on long-term succession of an aquatic environment that had progressed to an Arctic peatland was reported by Payette (1988). This succession followed the models of Connell and Slayter whereby the early occupants, identified in the peat, modified the environment to make it less suitable for other early successional species. This autogenic peatland succession was augmented by allogenic succession created by climatic changes in the past 5050 yr.

Evidence for the autogenic hypothesis was obtained by Harder (1917) who noted possible allelopathic influences in old cultures of *Nostoc*. Later, Akehurst (1931) suggested allelopathy as a factor in algal succession. He found that allelopathic substances produced by phytoplankton inhibited some algal species. Although Akehurst failed to demonstrate correlations between population sizes and abiotic factors, his findings have served as a basis for more recent investigations in algal allelopathy (Keating, 1977; Rice, 1984).

In this study it is unlikely that allogenic or noncompetitive allogenic factors had much influence on the dynamics of the algal succession. This is because the water within the stream was flowing at a relatively rapid rate. The rapid flow of water would have diffused

TABLE 1.—Stepwise regression results for the algae species along the thermal and temporal gradient. SL = *Synchococcus lividus*, SC = *S. cedrorum*, ML = *Mastogocladus laminosus*, PA = *Phormidium augustissimum*, PL = *P. laminosum*, PS = *P. subtruncatum*, PM = *P. molle*, OG = *Oscillatoria geminata*, OGT = *O. geminata v. tenella*, OGTM = *O. geminata v. tenella f. minor*, OA = *O. amphibia*, OL = *O. limosa*, OGFB = *O. geminata v. fragilis f. breve*, IP = *Isocystis pallida*. INT = intercept for the regression, TEMP = temperature, TEMP2 = quadratic temperature component, SEREC = predisturbance seral stage, SERE 1 through SERE 7 = the seral stages associated with the 1st through the 7th wk after the removal event, TSC through TS7 = the temperature by seral stage interactions, TSC-2 through TS7-2 = the second order temperature by seral stage interactions. The significance level for inclusion in the model was 0.15. Unless indicated by +, all parameters were significant at the 0.05 level

Parameter	Species						
	SL	SC	ML	PA	PL	PS	PM
INT	-67.710	0.035	-4.934	114.167	-122.583	1.297	0.016
TEMP	2.703		0.149	-4.055	5.347	-0.024+	
TEMP2	-0.025			0.036	-0.056		
SEREC	-5.393				-11.001		
SERE3	-0.370		-153.790+		-6.967		
SERE5			-3.567+				2.593
SERE7		0.254+					
TSC	0.099						
TS3			6.285				
TS5							-0.048+
TS7							
TSC-2		0.0002		0.0003	0.004		
TS3-2			-0.063		0.002		
TS5-2			0.002		-0.0003		
TS7-2	-0.0001+		0.001		-0.001		
R^2	0.820	0.182	0.620	0.671	0.797	0.056	0.122
n	15,755	22	5194	2950	8100	15	12

TABLE 1—Continued

Parameter	Species						
	OG	OGT	OGTM	OA	OL	OGFB	IP
INT	4.131	12.072	108.163	0.045	92.106	0.056	4.902
TEMP	−0.075	−0.223	−3.923		−3.461		−0.894
TEMP2			0.036		0.032		
SEREC		0.747				119.362	0.364+
SERE3	0.374+						
SERE5							
SERE7		1.046		−54.939+		232.854	8.296
TSC						−4.571	
TS3							
TS5							
TS7				2.317+		−8.866	−0.147
TSC-2						0.044	
TS3-2							
TS5-2							
TS7-2				−0.024+		0.084	
R^2	0.197	0.646	0.708	0.390	0.465	0.752	0.525
n	69	376	578	43	181	187	123

TABLE 2.—The sum of the number of significant (P < 0.05) positive and negative correlations between the various species of algae throughout the five successional stages. The species are identified as follows: 1 = *Synechococcus lividus*, 2 = *S. cedrorum*, 3 = *Mastigocladus laminosus*, 4 = *Phormidium angustissimum*, 5 = *P. laminosum*, 6 = *Pseudanabaena oblongata*, 7 = *Phormidium molle*, 8 = *Spirulina subtillissima*, 9 = *Oscillatoria geminata*, 10 = *O. geminata* v. *tenella*, 11 = *O. geminata* vs. *tenella* f. *minor*, 12 = *O. amphibia*, 13 = *O. limosa*, 14 = *O. geminata* v. *fragilis* f. *breve*, 15 = *Synechococcus miniscula*, 16 = *S. salina*, 17 = *Chroococcus minutus*, 18 = *C. minor*, 19 = *Isocystis pallida*, 20 = *Xenococcus minimus*, 21 = *Calothrix thermalis*, 22 = *Spirulina subtillissma* v. *thermalis* and 23 = *Phormidium subtruncatum*

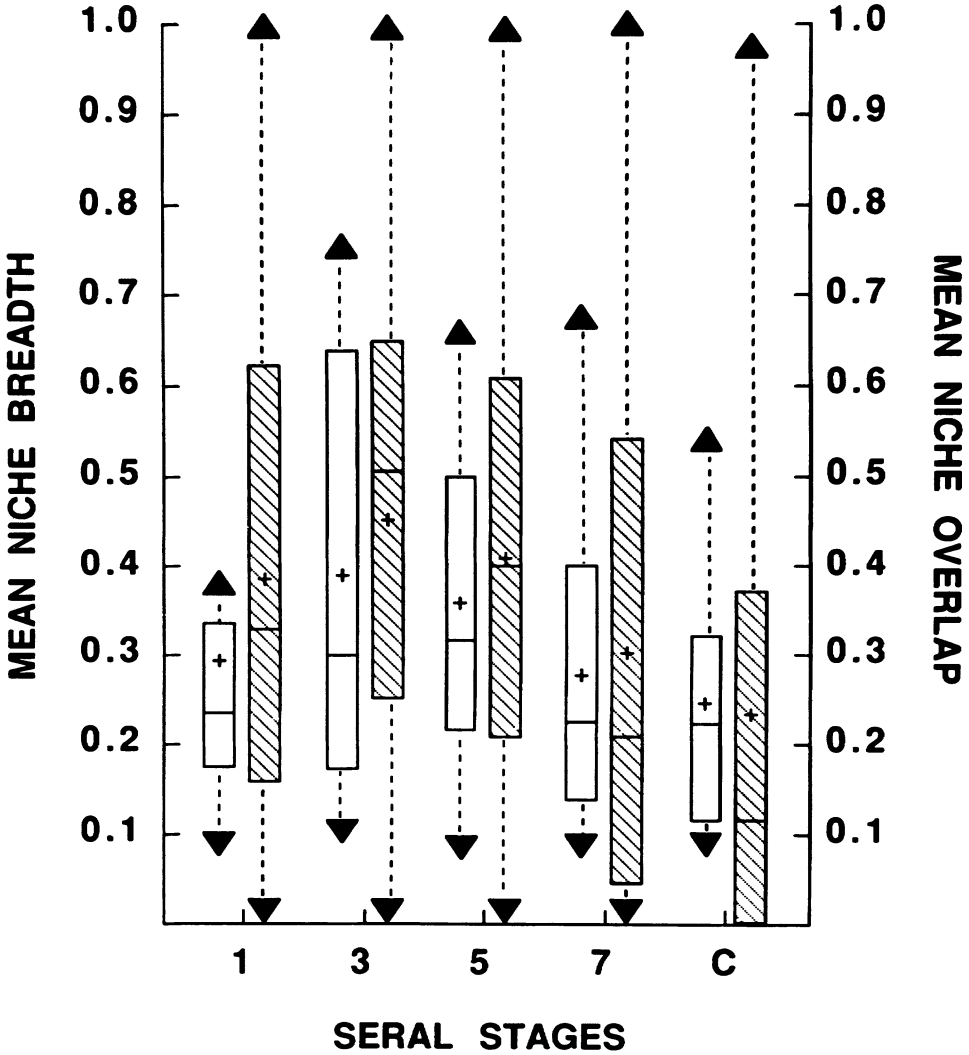| Species	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	0	3	-4	-1	-1	0	0	-2	-3	-4	0	-3	-2	0	0	0	-3	0	0	0	0	-1
2		0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
3			-2	-2	0	0	0	-2	-3	-3	0	-2	-1	0	0	0	-1	-1	0	0	0	-1
4				0	0	0	0	2	3	3	0	4	1	0	0	0	3	2	0	0	0	1
5					0	0	0	0	2	1	0	0	0	0	0	0	-1	1	1	0	0	0
6						0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0
7							0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8								0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9									1	2	0	0	0	0	0	0	2	2	0	0	1	0
10										4	0	0	0	0	0	1	0	3	3	1	0	0
11											0	3	1	0	0	0	1	2	0	0	0	0
12												0	0	0	1	1	2	0	0	0	0	0
13													3	0	1	0	2	0	0	0	0	1
14														1	1	0	0	0	0	1	0	1
15															0	1	1	0	0	0	0	0
16																0	1	0	0	0	1	0
17																	0	0	0	0	0	0
18																		0	1	0	0	0
19																			0	0	0	0
20																				0	0	0
21																					1	0
22																						0

FIG. 1.—Nonparametric schematic plots for the mean niche breadth values (open boxes) and mean niche overlap values (cross-hatched boxes). The extremes of each distribution are indicated by the dashed lines. Within each box, the upper horizontal line indicates the upper quartile, the middle horizontal line the median, and the lower horizontal line indicates the lower quartile. The plus sign in each box indicates the mean

the accumulation of any metabolic wastes. Even with the formation of an algal mat up to 1 cm thick, the diffusion of waste products would have been rapid, thus minimizing any potential allelopathic effects. Also, we believe the constant flow of water would minimize variations in nutrient supply and temperature. Data presented by Kullberg (1982) indicate the absence of a nutrient gradient along the entire stream. In addition, tests for nutrients performed in 1974 and 1978 found no significant differences in nutrient concentrations between the upper and lower reaches of the stream.

In other habitats algal succession can be affected by grazing. Brine flies may reduce algal mats in hot spring communities within the temperature range of 30–45 C (Brock et al., 1969; Wiegert and Mitchell, 1973; Wickstrom and Wiegert, 1980) but their upper temperature limit is 45 C, which falls below the minimum temperature studied here.

The constant influx of nutrients, the absence of grazers and the probable weakness of allelopathic effects leaves mainly the competition hypothesis to explain the patterns observed in this community. The probable limiting resource for these photosynthetic species is space (Tilman, 1982), where the quality of the space is determined primarily by temperature.

Strong positive or negative relationships exist only between a few of the many algae species (Table 2). The negative correlations, especially those with values of −4, may indicate either strong competitive interactions or dissimilar thermal optima, while the positive correlations may indicate similar thermal optima.

The changes observed in the distributions of mean niche breadths and mean niche overlaps are consistent with the predictions of the competition hypothesis. Between removal and the 3rd wk postremoval, both mean niche breadth and mean niche overlap increased, perhaps in response to the suddenly depleted populations and the subsequent ecological release. However, from the 3rd wk postremoval to the 7th wk postremoval, mean niche overlap and mean niche breadth decreased. We would expect that as the populations of the algae species increased and the available space decreased, interspecific competition would become more severe. Severe competition for a limiting resource can be accommodated by a reduction in niche breadth and a reduction in interspecific niche overlap (MacArthur, 1972). Similarly, the increased intensity of interspecific competition should result in more thermally restricted distributions for the algal species. This was apparently the case in this study as evidenced by the regression analyses. The distributions of the major algae species changed significantly with respect to temperature from the removal event to the final sampling. This trend is consistent with the idea that the intensity of interspecific competition increased with time, and that the algal species responded by limiting their respective distributions to temperatures with optimal growth and reduced competition.

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