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Lorin E. Squires
Brigham Young University

Mark C. Whiting
Oregon State University, Corvallis, Oregon

Jack D. Brotherson
Brigham Young University

Jack D. Rushforth
Brigham Young University

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COMPETITIVE DISPLACEMENT AS A FACTOR INFLUENCING PHYTOPLANKTON DISTRIBUTION IN UTAH LAKE, UTAH

Lorin E. Squires¹, Mark C. Whiting², Jack D. Brotherson¹, and Samuel R. Rushforth¹

ABSTRACT.—Phytoplankton studies during the summer of 1974 in Utah Lake, Utah, demonstrated the development of disjunct distributions of *Aphanizomenon flos-aquae* and *Ceratium hirundinella*. Differential response to environmental factors and competitive displacement are proposed as probable explanations for this phenomenon.

Theoretically, competitive displacement among organisms has occurred and is still occurring in all ecosystems. In terrestrial systems and particularly in plant communities, this process is often difficult to observe directly because these communities change so slowly through time. In most such communities, competition between organisms has undoubtedly contributed at some time to differential resource utilization and thus to separate niche development. Because environmental partitioning leads to a decrease in competition, the occurrence of competitive displacement has subsequently declined. However, in ecosystems where generation times are short, and successional sequences occur seasonally, community interactions are rapid and new settings are frequently provided for competitive confrontation. Phytoplankton systems exemplify such conditions and thus provide a possible arena for competitive displacement to be observed.

Competitive displacement has been of interest since the time of Darwin (1859), but has received greater attention and investigation in the last 30 to 40 years (Hardin 1960) following Gause's experimental evidence that no two species can exist indefinitely in the same niche (Gause 1969). Gause claimed that "as a result of competition two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has advantage over its com-

petitor." Additional refinement of this idea was presented by Hardin (1960), who suggested that if two sympatric noninterbreeding populations occupy the same ecological niche, the population with the breeding advantage will eventually displace the other.

The conditions necessary for competitive displacement to occur can be summarized as follows. First, environmental equilibrium must occur. Second, environmental equilibrium must last long enough for exclusion or displacement to occur. Third, in order to compete, species must use some of the same resources. And fourth, species using the same resources must have high enough densities for competition to occur.

Several recent ecological studies have attempted to define specific niche boundaries for sympatric species and demonstrate partitioning of the environment in terms of time, space, or food materials (MacArthur 1958, Jaeger 1971, Schoener 1968, Miracle 1974, Makarewicz and Likens 1975). Such partitioning leads to reduced interspecific competition, thus allowing species to coexist without displacement of one or the other. However, phytoplankton studies have been cited as demonstrating a possible exception to partitioning and niche separation. Hutchinson (1961) termed this phenomenon the "paradox of the plankton" because a high diversity of phytoplankton organisms coexist in an apparently homogenous limnetic environment.

¹Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

²Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331.

A number of theories have been introduced to explain planktonic systems. Hutchinson (1961) submitted that environmental equilibrium is not achieved because of highly fluctuating lentic environments and the short generation time of most plankton organisms. Richerson et al. (1970) postulated a plankton habitat of contemporaneous heterogeneity that is transitory in time. They suggested that certain species would have competitive advantage in each of the various contemporaneous patches in a lake's epilimnion. Petersen (1975) explained planktonic diversity by relating it to differential nutrient uptake. Titman (1976) demonstrated with laboratory experiments that Petersen's theory was plausible for at least the two plankton species *Cyclotella meneghiniana* and *Asterionella formosa*. Levandowsky (1972) presented the various causal factors affecting the plankton in terms of linking, separating, rarifying, reinforcing, and variational factors and suggested that biologists should widen their view in searching for explanations for plankton dynamics and diversity.

This paper reports the occurrence of two phytoplankters, *Ceratium hirundinella* and *Aphanizomenon flos-aquae*, which coexisted temporally in Utah Lake during the late summer of 1974 but became spatially disjunct. Competitive displacement is proposed as one factor causing the segregation of these species.

UTAH LAKE PHYTOPLANKTON

During the summer months of 1974, studies of the phytoplankton communities of Utah Lake, Utah (Whiting et al. 1978), were performed. We particularly examined seasonal succession and concomitant changes in environmental parameters. We found that the early summer communities were composed of a diverse group of diatoms and green and blue-green algae. During the same period of time, the environment in the lake was more heterogenous than at any other time. As the season progressed, environmental variation and algal diversity both decreased (Fig. 1). By August, algal communities were very homogenous, being composed of *Aphanizomenon flos-aquae* and *Ceratium hirundinella* almost exclusively. At that time,

these two species comprised from 89 to 100 percent of the algal standing crop at our sampling sites.

While making field collections on 15 August 1974, we noticed that the distribution of *Aphanizomenon flos-aquae* and *Ceratium hirundinella* had become disjunct. Calculation of relative densities of the two species and plotting their occurrence against each other confirmed spatial separation between the two (Fig. 2). Many stands were essentially unialgal. To assess any relationship between environmental parameters and distribution of these two species, we subjected the data to discriminant analysis (Klecka 1975). The discriminate function separated the two species completely on the basis of seven environmental variables (pH, phosphate [PO₄], Mg hardness, water temperature, total hardness, dissolved oxygen, and alkalinity). By far the most significant of these was pH. When the pH variable was removed and the stands were reevaluated, 100 percent environmental separation still existed between the two communities. However, upon examining the important discriminators, we became convinced that they were effects of the disjunct species distribution rather than causes. For instance, photosynthesis in aquatic systems often has the effect of increasing pH (Cole 1975). Consequently, the increased standing crop (Fig. 3) and thus elevated net photosynthesis in the *A. flos-aquae* stands would account for the higher pH and temperature levels in these stands. Furthermore, elevated pH and temperature levels are known to enhance precipitation of magnesium carbonates (Stum and Morgan 1970, Harvey 1969), which could account for lower measurable levels of magnesium hardness and total hardness in the same stands.

Correlation analyses (Snedecor and Cochran 1967) failed to indicate differential preferences of the two species for any of the variables identified in the discriminant analysis. The results of these analyses showed that abundance of both *A. flos-aquae* and *C. hirundinella* was positively correlated with the same environmental variables (turbidity, salinity, phosphate, pH and water temperature: $\alpha = .01$). This evidence, coupled with the increased lake homogeneity observed in mid-August (Fig. 1), suggests that the two algal

species may have been occupying the same environmental niche at that time. Thus, conditions were such that competitive exclusion or displacement could operate in the system.

It occurred to us that it might be possible to analyze competitive displacement using the niche overlap methods of Colwell and Futuyama (1971). Thus, we plotted niche breadth through the summer for each species (Fig. 4). The results indicated that *Ceratium* had a greater niche breadth than *Aphanizomenon* in early summer, but that the reverse was true later in the summer. Spatial niche overlap analysis for these two algae was also plotted against time (Fig. 5). Niche

overlap was low in the early summer when standing crop was low enough that the two species rarely occurred together in appreciable numbers. As the summer progressed, spatial niche overlap increased as standing crop increased in a tight linear relationship ($R^2 = .88$). However, between early and middle August, a major reduction in spatial niche overlap occurred so that the last data point (15 August) showed as little overlap as in the earliest summer communities. Colwell and Futuyama (1971) maintained that a high degree of overlap indicates a joint use of resources, whereas low overlap indicates low levels of resource sharing. They also stated

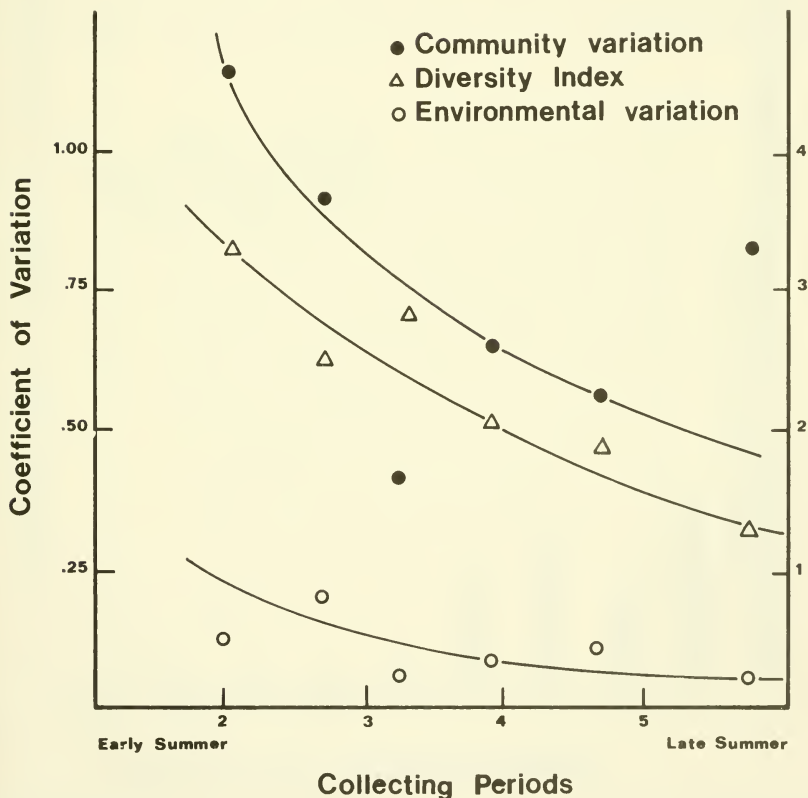


Fig. 1. Environmental and algal community gradients in Utah Lake, Utah, from 6 June to 15 August 1974.

that competitive displacement tends to reduce niche breadth and overlap among competing species. The niche breadth and overlap measurements of *C. hirundinella* and *A. flos-aquae* through summer 1974 in Utah Lake reflected just such conditions. The reduction in niche overlap observed on 15 August occurred concurrently with an exponential increase in the standing crop of *A. flos-aquae* (Fig. 3). These facts, plus the narrowed niche breadths for both *Aphanizomenon* and *Ceratium*, provide strong evidence for competitive displacement.

Two other explanations exist which could account for the disjunct distribution of these organisms that developed in August. The first is seasonal succession and the second is some unmeasured environmental variable creating a heterogenous environment.

Seasonal succession occurs when changes caused by progression of the season create new environmental conditions that promote the development of some species and depress the development of others. While competition is a factor in the interspecific relationship that occurs during seasonal succession, competitive displacement as such is largely due to changes in niche characteristics. Our niche breadth analysis (Fig. 4) shows that *C. hirundinella* reached a maximum breadth in July and thereafter declined, and *A. flos-aquae* reached a maximum breadth somewhat later. Even so, the actual standing crop of *C. hirundinella* increased from July through August, and in none of the samples were dead or dying cells encountered. Therefore, because the population of *Ceratium* showed no signs of decline, we con-

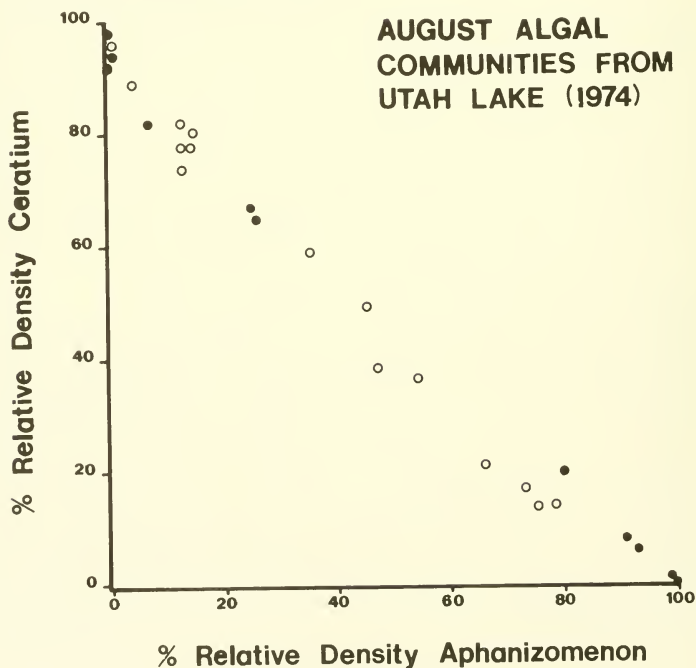


Fig. 2. Percent relative density of *Aphanizomenon flos-aquae* plotted against *Ceratium hirundella* for August 1974 algal communities. Clear circles designate 8 August collections; solid circles designate 15 August collections.

clude that the disjunct distribution was not due to seasonal replacement of *Ceratium* by *Aphanizomenon*.

The homogeneity of the limnetic environment in Utah Lake during late summer has already been discussed. However, the impor-

tance of wind and water currents in creating distributional patterns in the lake were not closely analyzed. The authors have noted for several years that during algal blooms in Utah Lake, local heavy concentrations of algae can develop, often taking the form of

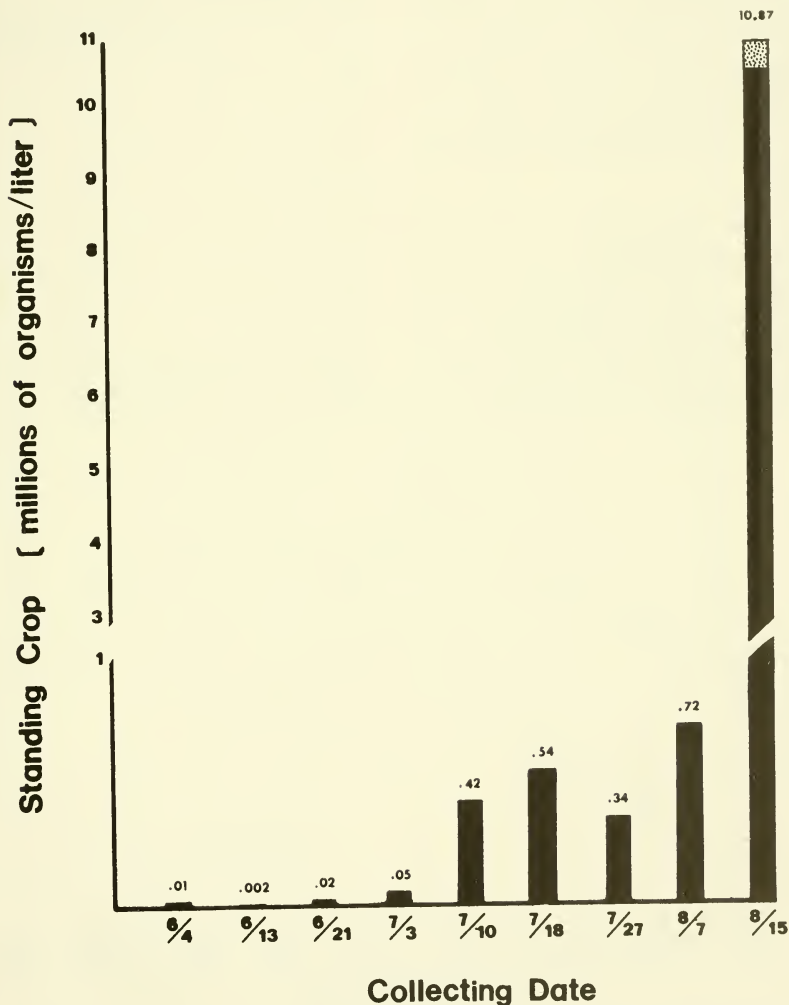


Fig. 3. Mean algal standing crop for collections during the summer of 1974. August 15 sample consisted almost completely of *Aphanizomenon* (solid area) and *Ceratium* (dotted area).

windrows and large amorphous patches. The windrows could possibly be explained by Langmuir circulation currents. The buoyancy of *A. flos-aquae* would cause it to concentrate where converging convection cells cause downwells. The motile *C. hirundinella* may be congregating in the areas of upwelling between the windrows in a manner similar to that reported by George and Edwards (1973) for *Daphnia*. The larger accumulations evident in the lake are more likely due to prevailing winds, which promote horizontal and vertical migrations of algae similar to those reported by Horne and Wrigley (1975) for blue-green algae in Clear Lake, California.

Because *C. hirundinella* is actively motile and *A. flos-aquae* is not, these two algae should respond differently to wind and water currents. Thus, it is possible that the disjunct distribution of these two organisms in Utah Lake is related to a physical parameter.

Because both *Ceratium* and *Aphanizomenon* are apparently well adapted to the environment existing in Utah Lake in August,

competition for the resources of space, light, and nutrients could be expected to occur whenever concentrations of organisms become sufficient to deplete these resources. The rapid increase in *A. flos-aquae* standing crop in the second week of August indicated that this alga had greater biotic potential than *C. hirundinella*. *Aphanizomenon* also may have had a competitive advantage because of its nitrogen-fixing capacity. Thus, when a confrontation occurs between these two organisms, *Aphanizomenon* would be expected to out-compete *Ceratium*.

We conclude that wind and water currents affecting Utah Lake were probable factors in the disjunct distribution of *Aphanizomenon flos-aquae* and *Ceratium hirundinella*. Furthermore, the segregation of these two species may have been augmented by competitive displacement of *Ceratium* by *Aphanizomenon*. The concentration of *A. flos-aquae* into local windrows and amorphous patches, coupled with its removal from other areas, allowed *C. hirundinella* to persist in the lake. The reproductive advan-

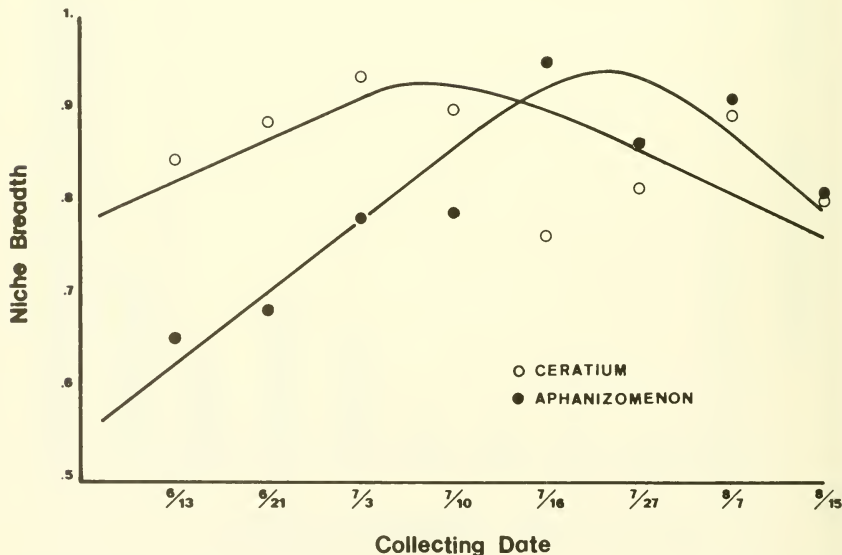


Fig. 4. Niche breadth indices for *Ceratium hirundinella* and *Aphanizomenon flos-aquae* during the summer of 1974.

tage of *A. flos-aquae* may well have resulted in the complete elimination of *C. hirundinella* had it not been for factors preventing its complete occupation of the water column. In the absence of the patchy distribution patterns of the two species, the shift in dominance from *Ceratium* to *Aphanizomenon* would have been attributed inaccurately to seasonal succession.

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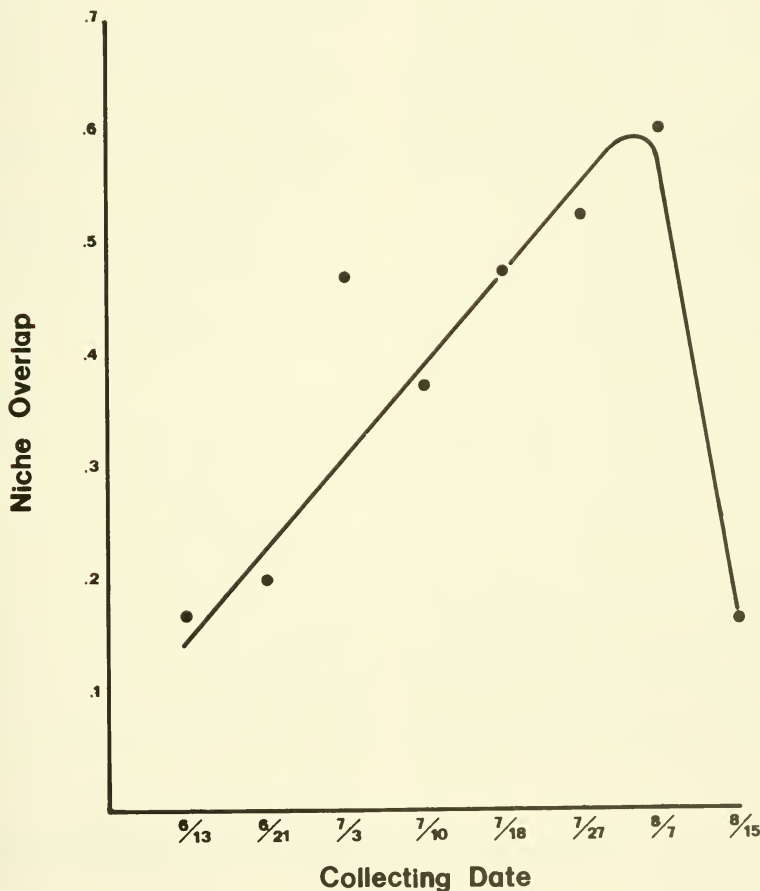


Fig. 5. Niche overlap indices for *Ceratium hirundinella* and *Aphanizomenon flos-aquae* during the summer of 1974.

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