Reprinted from *Journal of The Weed Science Society of America*, Volume 21, Number 1, January 1973

Biotic Interactions between Different Species of Algae[1]

CLAUDE E. BOYD[2]

Abstract. Species of green algae seldom grew as well in two-species cultures with other green algae, or with blue-green algae, as when cultured alone. Several species of algae apparently excreted one or more substances into the medium which inhibited the growth of the second species. Inhibition of growth of green algae was particularly great in two-species cultures with the blue-green algae, *Oscillatoria rubescens* Decandolle, *Anabaena flos-aquae* (Lyngbye) Breb., *Microcystis aeruginosa* Kutz., and *Coccochloris peniocystis* (Kutz.) Dr. and Daily. Green algae also failed to grow at normal rates in media prepared from filtrates of water from ponds which contained blooms of blue-green algae. Inhibitory substances are apparently an important factor in the development and persistence of relatively unialgal blooms of various species.

INTRODUCTION

THE species composition of phytoplankton communities in natural and impounded waters is often in a state of change. Seasonal changes and long-term changes in species composition have traditionally been attributed to the supply of available nutrients. This thesis was challenged on the grounds that sequences of species also occur in systems which continuously have an excess of nutrients (6). Fitzgerald (6) suggested that extracellular substances produced by one species of algae influenced the growth of other species. There is some evidence to support this hypothesis. Filtered water from a pond that contained a bloom of blue-green algae was toxic to *Haematococcus pluvialis* (Girod.) Rostof (16). A number of algae grew poorly in media prepared from filtered water which had contained a large population of *Aphanizomenon gracile* Lemm. (20). *Microcystis aeruginosa* Kutz. inhibited the growth of several species in laboratory cultures and apparently reduced the production of other algae in three Missouri ponds (21). Several algae failed to grow as well in two-species cultures as when cultured alone (10, 14, 15, 17, 21). Failure of certain algae to grow in natural waters was attributed to growth inhibitors of algal origin (11, 12, 16, 18, 20, 21).

In a review of the literature on factors which regulate the growth of algae in laboratory cultures and in nature, Fogg (7) found insufficient data upon which to formulate a conclusion regarding the general importance of biotic interactions between species of algae. Dense blooms of algae cause many water quality problems, and information on factors responsible for the development and persistence of algae blooms is of practical value to water resource managers.

The present research was initiated to evaluate further the biotic relationships between various species of algae. Particular attention was given to the influence of blue-green algae on the growth of green algae. Data were also obtained on the community structure of phytoplankton blooms in ponds.

MATERIALS AND METHODS

Algae used in these experiments were obtained from culture collections at Indiana University and the University of Wisconsin (Table 1). These cultures contained only one species of algae and only three cultures, *Nostoc muscorum* Kutz., *Microcystis aeruginosa* and *Oscillatoria rubescens* Decandolle, were contaminated with bacteria.

Stock liquid cultures of green algae were maintained in a modified Beyerinck's solution (3), while stock cultures of blue-green algae were grown in a modification of Zehnder and Gorham's No. 11 medium (22). Nutrient concentrations in the two media are listed in Table 2. These cultures were transferred to new media at 7 to 14-day intervals to insure that they contained young, rapidly dividing cells which would grow quickly when placed in experimental media.

[1]Received for publication April 28, 1972. Investigation supported by Project AID/csd 2780 to the International Center for Aquaculture, Auburn University.

[2]Assoc. Prof., Dep. of Fisheries and Allied Aquacultures, Agr. Exp. Sta., Auburn Univ., Auburn, Alabama 36830.

Table 1. Stock cultures of algae used in studies of biotic interactions between different species of algae.

Species	Culture collection identification[a]
Green algae	
Ankistrodesmus falcatus (Corda) Ralfs	I.U. - 749
Chlorella pyrenoidosa Chick	I.U. - 26
Coelastrum microporum Naegeli	I.U. - 280
Scenedesmus dimorphus Kutz	I.U. - 746
Cosmarium subtumidum Nordst	I.U. - 297
Chlamydomonas sp	I.U. - 624
Staurastrum sp	I.U. - 173
Blue-green algae	
Anabaena flos-aquae (Lyngbye) Breb	I.U. - 1444
Nostoc muscorum Kutz	I.U. - 1037
Coccochloris peniocystis (Kutz.) Dr. and Daily	I.U. - 1548
Phormidium sp	I.U. - 485
Lyngbya sp	I.U. - 488
Oscillatoria rubescens Decandolle	U.W. - 2000
Microcystis aeruginosa Kutz	U.W. - 1036

[a]Cultures identified by the letters I.U. and U.W. are from algae collections at Indiana Univ. and the Univ. of Wisconsin, respectively.

Table 2. Concentrations of nutrients in media used in studies of biotic interactions between different species of algae.

Reagent	Concentration	
	Modified Beyerinck's solution	Modified Zehnder and Gorham's No. 11 solution
	(mg/L)	(mg/L)
NH_4NO_3	250.00	
$NaNO_3$		496.00
K_2HPO_4	100.00	30.00
$MgSO_4 \cdot 7H_2O$	100.00	75.00
$CaCl_2 \cdot 2H_2O$	50.00	36.00
Na_2CO_3		20.00
$Na_2SiO_3 \cdot 9H_2O$		58.00
EDTA		1.00
Ferric citrate		6.00
Citric acid		6.00
H_3BO_3	2.50	2.50
$MnCl_2 \cdot H_2O$	1.50	1.50
$ZnCl_2$	0.10	0.10
$CuCl_2 \cdot 2H_2O$	0.05	0.05
MoO_3	0.05	0.05

Two-species combinations. The influence of one species upon the growth of a second species was evaluated by the procedure used by Proctor (16, 17) and Vance (21). Two species were grown in combination and individually. Any significant increase or decrease in growth of one species in a two-species combination, as compared to its growth in a single-species culture, was attributed to an influence of the second species. Beyerinck's solution (Table 2) was used as the nutrient solution for the combinations of different species of green algae and in the single species controls. Combinations of green and blue-green algae were cultured in a modified Zehnder and Gorham's No. 11 medium (Table 2). Cultures of individual species of green or blue-green algae which were used as controls for two-membered combinations of green and blue-green algae were also cultivated in the modified Zehnder and Gorham's No. 11 medium. Fifty ml volumes of nutrient solution in 125-ml, cotton stoppered, erlenmeyer flask were inoculated with the desired species. A determination was made for each species of the initial density of individuals which was required to produce moderate growth within 4 days in fresh media. A quantity of the stock liquid culture which contained the calculated number of individuals of a species for moderate growth was inoculated into the fresh experimental media in each instance. After inoculation the initial concentration of each species in a two-species culture was equal to that in the single-membered cultures which served as controls. Three replications were prepared for each control and two-species combination. Aspectic techniques were used throughout. The algae cultures were incubated for 4 days at 26 C under uniform lighting (16 hr in light and 8 hr in darkness) and were swirled twice daily. Combinations of green algae and appropriate controls were placed under 4300 lux illumination. Several species of blue-green algae did not grow well at 4300 lux. Experiments involving combinations of green and blue-green algae were conducted under 1600 lux. Green algae grew well at either light intensity.

After 4 days the number of individuals, single cells, or colonies was determined. Small algae, *Chlorella pyrenoidosa* Chick, *Ankistrodesmus falcatus* (Corda) Ralfs, and *Scenedesmus dimorphus*, Kutz. were enumerated with a Spencer Bright-Line hemacytometer. Other species of green algae were counted in a Sedgwick-Rafter counting cell. Most species of blue-green algae were filamentous and grew in dense clumps. No suitable procedure was found for enumerating these organisms. The quantity of a blue-green alga in a particular treatment was compared visually with the quantity of this alga in the appropriate control. The inability to obtain good quantitative data for blue-green algae was not a serious limitation since the influence of blue-green algae on the growth of green algae was the primary objective of this study.

Original data (individuals per ml) were used to make t-test comparisons of significance between the growth of a species alone and in a particular two-species combination. However, to simplify presentation, the growth of a particular species in unialgal culture was taken as 100% for comparison with growth of this species in any given species combination.

Filtrate experiments. Nine samples of water which contained either dense populations of blue-green algae or moderate densities of green algae and diatoms were obtained from ponds on the Fisheries Research Unit, Auburn University. Each water sample was filtered through a 20-cm column of glass wool to remove the algal community. A test medium and a control medium (modified Beyerinck's solution) were prepared with each filtrate and glass distilled water, respectively. These media were not sterilized, but the flasks were stoppered with cotton to prevent contamination with air-borne algal cells or spores. Two replicates of each media were inoculated with *S. dimorphus, C. pyrenoidosa,* and *Chlamydomonas* sp. Algal cultures were incubated for 4 days at 26 C under 4300 lux on a mechanical shaker set at 60 oscillations per minute.

Observations on algal communities in ponds. The water samples were collected from various ponds on the Fisheries Research Unit during the summer of 1971. Samples were secured with a 90-cm water column sampler (4). Algae were enumerated by the drop-sedimentation technique (1). Species diversity was calculated by the equation:

$$\text{Species diversity} = -\sum_i P_i \log e\, P_i$$

where P_i = the decimal fraction of the proportion of the total individuals which belonged to the ith species (13). A community composed of 99% of one species and 1% of a second species has a diversity of 0.056, while a community composed of 10% each of 10 species has a diversity of 2.300. Chlorophyll concentrations in pond waters were measured by the method of Golterman and Clymo (8).

RESULTS

Data for the growth of four species of green algae in two-species combinations are presented in Table 3. In two

Table 3. Growth of four species of algae in various two-species combinations compared with growth of each species in single-species cultures (controls).

Combination	Relative growth[a]
	(% of control)
Chorella pyrenoidosa	34.2**
Coelastrum microporum	75.5*
C. pyrenoidosa	45.9*
Chlamydomonas sp.	91.7
C. pyrenoidosa	30.2**
Scenedesmus dimorphus	112.7
S. dimorphus	67.7*
C. microporum	36.7**
S. dimorphus	52.1**
Chlamydomonas sp.	84.1
Chlamydomonas sp.	88.6
C. microporum	39.4**

[a]*t—value significant at 0.05 level; **t—value significant at 0.01 level.

of six combinations, neither species grew as well in combination as alone. In the other four combinations, one species grew as well in combination as alone, but the second species was clearly inhibited. *Chlorella pyrenoidosa* was inhibited by each of the other three species, while *Chlamydomonas* sp. inhibited the growth of *Scenesdesmus dimorphus, Coelastrum microporum* Naegeli, and *Chlorella pyrenoidosa.*

Results from two-species cultures of green and blue-green algae are summarized in Table 4. *Nostoc muscorum* did not inhibit any of the seven species of green algae, while *Oscillatoria rubescens* and *Microcystis aeruginosa* inhibited all seven species. The growth of some green algae was inhibited in cultures containing *Phormidium* sp., *Lyngbya* sp., *Anabaena flos-aquae* (Lyngbye) Breb., or *Coccochloris peniocystis* (Kutz.) Dr. and Daily. *Chlamydomonas* sp. attained a greater density in combination with *Anabaena flos-aquae* than alone. Inhibition of growth of green algae was noted in 37 of the 49 two-species combinations. In 11 of the combinations, the growth of green algae was reduced at least 80%. Blue-green algae grew profusely in all two-species combinations with green algae. Careful visual observation did not reveal a single instance in which the growth of blue-green algae appeared less in the combinations than in controls.

Some factor was present in filtrates of water from nine different ponds which influenced the growth of one or more of three species of green algae (Table 5). Several instances of growth inhibition occurred in filtrates of water from

Table 5. The growth of three species of green algae in Beyerinck's solutions prepared from algae-free filtrates of water samples from nine different ponds as compared to growth in controls (Beyerinck's solutions prepared from distilled water).

Dominant algae in water sample	Green algae[a]		
	Chlorella pyrenoidosa	*Chlamydomonas* sp.	*Scenedesmus dimorphus*
	(% of control)		
Spirulina princeps	60.3*	46.4*	30.3*
Spirulina princeps	8.9**	54.5*	89.3
Anabaena sp.	112.5	21.4*	57.8*
Anabaena sp.	67.2*	72.7	86.1
Anabaena circinalis	46.3*	48.2*	155.8**
Anacystis incerta	101.1	13.2*	155.8**
Chlorella sp.	81.2	82.6	120.3
Chlorella sp.	143.8*	112.8	93.4
Diatoms	119.6*		75.9*

[a]*t—value significant at 0.05 level; **t—value, significant at 0.01 level.

ponds containing dense growths of the blue-green algae, *Spirulina princeps* (West and West), *Anabaena* sp., *Anabaena circinalis* Rab., or *Anacystis incerta* (Lemm.) Dr. and Daily. The patterns of inhibition were not consistent. For example, one filtrate from water which contained *Spirulina princeps* inhibited all three species of green algae, but the filtrate from water of a second pond which contained *Spirulina princeps* was not toxic to *Scendesmus dimorphus.* Furthermore, the degree of inhibition of a particular species of green algae was different in the two filtrates mentioned above. Similar differences in the pattern and degree of inhibition were also obtained for the two filtrates which represented *Anabaena* sp. The water samples all contained populations of algae in addition to the dominant species listed in Table 5. Therefore, inconsistencies in the pattern and amounts of inhibition are not surprising since extracellular substances from a number of species of algae were likely present in the filtrates. No inhibitory effects were noted in filtrates from waters which contained populations of green algae or diatoms. Several filtrates stimulated growth of one or the other of the three species of green algae.

Algal communities in ponds on the Fisheries Research Unit were divisible into three groups (Table 6); (a) mixed algal populations consisting of green algae, blue-green algae, yellow-green algae, and diatoms with no one species being particularly dominant; (b) communities in which one or sometimes two species of green algae were dominant; and (c) communities comprised of a high proportion of one species of blue-green algae. All communities were of sufficient density to discolor the water and to be classified as blooms. The number of species in mixed algal blooms averaged 14.8. Averages of 5.0 and 10.0 species were obtained for blooms of blue-green and green algae, respec-

Table 4. Growth of seven species of green algae in two-species combinations with seven species of blue-green algae compared to the growth of the green algae in single-species control cultures.

Green algae	Blue-green algae[a]						
	Oscillatoria rubescens	*Anabaena flos-aquae*	*Microcystis aeruginosa*	*Coccochloris peniocystis*	*Lyngbya sp.*	*Phormidium sp.*	*Nostoc muscorum*
	(% of control)						
Scenedesmus dimorphus	28.7**	26.5**	18.0**	34.7**	61.5**	101.4	107.5
Chlorella pyrenoidsa	2.6**	8.1**	48.9**	50.2**	70.5**	66.5**	92.3
Chlamydomonas sp.	1.8**	124.2**	26.3**	103.7	65.9**	100.6	112.3
Coelastrum microporum	1.8**	8.2**	14.3**	41.9**	74.0**	41.4**	93.0
Ankistrodesmus falcatus	40.2**	12.1**	29.8**	33.2**	95.4	95.9	92.7
Staurastrum sp.	18.2**	52.6**	31.6**	18.8**	47.1**	23.5**	94.1
Cosmarium subtumidum	16.0**	35.3**	55.0**	31.4**	43.3**	37.4**	86.4

[a]*t—value significa 1.05 level; **t—value significant at 0.01 level.

Table 6. Characteristics of phytoplankton communities in fish ponds on the Fisheries Research Unit, Auburn Univ.

Dominant algae	Abundance of dominant algae	Species present	Species diversity[a]	Chlorophyll
	(%)	(No.)	(Unitless)	(μg/L)
	Mixed algal blooms			
None		16	2.099	11.2
None		14	2.088	41.6
None		13	2.037	18.9
None		15	2.140	20.2
None		16	2.191	47.2
	Green algae blooms			
Cosmarium	92.2	9	0.938	21.4
Nephrocytium	84.5	9	0.737	24.8
Coelastrum	62.8	9	1.090	51.7
Scenedesmus	78.5	12	0.998	50.6
Closterium	47.3	11	1.611	24.7
	Blue-green algae blooms			
Oscillatoria	97.1	3	0.150	60.7
Oscillatoria	78.8	5	0.689	65.2
Anabaena	66.3	6	0.902	128.5
Anabaena	96.0	3	0.194	69.2
Spirulina	95.0	5	0.252	57.3
Spirulina	88.0	5	0.442	127.6
Microcystis	70.0	8	1.029	25.8
Microcystis	95.5	5	0.264	
Merismopedia	65.5	5	0.870	28.1

[a]Species diversity $= -\Sigma P_i \log e P_i$, where P_i = the decimal fraction of the proportion of the total individuals which belonged to the ith species.

tively. The number of species reported for a particular pond does not include all species in the pond. This number includes only those species which occurred in the upper 90 cm of the water column in sufficient abundance to be collected and counted by the techniques employed. These were the ecologically important phytoplankton species at the time of sampling.

Species diversity was high (2.037 to 2.191) in the mixed-species blooms, intermediate in blooms of green algae (0.737 to 1.1611), and low in blooms of blue-green algae (0.150 to 1.029). The individuals in a community with high diversity are more uniformly distributed among the different species than in a community with low diversity. One species comprised 75% or more of the total individuals in several communities (Table 6).

Blooms of blue-green algae in ponds often persist for long periods. A population of *Spirulina princeps* was present at a level of 50% or more of the total phytoplankton for over 3 months. An *Oscillatoria* sp. population was observed at an abundance of over 75% of the total phytoplankton for more than 2 months (Table 7).

Table 7. The relative abundance of *Spirulina princips* and *Oscillatoria* sp. in two different ponds during a 20 week period. Values indicate the percentages of the total phytoplankton communities which were comprised of the two species.

Date	*Spirulina princeps*	*Oscillatoria* sp.
	(%)	(%)
July 9		94.2
July 29	52.4	98.0
August 17	94.9	75.2
September 2	98.0	88.0
September 15	69.7	92.9
September 20	69.1	57.5
September 27	52.3	1.1
October 7	56.9	0.0
October 24	72.9	
November 12	89.6	
November 30	6.6	

Discussion

Vance (21) reported that the green algae, *Chlamydomonas moewusii* Gerloff and *Haematococcus lacustris* did not grow in combination with *Microcystis aeruginosa.* Proctor (17) found that four species of green algae either grew poorly or died in two-membered cultures with *Anacystis nidulans* Dr. and Daily. The present study confirms that additional species of blue-green algae inhibit the growth of green algae. Findings reported in Table 3 corroborate previous observations which indicated that certain species of green algae inhibited the growth of other green algae in two-species cultures (10, 11, 17).

A cursory examination of data on the growth of algae in two-species combinations might suggest that competition for nutrients caused the observed inhibition. However, the nutrient solutions were sufficiently concentrated to support very dense growths of algae. Species used in the two-membered cultures attain maximum density after 2 to 3 weeks. Growth after 4 days (the incubation period for the experiments) is much less than maximal. For example, a 21-day-old culture of *Scenesdesmus dimorphus* contained 133×10^4 individuals per milliliter, while a 4-day-old culture contained only 275×10^3 individuals per milliliter. Trace element concentrations in the media were low, but it is doubtful that one species accumulated the available supply of one or more trace elements at the expense of the second species. Stock cultures of green algae grew well in media prepared without additions of trace elements (5). Sufficient trace elements were supplied as impurities in the reagents and distilled water. Although the cultures were swirled twice daily, CO_2 concentrations were possibly in short supply in the cotton-plugged flasks. One species in a two-species culture might have absorbed CO_2 more rapidly or have been able to use lower concentrations of CO_2 than the second species and therefore monopolized the available CO_2. Blue-green algae can use lower concentrations of CO_2 than green algae and often occur in environments where CO_2 concentrations are low (9). If this had been the mechanism of competition between green and blue-green algae, the patterns of inhibition would have been more consistent and blue-green algae would have grown poorly in cultures where green algae were not inhibited.

Inadequate light penetration was not responsible for reduced growth of green algae in any two-species combination. All green algae were well dispersed in the solutions. None of the blue-green algae floated to the surface and *Oscillatoria rubescens, Anabaena flos-aquae, Lyngbya* sp., *Phormidium* sp., and *Nostoc muscorum* grew at the bottom of the flasks.

The role of bacteria in the inhibition of green algae can not be ruled out in two-species cultures containing those blue-green algae *(Microcystis aeruginosa* and *Oscillatoria rubescens)* which were contaminated with bacteria. However, the presence of bacteria in experiments containing *Nostoc muscorum* did not cause a decrease in growth of green algae. There was no evidence of inhibition of growth in seven species of green algae which were intentionally infected with bacteria (5).

If two-species cultures were incubated for long periods, one species would grow faster and compete more effectively for nutrient resources than the second species. However, from the standpoint of resources, a species was expected to grow as well for 4 days in a culture with a second species as when grown alone. The observed instances of reduced growth of a species in two-species cultures were related to

the presence of the second species. Inhibition of growth was apparently caused by the excretion of one or more substances by one alga that reduced the growth of the other alga. There were several two-species combinations of green and blue-green algae in which the growth of the green alga was not inhibited. Talling (19) found no evidence of inhibition of growth when two species of diatoms were grown in combination.

Filtrate experiments (Table 5) were conducted under the same culture conditions as two-species cultures. The inhibition of green algae was caused by some substance present in the filtrates of pond waters that was not present in the controls. Since only filtrates from waters which contained blue-green algae inhibited growth of green algae, the inhibitory factor was assumed to have originated from blue-green algae. Other workers have reported that filtrates from waters which contained blue-green algae were toxic to green algae (16, 20, 21).

The patterns of inhibition indicate that the same inhibitory agent is not produced by all species of blue-green algae. For example, growth of *Chlamydomonas* sp. was inhibited by *Oscillatoria rubescens, Microcystis aeruginosa,* and *Lyngbya,* sp., promoted by *Anabaena flos-aquae,* and was not influenced by *Coccochloris peniocystis.* Both *Anabaena flos-aquae* and *Coccochloris peniocystis* inhibited the growth of the six species of green algae.

Lyngbya sp. and *Phormidium* sp. reduced the growth of some green algae but not others. These two species of blue-green algae were generally less detrimental to the growth of green algae than *Oscillatoria rubescens, Anabaena flos-aquae, Microcystis aeruginosa,* and *Coccochloris peniocystis.* Apparently, *Lyngbya* sp. and *Phormidium* sp. produced lower levels of an inhibitory substance than some other blue-green algae. Certain species of green algae were more tolerant to the presence of a particular blue-green alga than others. For example, *Coelastrum microporum* was inhibited more than *Ankistrodesmus falcatus* by the presence of *Oscillatoria rubescens* (Table 4).

Some workers have speculated on the chemical nature of inhibitory substances produced by algae. Proctor (17) concluded that fatty acids liberated from dead *Chlamydomonas* cells inhibited the growth of *Haematococcus.* Low concentrations of several purified fatty acids were toxic to species of green and blue-green algae in cultures. According to Fogg (7), Jakob found that *Nostoc muscorum* produced a dihydroxy-anthroquinone which inhibited the growth of other algae. *Nostoc muscorum* did not exhibit inhibitory effects in the present study.

Chlamydomonas sp. grew better in combination with *Anabaena flos-aquae* than alone. Filtrates from some waters which contained either green or blue-green algae also promoted the growth of green algae (Table 5). Some algae reportedly produce substances which promote growth of other algae (2). Growth promoting substances were likely involved in the *Anabaena-Chlamydomonas* combination (Table 4). However, one can only speculate that substances of algal origin caused increased growth in several of the filtrates because other microorganisms were present.

The present findings and results of previous workers have established that one species of algae (especially blue-green algae) may be toxic to a second alga in laboratory cultures. Furthermore, filtrates from pond waters containing dense blooms of blue-green algae are inhibitory to green algae. The ecological role of these inhibitors in natural phytoplankton communities has not been demonstrated.

Dense blooms of phytoplankton obviously develop in response to high nutrient levels. It is not clear why the blooms are often relatively unialgal (Table 6) nor is it clear why a given species is responsible for the bloom in a particular habitat. Blooms in groups of ponds that received applications of fish feeds or fertilizers and located side by side in a series are often caused by different species of algae. These differences in algal communities were not related to nutrient concentrations. Temporal changes in species composition of algal communities in waste stabilization ponds and other eutrophic habitats were not related to nutrient concentrations. (6).

A great many factors, including chance, affect the species compositions of phytoplankton communities. Growth inhibitors of algal origin are likely one of these factors. An alga probably attains a cell density sufficient to produce high enough concentrations of the growth inhibitor(s) to adversely affect other species. This alga is able to increase at a greater rate and concentrations of the inhibitor(s) rise. The inhibitory substance(s) hold other species at low levels of abundance and prevents them from competing effectively with the dominant species for resources. As long as environmental conditions are tolerable, the bloom remains essentially unialgal. Proof of this hypothetical sequence of events will be difficult or impossible to obtain, but the circumstantial evidence indicates that inhibitory substances of algal origin likely play an important role in the development of the algal flora in many natural waters.

ACKNOWLEDGMENTS

The technical assistance of Mrs. Lynda Tillery is appreciated. Dr. G. P. Fitzgerald kindly supplied cultures of *Microcystis aeruginosa* and *Oscillatoria rubescens.*

LITERATURE CITED

1. AMERICAN PUBLIC HEALTH ASSOCIATION. 1971. Standard methods for the examination of water and wastewater. Amer. Public Health Assoc., New York. 874 p.
2. BENTLEY, J. A. 1958. Role of plant hormones of algal metabolism and ecology. Nature (London) 181:1499–1502.
3. BOLD, H. C. 1942. The cultivation of algae. Bot. Rev. 8:69–138.
4. BOYD, C. E. 1972. Summer algal communities and primary productivity in fish ponds. Hydrobiologia (In press).
5. BOYD, C. E. 1972. Sources of CO_2 for nuisance blooms of algae. Weed Sci. 20:492–497.
6. FITZGERALD, G. P. 1964. The biotic relationships within water blooms. Pages 300–306 *in* D. F. Daniel, ed. Algae and man. Plenum Press, New York.
7. FOGG, G. E. 1965. Algal cultures and phytoplankton ecology. Univ. Wisconsin Press, Madison. 126 p.
8. GOLTERMAN, H. L. and R. S. CLYMO. 1969. Methods for chemical analysis of freshwaters. Int. Biol. Program Handbook No. 8, Blackwell Sci. Publ., Oxford. 172 p.
9. KING, D. L. 1970. The role of carbon in eutrophication. J. Water Pollution Contr. Fed. 42:2035–2051.
10. KROES, H. W. 1971. Growth interactions between *Chlamydomonas globosa* Snow and *Chlorococcum ellipsoideum* Deason and Bold under different experimental conditions, with special attention to the role of pH. Limnol. Oceanogr. 16:869–879.
11. LEFÈVRE, M. and H. JAKOB. 1949. Sur quelques propriétés des substances actives sirées d'alques d'eau douce. C. R. Acad. Sci., Paris 229:234–236.

12. LEFÈVRE, M., H. JAKOB and M. NISBET. 1952. Auto - et hétéroantagonisme chez les alques d'eau douce - in vitro et dans les collections d'eau naturelles. Ann. Sta. Cent. Hydrobiol. Appl. 4:5–198.
13. MACARTHUR, R. H. and J. W. MACARTHUR. 1961. On bird species diversity. Ecology 42:594–598.
14. MCVEIGH, I. and W. H. BROWN. 1954. In vitro growth of *Chlamydomonas chlamydogama* Bold and *Haematococcus pluvialis* Flotow em. Wille in mixed cultures. Bull. Torrey Bot. Club 81:218–233.
15. PRATT, D. M. 1966. Competition between *Skeletonema costatum* and *Olisthodiscus luteus* in Narragansett Bay and in culture. Limnol. Oceanogr. 11:477–455.
16. PROCTOR, V. W. 1957. Some controlling factors in the distribution of *Haemotococcus pluvialis*. Ecology 38:457–462.
17. PROCTOR, V. M. 1957. Studies of algal antibiosis using *Haematococcus* and *Chlamydomonas*. Limnol. Oceanogr. 2:125–139.
18. RICE, T. R. 1954. Biotic influences affecting population growth of planktonic algae. Fish. Bull., U. S. Fish and Wildlife Serv. 54:227–245.
19. TALLING, J. F. 1957. The growth of two plankton diatoms in mixed culture. Physiol. Plant. 10:215–223.
20. TASSIGNY, M. and M. LEFÈVRE. 1971. Auto., hétéroantagonisme et autres conséquences des excretions d'algues d'eau douce ou thermale. Mitt. Internat. Verin. Limnol. 19:26–38.
21. VANCE, B. D. 1965. Composition and succession of cyanophycean water blooms. J. Phycol. 1:81–86.
22. ZEHNDER, A. and P. R. GORHAM. 1960. Factors influencing the growth of *Microcystis aeruginosa* Kutz. Emend. Elenkin. Can. J. Microbiol. 6:645–660.