Oecologia (Berl.) 29, 257–267 (1977)

Oecologia

Some Factors Effecting Algal Densities in a Eutrophic Farmland Stream

James W. Moore*

School of Biological Sciences, University of Bath, Bath, England

Summary. Population dynamics of attached algae in a eutrophic farmland stream (Wellow Brook, England) were correlated through multiple regression analyses with changes in 7 physico-chemical parameters (temperature, light, water velocity, pH, NO_3-N, P_2O_5-P, SiO_2-Si). Samples were taken every 2 weeks for 25 consecutive months between June 1973 and June 1975. The relative significance of the 7 parameters in controlling densities varied widely depending on species. Overall light was most important, accounting for 28 and 17% of density changes in the epipelon and epilithon respectively. While winter flooding caused a sharp reduction in the density of these 2 communities, the concentration of P_2O_5-P and NO_3-N and pH usually had little effect on numbers. The 7 parameters did not exert major control over the epiphyton, normally accounting for $<30\%$ of densities variation. Grazing by the protozoan *Frontonia acuminata* may have significantly reduced the density of the epipelon for 2 months during the spring but otherwise was of no importance to any community.

Introduction

While much has been written on the factors controlling phytoplankton dynamics, attached communites have received far less attention (Round, 1972). This is largely due to the problems associated with the frequent large-scale shifts in environmental condition of rivers and the inadequacy of sampling techniques (Round, 1970; Jones, 1974). It is also difficult to determine the importance of herbivorous grazing in controlling algal numbers, due both to the problems associated with estimating feeding rates (Moore, 1977) and population densities (Williams and Hynes, 1974). The purpose of this study was therefore to describe some of the factors influencing population cycles of attached algae in Wellow Brook, a eutrophic farmland stream situated in southern England.

* *Present address:* Environmental Protection Service, P.O. Box 2310, Yellowknife, Northwest Territories XOE 1HO, Canada

Materials and Methods

Wellow Brook is 20 km long falling 130 m to its juncture with the Avon River. It flows mainly through pasture but several towns are situated along its banks. A few streams flow into Wellow Brook but lakes and ponds are absent. The collection area (51°18′ N; 2°24′ W) was situated near Radstock in a rural area about 10 km from the source. The stream at this point was unshaded, 10 m in width, and much of its bed was covered with large rounded rocks (10–30 cm diameter) that supported extensive growths of *Cladophora glomerata* (Lyngby.) Kz. Samples of epipelon (algae associated with sediments) and epilithon (with rocks) were taken from the same site located 1 m from shore every 2 weeks (June 1973–June 1975) as outlined in Moore (1976). Simultaneous collections of the epiphyton associated with *C. glomerata* were made (Moore, 1976) in 4 areas just upstream from this station. Each area had a different but normally stable current speed, i.e., Site I (66–85 cm/s), Site II (46–65 cm/s), Site III (26–45 cm/s), and Site IV (10–25 cm/s). The first site was situated in mid-stream and the others were located at respective distances of 3, 1, and 0.5 m from shore. During periods of high water in winter (Fig. 1), current speed in all 4 areas ranged from 45 to 100 cm/s.

The methods of collection and analysis of each algal assemblage and the determination of physico-chemical parameters were identical to those outlined earlier (Moore, 1976). To estimate the quantity of material that had settled on *C. glomerata*, the samples from each site were washed lightly with distilled water and the dislodged material was dried by sublimation (−40° C) to constant weight. Microscopic examination of the filaments indicated that virtually all the material was removed and, although a few epiphytes were also dislodged, their contribution to the estimate of settled material was considered negligible. The density of protozoans on the sediments was determined by diluting the samples used for the analysis of epipelic algae in distilled water to 100 ml. Three 10 ml aliquots were taken and all the animals in each aliquot counted.

Multiple regression analyses were used to determined the effect of the 7 physico-chemical parameters on the density of predominant algae. Since herbivorous grazing usually had little influence on the population cycles, as outlined later, it was not included in the analyses. The importance of light as an ecologic factor was estimated using the time between sunrise and sunset.

Results

Physico-chemical analysis. Water temperatures varied from 4 to 19° C with a maximum daily range of 1.5° C occurring in summer. Nutrients (P_2O_5-P, NO_3-N, SiO_2-Si) always occurred abundantly (Fig. 1). pH was usually near 8 with total alkalinity ranging from 260 to 390 mg/l as $CaCO_3$. The organic content of the sediments fluctuated between 5 and 8% of the total dry weight. Daily observations at Wellow Brook indicated that all periods of elevated discharge were recorded as in Figure 1. Discharge averaged 2.5 m^3/s with maximum and minimum values of 15 and 2 m^3/s respectively.

Epipelon and epilithon. A recurring pattern in the seasonal abundance of predominant epipelic and epilithic species was not evident (Fig. 2). Although *Navicula viridula* v. *minor* V.H. and *Surirella ovata* v. *minuta* Bréb., for example, reached maximum numbers during the spring bloom (April) in 1974, density values were much lower at a comparable time in 1975. Similarly while *Navicula tripunctata* (O. F. Müll.) Bory occurred in relatively large numbers during the summer and fall of 1973, this species failed to attain comparable development at any other time, a feature noted for several other plants (Fig. 2). Multiple regression analyses indicated that 19–54% of the dynamics of most species could be related to the physico-chemical parameters measured (Table 1). Of these, water velocity and the concentration of SiO_2-Si were usually the most important, particularly in the epipelon, while P_2O_5-P was of least significance.

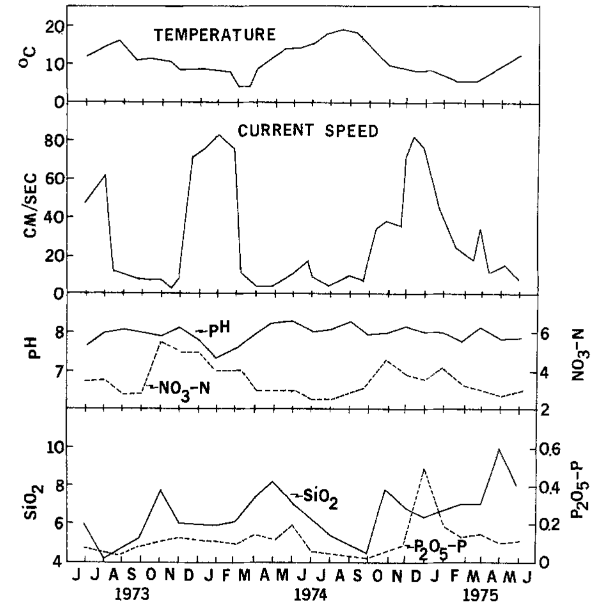

Fig. 1. Seasonal changes in physico-chemical properties of Wellow Brook. Current speed was measured over the area used for collection of epipelic algae. All nutrients are expressed as mg/l

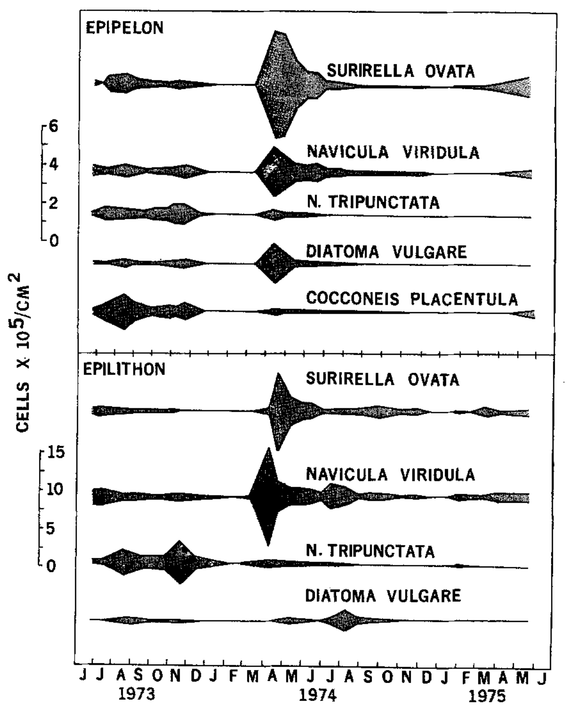

Fig. 2. Seasonal changes in the density of common epipelic and epilithic algae in Wellow Brook

Table 1. Multiple regression analyses of some factors influencing population dynamics of epipelic and epilithic algae in Wellow Brook. MR^2 (%) = accumulated variation of of dependent variable accounted for by the step-wise addition of the independent variables

Independent variable	Rank	MR^2	Independent variable	Rank	MR^2	Independent variable	Rank	MR^2
			Epipelon					
a) Dependent variable – *Surirella ovata* v. *minuta*			b) Dependent variable – *Navicula viridula*			c) Dependent variable – *Navicula tripunctata*		
Water velocity	1	12.9	SiO_2-Si	1	28.0	Temperature	1	5.9
SiO_2-Si	2	22.9	Water velocity	2	54.1	Water velocity	2	9.8
NO_3-N	3	28.5	Temperature	3	62.7	Light	3	13.3
pH	4	32.9	NO_3-N	4	70.7	pH	4	15.3
Temperature	5	35.8	Light	5	74.0	NO_3-N	5	16.9
Light	6	37.3	pH	6	75.0	SiO_2-Si	6	18.0
P_2O_5-P	7	37.3	P_2O_5-P	7	75.2	P_2O_5-P	7	18.7
d) Dependent variable – *Diatoma vulgare*			e) Dependent variable – *Cocconeis placentula*			f) Dependent variable – Total epipelic density		
Water velocity	1	12.8	Temperature	1	17.2	Light	1	28.0
Temperature	2	17.8	Light	2	33.6	Water velocity	2	55.6
SiO_2-Si	3	20.3	SiO_2-Si	3	43.7	NO_3-N	3	60.5
Light	4	22.3	NO_3-N	4	50.1	SiO_2-Si	4	65.6
pH	5	23.6	pH	5	51.1	Temperature	5	69.6
P_2O_5-P	6	24.2	Water velocity	6	51.4	P_2O_5-P	6	70.4
NO_3-N	7	24.8	P_2O_5-P	7	51.4	pH	7	70.4
			Epilithon					
a) Dependent variable – *Surirella ovata* v. *minuta*			b) Dependent variable – *Navicula viridula*			c) Dependent variable – *Navicula tripunctata*		
Temperature	1	11.2	Water velocity	1	14.6	NO_3-N	1	26.1
SiO_2-Si	2	18.3	NO_3-N	2	19.4	Water velocity	2	30.6
pH	3	25.2	SiO_2-Si	3	21.1	SiO_2-Si	3	34.9
Light	4	28.1	Temperature	4	21.7	Light	4	37.6
Water velocity	5	30.9	pH	5	21.8	Temperature	5	38.0
NO_3-N	6	32.1	P_2O_5-P	6	21.8	P_2O_5-P	6	38.2
P_2O_5-P	7	32.2	Light	7	21.8	pH	7	38.3
d) Dependent variable – *Diatoma vulgare*			e) Dependent variable – Total epilithic density					
Temperature	1	44.4	Light	1	17.0			
SiO_2-Si	2	51.1	Temperature	2	31.2			
Water velocity	3	52.2	Water velocity	3	38.7			
Light	4	53.1	SiO_2-Si	4	40.6			
No_3-N	5	53.4	NO_3-N	5	41.0			
pH	6	53.7	pH	6	41.0			
P_2O_5-P	7	53.8	P_2O_5-P	7	41.0			

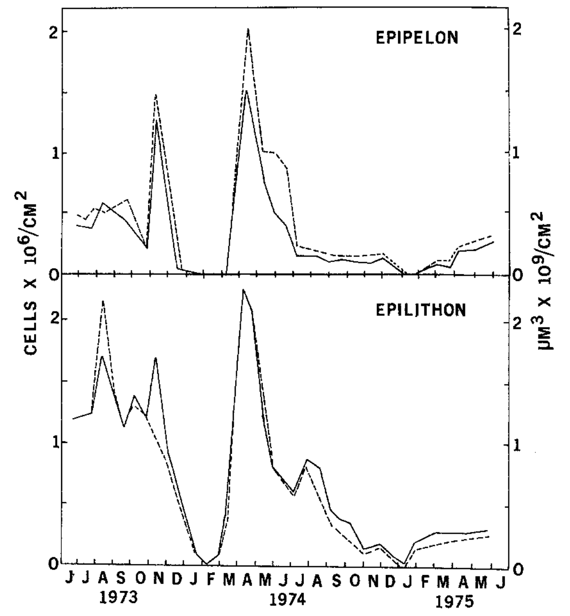

Fig. 3. Seasonal changes in the standing crop of the epipelon and epilithon in Wellow Brook. ——— numbers, – – – – cell volume

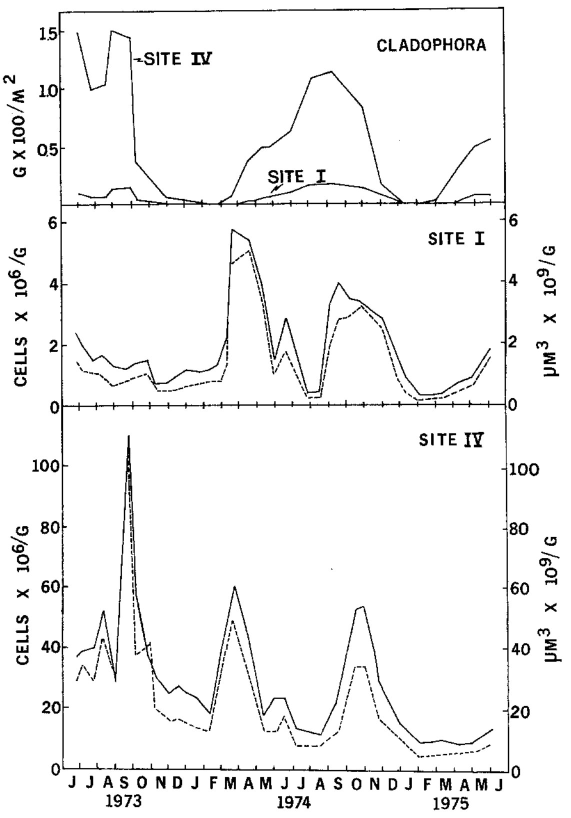

Fig. 4. Seasonal changes in the standing crop of *Cladophora glomerata* and its epiphytic flora at sites I and IV in Wellow Brook. ——— numbers, – – – – cell volume

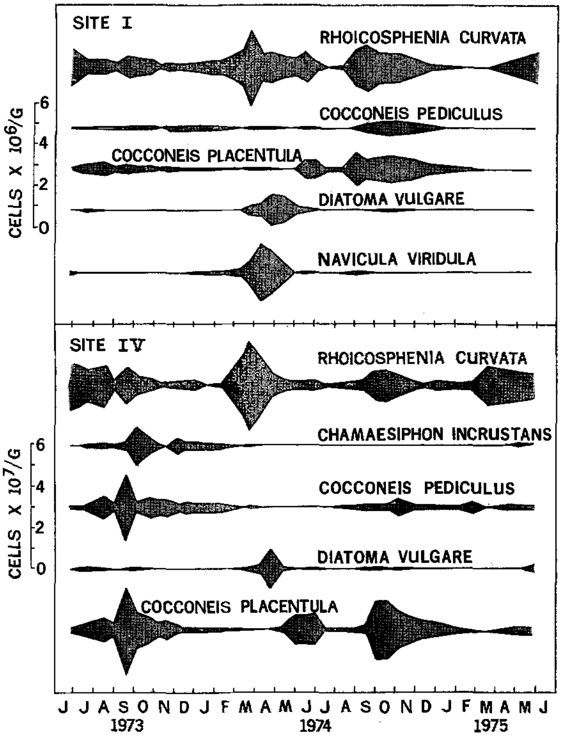

Fig. 5. Seasonal changes in the standing crop of epiphytic algae at Sites I and IV in Wellow Brook

Population dynamics of the total standing crop, although generally similar throughout 1974, differed considerably during 1973 (Fig. 3). Thus, while the epilithon increased sharply in numbers in August, comparable development failed to occur on the sediments with virtually the opposite pattern taking place in November. About 70% of the seasonal variation in the density of the epipelon could be accounted for by the physico-chemical parameters measured (Table 1). Of these, light and water velocity were most important while the concentration of nutrients played an insignificant role in controlling numbers. Seasonal variation in the epilithon was weakly influenced by light, temperature, and water velocity with the other parameters accounting for only 2.3% of density changes (Table 1). Poorest development in both communities invariably occurred during high water while periods of maximum growth were observed when the population of *C. glomerata* was either low or waning.

Epiphyton. The standing crop of *Cladophora glomerata* varied seasonally with a maximum value of 150 g (dry weight)/m^2 being recorded at Site IV (Fig. 4). Temperature strongly influenced this plant, accounting for 69% of density variations, followed by light (10%), SiO_2-Si (1.7%), and NO_3-N (1.5%). The quantity of detritus associated with *C. glomerata* increased inversely with water velocity. Thus in the fastest flowing reaches of Wellow Brook values seldom exceeded 0.02 g/g dry weight of *C. glomerata* while in relatively calm areas weights of up to 2 g/g were recorded.

Table 2. Multiple regression analyses of some factors influencing population dynamics of epiphytic algae at Sites I and IV in Wellow Brook

Independent variable	Rank	MR^2	Independent variable	Rank	MR^2	Independent variable	Rank	MR^2
			Site 1					
a) Dependent variable – *Rhoicosphenia curvata*			b) Dependent variable – *Cocconeis pediculus*			c) *Cocconeis placentula*		
P_2O_5-P	1	6.6	P_2O_5-P	1	16.0	Temperature	1	18.0
Light	2	11.5	NO_3-N	2	24.5	P_2O_5-P	2	27.5
Water velocity	3	13.9	Light	3	32.9	NO_3-N	3	33.0
SiO_2-Si	4	15.9	Temperature	4	37.3	pH	4	37.4
NO_3-N	5	17.7	SiO_2-Si	5	38.7	Water velocity	5	41.7
Temperature	6	19.3	Water velocity	6	39.8	SiO_2-Si	6	43.5
pH	7	20.0	pH	7	39.9	Light	7	43.5
d) Dependent variable – *Diatoma vulgare*			e) Dependent variable – *Navicula viridula*			f) Dependent variable – Total density		
Water velocity	1	8.2	Water velocity	1	6.6	P_2O_5-P	1	5.5
pH	2	14.2	NO_3-N	2	10.6	pH	2	10.5
Light	3	17.8	SiO_2-Si	3	11.8	SiO_2-Si	3	14.7
Temperature	4	20.7	pH	4	12.9	Temperature	4	16.7
NO_3-N	5	22.7	P_2O_5-P	5	13.1	Water velocity	5	18.7
P_2O_5-P	6	22.8	Light	6	13.2	NO_3-N	6	19.9
SiO_2-Si	7	22.8	Temperature	7	13.2	Light	7	20.9
			Site IV					
a) Dependent variable – *Rhoicosphenia curvata*			b) Dependent variable – *Cocconeis pediculus*			c) Dependent variable – *Cocconeis placentula*		
Light	1	10.6	NO_3-N	1	25.5	SiO_2-Si	1	11.5
NO_3-N	2	19.3	SiO_2-Si	2	37.6	Temperature	2	23.0
pH	3	23.8	pH	3	42.5	Light	3	26.0
SiO_2-Si	4	26.2	P_2O_5-P	4	44.6	pH	4	27.2
Temperature	5	27.3	Temperature	5	45.9	NO_3-N	5	28.1
Water velocity	6	27.4	Light	6	46.9	P_2O_5-P	6	28.3
P_2O_5-P	7	27.4	Water velocity	7	46.9	Water velocity	7	28.3
d) Dependent variable – *Diatoma vulgare*			e) Dependent variable – *Chamaesiphon incrustans*			f) Dependent variable – Total density		
SiO_2-Si	1	6.8	SiO_2-Si	1	14.3	SiO_2-Si	1	12.0
pH	2	11.9	pH	2	22.3	pH	2	16.5
Temperature	3	16.0	Light	3	27.6	NO_3-N	3	18.0
Water velocity	4	19.5	Water velocity	4	31.3	Water velocity	4	19.5
NO_3-N	5	23.0	NO_3-N	5	34.6	Light	5	20.8
P_2O_5-P	6	23.1	Temperature	6	35.6	P_2O_5-P	6	21.8
Light	7	23.2	P_2O_5-P	7		Temperature	7	21.9

Although *Rhoicosphenia curvata* (Kz.) Grun. ex Rabh. was the predominant epiphyte in the rapid water collection area, several other species occasionally achieved high densities (Fig. 5). The relative abundance of *R. curvata* decreased in slower flowing areas with *Cocconeis* spp and *Chamaesiphon incrustans* Grun. becoming much more important (Fig. 5). The pattern of seasonal change in the density of the epiphytic communities was usually similar regardless of ambient water velocity (Fig. 4). Thus peak development in all 4 populations occurred when the standing crop of *C. glomerata* was either low or declining, as exemplified by the data from Sites I and IV (Fig. 4). The assemblage growing in relatively calm reaches of Wellow Brook was, however, always much larger than the population inhabiting rapid water areas. The relative importance of the 7 environmental parameters in controlling densities varied depending on ambient water velocity (Table 2). P_2O_5-P, for example, was often of primary significance at Site I but was replaced with SiO_2-Si at Site IV. In contrast to the epipelon and epilithon, water velocity had little effect on population changes.

Discussion

The periodicity of *C. glomerata* during 1973 parallels the situation in other temperate zone rivers where 2 distinct periods of intensive growth occur (Whitton, 1970; Bellis and McLarty, 1971). This feature, which is often related to high mid-summer temperatures, contrasts with the uninterrupted rise and fall in numbers in 1974. Since changes in temperature were well correlated with shifts in the density of *C. glomerata*, the bimodal growth of 1973 was due to a cooling of the water rather than excessively high temperatures. The poor development of *C. glomerata* in the rapid water collections site contrasts markedly with certain other populations (Zimmerman, 1961), and at present no explanation can be offered to account for this discrepancy.

The inverse relationship that often existed between the density of the microflora and that of *C. glomerata* was probably due to a number of factors. Firstly competition for at least one component of the environment may have controlled the abundance of the smaller algae. It is known, for example, that vascular plants as well as *C. glomerata* normally compete more successfully for nutrients than unicellular algae (Fitzgerald, 1969). Since, however, N, P, and Si always occurred abundantly in Wellow Brook, some other substance may have restricted development, as previously observed for planktonic algae (Lund, 1971). It should be noted that the microflora sometimes showed an elevation in numbers when the standing crop of *C. glomerata* was high. During these periods *C. glomerata* was always waning and invariably dropped to very low densities within a few weeks. Thus most of the population was either dead or dying implying that there would be little nutrient use. In addition to this factor, production of toxic metabolites by *C. glomerata* and differential growth between *C. glomerata* and the microflora would account for the inverse density relationship.

There were several other instances in which development of certain species was correlated. For example, in the epilithon, the abundance of *S. ovata* increased only after *N. viridula* had waned. As in *C. glomerata*, the production of toxic metabolites could account for these relationships. Perhaps (and more likely), however, they are simply due to differential response to abiotic factors.

The generally small contribution of nutrient concentration to the dynamics of all 3 communities is similar to other eutrophic farmland rivers (Backhaus, 1968a, b; Marker, 1976a, b). This can be related to the fact that the high level of dissolved material in such areas seldom restricts growth. The broad variation in temperature should probably have caused wider fluctuations in the density of the flora than were observed (Moss, 1973). Perhaps under nutrient-enriched conditions algae are able to tolerate variations in other parameters such as temperature. The significant contribution of light to the epipelon and epilithon parallels the situation in other temperate zone populations (Gruendling, 1971; Marker, 1976a). Since Wellow Brook was unshaded, the summer reduction in densities was not due to leaf cover, which, in some streams, can severely limit development (Godward, 1934; Whitton, 1970). Is should perhaps be pointed out here that the overall MR^2 values for all 3 communities are largely a reflection of the variability induced by a few predominant species. In other streams where different species exist, the importance of the various independent variables could be dissimilar to those observed in this study.

Most of the common epipelic and epilithic species were similar to those recorded for other areas of England (Round, 1960, 1961; Moss and Round, 1967). For epiphyton, the importance of *Cocconeis* spp. and *Chamaesiphon incrustans* in the calmer areas contrasts with the data of Chudyba (1968). In this latter study, *Cocconeis pediculus* was predominant in fast-flowing water while the abundance of *C. placentula* v. *euglypta* remained relatively constant regardless of water velocity. Furthermore, *Rhoicosphenia curvata* showed considerable development at one of the calmer sites in Chudyba's study. Although the reason for these differences is not apparent, it should be noted that the pattern of seasonal distribution did, for short periods in the present study, parallel those described by Chudyba.

Since the predominant epiphytic species in Wellow Brook characteristically possessed well-developed attachment mechanisms such as stalks, water velocity, even during flooding, had little effect on density changes. In contrast several common epipelic and epilithic species were only poorly attached to the substrate and thus flow was more important in controlling densities. It should be noted that while several epipelic species did possess stalks, high periods of discharge scoured both the plant and substrate, contrasting with the epiphytic substrate (*C. glomerata*, which was not influenced by flooding. Because the density of the epiphyton increased with the amount of detritus on the filaments, this factor was not primarily responsible for limiting algal growth.

Although herbivores were generally rare on the sediments, the protozoan *Frontonia acuminata* Ehr. did occur abundantly during March and April 1974 and was absent at other times. They contained an average of 8.2 ± 1.7 ($\pm 95\%$ confidence limits) diatom cells per individual and, since their density was estimated at $13{,}600 \pm 1{,}400/cm^2$, about 1.1×10^5 cells/cm^2 were contained in these organisms. This value represents about 10% of the total standing crop of the epipelon at this time. While feeding rates were not determined due to the high degree of error involved with such estimates (Moore, 1977; Saunders, 1969), the large quantity of ingested algae (cf. Moore, 1972, 1975) indicates that significant herbivory may have taken place.

The diatom *Navicula viridula* v. *minor* accounted for 50% by number of the algae in the gut of *F. acuminata*, followed by *Surirella ovata* v. *minuta* at 35%. Since this latter species was more abundant in the environment than *N. viridula*, there was some degree of food selection. This feature can be explained by the fact that *S. ovata* is well attached to the substrate by a gelatinous stalk whereas *N. viridula* possesses, a less efficient mechanism for attachment and is thus easier to dislodge. It is also possible, however, that *N. viridula* was originally predominant in the environment but was greatly reduced in numbers through the grazing of *F. acuminata*. In some habitats protozoans are non-selective feeders (Goulder, 1972). In contrast to the effects of grazing by protozoans, the large numbers of *Asellus aquaticus* and *Gammarus pulex* found among the growths of *C. glomerata* did not significantly reduce the standing crop of the epiphyton (Moore, 1975).

References

Backhaus, D.: Ökologische Untersuchungen an den Aufwuchsalgen der obersten Donau und ihrer Quellflüsse. II. Die räumliche und zeitliche Verteilung der Algen. Arch. Hydrobiol., Suppl. **34**, 24–73 (1968a)

Backhaus, D.: Ökologische Untersuchungen an den Aufwuchsalgen der obersten Donau und ihrer Quellflüsse. III. Die Algenverteilung und ihre Beziehungen zur Milieuofferte. Arch. Hydrobiol., Suppl. **34**, 130–149 (1968b)

Bellis, V.J., McLarty, D.A.: Ecology of *Cladophora glomerata* (L.) Kz. in southern Ontario. J. Phycol. **3**, 57–63 (1967)

Chudyba, H.: *Cladophora glomerata* and concomitant algae in the river Skawa. Distribution and condition of appearance. Acta Hydrobiol. **10**, 39–84 (1968)

Fitzgerald, G.P.: Some factors in the competition or antagonism among bacteria, algae and aquatic weeds. J. Phycol. **5**, 351–359 (1969)

Godward, M.B.: An investigation of the causal distribution of algal epiphytes. Beih. bot. Zbl. **52**, 506–539 (1934)

Goulder, R.: Grazing by the ciliated protozoan *Loxodes magnus* Stokes on the the alga *Scenedemus* in a eutrophic pond. Oikos **23**, 109–115 (1972)

Gruendling, G.K.: Ecology of epipelic algal communities in Marion Lake, British Columbia. J. Phycol. **7**, 239–249 (1971)

Jones, J.E.: A method for observation and enumeration of epilithic algae directly on the surface of stones. Oecologia (Berl.) **16**, 1–8 (1974)

Lund, J.W.G.: An artificial alteration of the seasonal cycle of the plankton diatom *Melosira italica* subsp. *subarctica* in an English lake. J. Ecol. **59**, 521–533 (1971)

Marker, A.F.H.: The benthic algae in some streams in southern England. II. The primary productivity of the epilithon in a small chalk stream. J. Ecol. **64**, 359–373 (1976a)

Marker, A.F.H.: The benthic algae in some streams in southern England. I. Biomass of the epilithon in some small streams. J. Ecol. **64**, 343–358 (1976b)

Moore, J.W.: Composition and structure of algal communities in a tributary stream of Lake Ontario. Canad. J. Bot. **50**, 1663–1674 (1972)

Moore, J.W.: The role of algae in the diet of *Asellus aquaticus* L. and *Gammrus pulex* L. J. Anim. Ecol. **44**, 719–730 (1975)

Moore, J.W.: Seasonal succession of algae in rivers. I. Examples from the Avon, a large slow-flowing river. J. Phycol. **12**, 342–349 (1976)

Moore, J.W.: Some aspects of the feeding biology of benthic herbivores. Hydrobiologia **53**, 139–146 (1977)

Moss, B., Round, F.E.: Observations on standing crops of epipelic and episammic algal communities in Shear Water, Wilts. Br. Phycol. Bull. **3**, 241–248 (1967)

Round, F.E.: Studies on bottom-living algae in some lakes of the English lake district. IV. The seasonal cycles of the Bacillariophyceae. J. Ecol. **48**, 529–547 (1960)

Round, F.E.: Studies on bottom-living algae in some lakes in the English lake district. V. The seasonal cycles of the Cyanophyceae. J. Ecol. **49**, 31–38 (1961)
Round, F.E.: The biology of the algae. London: Ed. Arnold 1970
Round, F.E.: Patterns of seasonal succession of freshwater epipelic algae. Br. Phycol. J. **7**, 213–220 (1972)
Saunders, G.W.: Some aspects of feeding in zooplankton. In: Eutrophication: causes, consequences, correctives, pp. 556–573. Washington: Natl. Acad. Sci. 1969
Whitton, B.A.: Biology of *Cladophora* in freshwaters. Wat. Res. **4**, 457–476 (1970)
Williams, D.D., Hynes, H.B.N.: The occurrence of benthos deep in the substatum of a stream. Freshwat. Biol. **4**, 233–256 (1974)
Zimmerman, P.: Experimentelle Untersuchungen über die ökologische Wirkung der Strömungsgeschwindigkeit auf Lebensgemeinschaften des fließenden Wassers. Schweiz. Z. Hydrol. **23**, 1–81 (1961)

Received February 10, 1977