Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Population and Production Dynamics of Benthic Algae in an Artificial Recirculating Hard-Water Stream

A. F. H. Marker and H. Casey

Phil. Trans. R. Soc. Lond. B 1982 **298**, 265-308
doi: 10.1098/rstb.1982.0085

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: **http://rstb.royalsocietypublishing.org/subscriptions**

This journal is © 1982 The Royal Society

Downloaded from rstb.royalsocietypublishing.org

Phil. Trans. R. Soc. Lond. B **298**, 265–308 (1982) [265]
Printed in Great Britain

THE POPULATION AND PRODUCTION DYNAMICS OF BENTHIC ALGAE IN AN ARTIFICIAL RECIRCULATING HARD-WATER STREAM

BY A. F. H. MARKER AND H. CASEY
Freshwater Biological Association, River Laboratory, East Stoke, Wareham, Dorset BH20 6BB, U.K.

(*Communicated by W. D. P. Stewart, F.R.S. – Received* 16 *July* 1981)

CONTENTS

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
The Royal Society is collaborating with JSTOR to digitize, preserve, and extend access to *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences.* www.jstor.org

Downloaded from rstb.royalsocietypublishing.org

An artificial stream has been used to examine the population and production dynamics of benthic algae that grow in the hard-water, nutrient-rich streams of southern England. The channel, made of glass-reinforced plastic is *ca.* 60 m in circumference and filled with flints *ca.* 40 mm in diameter. Water 0.3 m deep above the gravel was recirculated at 0.4 m s^{-1} by an archimedean screw pump. Water was supplied from the aquifer at a rate of 4.2 m^3 h^{-1} and left the channel from an overflow notch.

The chemical composition of the inflow water was relatively constant so that differences between inflow and outflow could be directly related to biological and non-biological changes in the channel. Experiments in the dark showed that calcium carbonate precipitated, reducing calcium concentration and alkalinity to 80% of inflow values. Reactive phosphate precipitated to 28% of inflow concentrations.

Preliminary experiments were done in the light between April and December 1976 and detailed experiments between April 1977 and July 1978. The initial colonization phase, in both 1976 and 1977, was dominated by diatoms. Chlorophyll densities increased by over 300-fold in 14 days in 1977. The change in cell numbers of four dominant species, over a 7 day period, confirmed doubling times of less than 2 days. Maximum densities of 500–600 mg chl *a* m^{-2} were reached 5 weeks after the dark covers had been removed. The biomass remained constant for the next 14 days and during this phase the rate of silicon uptake was 4.5 g m^{-2} day^{-1}. Substantial uptake was also recorded, while the biomass was declining, between the seventh and ninth weeks. Over a period of 60 days, 107 g Si m^{-2} were taken up and photosynthetic studies indicated that 137 g C m^{-2} has also been taken up. In terms of biomass this would correspond to 2.3–4.6 g chl *a* m^{-2}, whereas the maximum observed biomass was 0.5–0.6 g m^{-2}. Loss of fine particulate material over 60 days was 0.0558 g of pigment per square metre and sedimentation into the lower layers of the gravel was 0.735 g of pigment per square metre. During weeks 10, 11 and 12 substantial quantities of silicon and phosphorus were released into the water and for a brief period calcium bicarbonate concentrations in the channel approached inflow concentrations.

The diatoms of the initial colonization phase were succeeded by a lime-encrusted growth of blue-green and green algae (*Lyngbya kützingii*, *Chamaesiphon polymorphus* and *Gongrosira incrustans*) with densities through the winter of 1977 of *ca.* 200 mg chl *a* m^{-2}. *Cladophora glomerata* developed in the autumn of 1977 and its epiphytic algal flora was substantially different from the epilithic flora. Diatoms recurred in large numbers in the spring of 1978. In terms of biomass the principal diatoms were *Achnanthes minutissima*, *Fragilaria virescens*, *Gomphonema rhombicum*, *Meridion circulare*, *Nitzschia fonticola* and *Synedra ulna*.

Regression analysis showed that suspended chlorophyll *a* concentration was not related to benthic algal biomass (estimated as chlorophyll *a*) but more closely related to benthic diatom volume or dissolved silicon concentration.

The seasonal succession of algae in the channel was very similar to that which occurs in local streams. The initial colonization phase by diatoms bears a striking resemblance to the spring outburst of benthic diatoms in local streams. In the channel (and in natural streams, by inference) this succession cannot be controlled by changes in discharge, water velocity or chemical composition of the water. The onset of diatom growth in the spring in streams is probably largely controlled by light intensity. The absence of large numbers of insect larvae, until mid-April, probably allows the biomass to develop. After April the impact of insect larvae on diatom populations may be considerable.

1. Introduction

Good quantitative estimates of the seasonal changes in benthic river algae, compared with lake phytoplankton, are few. A survey of the literature suggests that three types of stream can be recognized. The first type of stream is subject to very high discharge during the spring and early summer due to snow melt in the upper reaches; such streams generally develop a maximum algal biomass in the late summer and autumn or during the winter (Gumtow 1955; Koboyasi

Downloaded from rstb.royalsocietypublishing.org

1961*a*; Tominaga & Ichimura 1966; Bombowna 1972; Ertl *et al.* 1972). The second type of stream is relatively nutrient-rich from the source and not subject to such large and rapid changes in discharge in the spring; in these streams algae show a characteristic seasonal pattern with a diatom maximum in the spring and sometimes another in the autumn (Butcher 1949; Blum 1957; Backhaus 1968; Marker 1976*a*; Moore 1976; Sumner & Fisher 1979). In some streams, however, rapid and unpredictable changes in discharge effectively control the algal biomass which, therefore, shows no regular seasonal patterns (Douglas 1958; Tett *et al.* 1978).

The hard-water chalk streams of southern England are within the second category. The submerged macrophyte, *Ranunculus penicillatus* var. *calcareus* (R. W. Butcher) C. D. K. Cook, often dominates the flora, together with variable quantities of emergent macrophytes (Ladle & Casey 1971; Westlake *et al.* 1972). Chalk streams are nutrient-rich and there is no evidence of nutrient limitation during the year (Casey 1969; Westlake *et al.* 1972). Their benthic algae show a pronounced seasonal variation with a maximum biomass in the spring, largely composed of diatoms (Marker 1976*a*). Diatoms can also recur at other times of the year but the period of recurrence is less regular and shorter than that of the spring 'outbursts' (Marker 1976*a*; Marker & Gunn 1977). The analysis of dissolved silicon concentrations over 13 years, however, suggests that a small but significant late-summer growth of diatoms does occur in some of these streams (Casey *et al.* 1981).

Although the algae of chalk streams are only a small proportion of the total plant biomass, primary production by algae is high, suggesting that there must be a rapid turnover (Marker 1976*b*). Invertebrates may have a considerable impact on algal biomass because treatment with insecticides leads to a rapid increase in the biomass of algae (Eichenberger & Schlatter 1978). Moreover, chironomids are important during times of the year when diatoms are a significant proportion of the flora (Williams 1981).

Apart from depletion by grazing, algae are also lost through drift and sedimentation. Suspended algae in small streams are largely derived from benthic populations (Butcher 1932), but in chalk streams they appear to reflect changes in the benthic diatoms more closely than changes in the benthic algal flora in general (Marker & Gunn 1977; Casey *et al.* 1981). The situation is highly complex, with a wide variety of factors affecting the resuspension and sedimentation of algae. Without a knowledge of how long the algae remain in suspension and hence to which part of the river bed they relate, any comparison between the attached flora and the suspended solids can only be of limited value.

Channels have been used for many years for the experimental control of the physical and chemical variables that determine the pattern of biological events in streams. Some of these studies have been on the growth and production of blue-green algae in thermal streams (Stockner 1968; Wiegert & Fraleigh 1972; Fraleigh & Wiegert 1975). Laboratory streams were used for numerous studies on the effect of temperature and irradiance on the respiration and photosynthesis of benthic algae in temperate streams (McIntire 1966, 1968; McIntire *et al.* 1964; McIntire & Phinney 1965; Phinney & McIntire 1965). The channels used by Eichenberger (1967*a*, *b*, 1972*a*, *b*) included more features of temperate streams because they were in the open, subject to natural daylight and colonization by insects with aquatic larval stages. All these channels, however, were operated as direct, through-flow systems. The amount of water pumped directly controlled water velocity and depth and the retention time of the water could only be controlled by changing the velocity of the water or the length of the channel. Consequently most of these systems were narrow with shallow water (a few centimetres)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

and were far removed from natural stream conditions. Moreover, they were not generally suitable for destructive sampling owing to their small size. None of the studies in temperate or cool temperate waters included quantitative studies on the streams from which the water was drawn to operate the channels, so that a direct comparison, to see how far the experimental system reflected natural streams, was not possible. None of the experiments attempted parallel studies on flora, fauna and water chemistry.

For the studies described in this paper, a recirculatory channel system has been developed that allows for more intensive destructive sampling (Ladle *et al.* 1981). It resembles a natural stream much more closely in dimensions, substrate type, water depth and water velocity than do most of the channels described hitherto. The system was kept relatively simple with the omission of mobile fine sediments, macrophytes and a comprehensive invertebrate fauna. By recirculating the water the effective period of contact for non-gaseous chemicals is increased without altering the length of the channel; consequently the sampling programme is not bedevilled with changes in the flora along the length of the channel but can still be used to study changes in the water chemistry.

The studies reported here concern: (i) the effect of the developing algal flora on the water chemistry; (ii) the factors that control the seasonal cycle of benthic diatoms; (iii) the summer succession to crusts of green and blue-green algae (Marker 1976*a*); (iv) the relation between primary production and biomass (Marker 1976*b*); (v) the relation between suspended and benthic algae (Marker & Gunn 1977); (vi) a budget for the production and loss of algae in a relatively well defined system.

Studies on the interaction between the primary and secondary trophic levels will be reported elsewhere.

2. Methods

2.1. *The recirculating channel*

The channel has already been described in detail (Ladle *et al.* 1977). The system is annular, and 53 m in length overall. The channel itself is 2 m wide at the top and 1 m wide at the bottom. Water was recirculated by an archimedean screw pump and, in the experiments described in this paper, travelled at a mean velocity of 0.4 m s^{-1}. This means that the water recirculated in just over 2 min. Water was supplied to the channel from a borehole sunk into the chalk (soft Cretaceous limestone) aquifer. For most of the period fresh water was supplied to the channel, continuously, from one of two pumps and entered the channel just upstream of the screw pump. Water left the channel from a small slit exit on the side of the channel, about 45 m downstream of the screw pump. The larger pump supplied water at a rate of *ca.* 10.2 m^3 h^{-1}, the smaller at a rate of *ca.* 4.2 m^3 h^{-1}. The advantage of this system is that throughflow (rate of inflow and outflow) can be controlled independently of water velocity; recirculation provides a relatively large volume of water moving at comparatively high velocities over sufficient substrate without either depleting the aquifer or interfering with the natural drainage system of the area. The replenishment of water from the chalk aquifer allows the total throughput of nutrients to be calculated accurately because the chemistry of the input is relatively constant and continuous monitoring is unnecessary.

A salt (NaCl) dilution method was used to calculate the volume of water in the channel. The inflow and outflow points on the channel were stopped off and a known quantity of NaCl

Downloaded from rstb.royalsocietypublishing.org

was added. The concentration remained constant after 1 h and no change was detected after a further 24 h. The rate of exchange between the main body of water and the interstitial water was, therefore, assumed to be rapid. The retention time of the water in the channel was estimated by measuring the rate of dilution of the NaCl after the exit had been reopened and through-flow recommenced. At the beginning of 1976 the channel was filled with clean gravel (mean diameter 40 mm, supplied from a local quarry mining tertiary deposits), to a depth varying from 0.50 m at the outfall of the pump to 0.30 m at the inflow of the pump (gradient *ca.* 1:250). The mean depth of the water above the gravel was 0.36 m. For ease of sampling, small samplers 100 mm in diameter and 100 mm deep with a circular wooden base and sides of plastic 'garden mesh' (5 mm) were constructed (Ladle *et al.* 1980). These samplers allowed a free exchange of interstitial water and were sunk into the gravel with their tops level with the surface gravel. About 500 were evenly placed in rows of five across the channel. A few flints from the adjoining stream (< 50 m away) were placed at the outfall of the screw pump to 'seed' the system with naturally occurring algae. The growth of algae was then followed from April to December 1976. At the end of 1976 the upper 200 mm of gravel were removed and replaced with clean gravel; the sampling pots were replaced at the same time. By covering the channel with black polyethylene, experiments were done in the dark during February and March, in both 1976 and 1977, to establish non-phototrophic effects on water chemistry. The dark covers were removed in April and the growth of algae followed until July 1978. A three-way direct comparison could then be made between algal development during the initial colonization phase in the channel, growth the following spring when the substratum remained undisturbed by changes in discharge (also in the channel) and seasonal changes in natural streams (Marker 1976*a*).

2.2. *Temperature*

The temperature of the channel water, ground water and the water of the adjacent natural stream was measured by means of thermisters coupled to a Grant chart recorder during 1976 and 1977 and then to a Solatron 3430 Compact Logger during the summer of 1978.

2.3. *Chemistry*

Alkalinity, pH, and concentrations of Ca, Mg, K, Na, NO_3-N, PO_4-P, SiO_2-Si were measured in the inflow water, outflow water and the adjacent natural stream at least weekly and more frequently during periods of intense biological activity. The methods were generally those of Casey & Newton (1973), except for silicon (Mullin & Riley 1955).

2.4. *Estimation of benthic chlorophyll a*

Samplers, containing gravel, were removed at random at weekly intervals during the initial colonization phase and every 2 weeks thereafter. Normally 10 samplers were removed on each occasion but sometimes 15 were taken, if the 95% confidence intervals increased above 15% of that of the preceding set of samples. *Cladophora* was removed initially and treated separately. The gravel from each sampler was transferred to two, wide-necked, screw-top glass jars which effectively divided it into an upper 50 mm and a lower 50–100 mm sample. Chlorophyll *a* was estimated following extraction into 275 ml of methanol overnight at 5 °C (Marker 1972, 1976*a*).

Tests showed that neither cold nor hot methanol extracted more than 25% of the chlorophyll *a* from *Cladophora*. Prefreezing of the sample increased the subsequent extraction to more than

Downloaded from rstb.royalsocietypublishing.org

95% without apparent loss of pigment (Marker 1980). However, freezing had no significant effect on the extraction from gravel samples. Consequently chlorophyll *a* was usually extracted from fresh gravel samples but from frozen *Cladophora* samples.

2.5. *Examination of benthic flora*

The composition of the algae, growing on stones, was examined on each occasion that chlorophyll was estimated by removing 15 stones at random from the bed of the channel. A sample comprised one stone and the algae attached to it. Several methods were then used successively to remove algae from the stones.

(i) *Cladophora*, which was not present on all stones, was removed and examined separately.
(ii) Very loosely attached algae (largely diatoms) were removed by brushing with a test tube brush.
(iii) More firmly attached algae were removed with a stiff nylon tooth brush.
(iv) Encrusted algae were scraped off with a scalpel.
(v) Finally the stone was abraded vigorously with a wire brush. This treatment undoubtedly macerated some of the algae but was only used as the final step.

The algae removed by treatments (ii)–(v) were pooled.

Because the concept of substrate surface area is somewhat obscure and the interstitial spaces of the gravel are not filled with soft sediment thus extending the colonizable surface area significantly into the third dimension, the area of channel bed, rather than the area of substrate surface, was used as the basis of comparisons between different variables. The area subtended by each stone was estimated from photographs.

The wide variety of morphological types of algae growing close together on the stones made microscopical examination difficult. Smaller species of *Chamaesiphon*, *Pleurocapsa* and *Lyngbya* etc. did not readily separate out into individual cells or trichomes before cells of species like *Gongrosira incrustans* and *Chamaesiphon polonicus* had been macerated. Moreover, the estimation of numbers of filaments was not considered valid because their length and hence, in part, their numbers would have been a reflection of the degree of homogenization. Homogenization was not complete and not only were clumps of individual species very difficult to count but their non-random distribution would have introduced unquantifiable errors. It was, therefore, not possible to disperse the attached algae sufficiently to count cells with the use of either sedimentation chambers or Sedgewick Rafter chambers.

Samples were preserved in 2% glutaraldehyde. Formaldehyde was avoided because of toxins arising from samples treated later with HCl (Dewhurst 1976). Some material was always examined live.

With use of a spatula and a glass rod samples were homogenized as far as was possible without macerating the algae and a small volume was placed under a coverslip. By using a grid-intersection micrometer eyepiece, fields were selected at random and the species present at the grid intersections were noted. At least 200 positive records were made for each sample so that over 3000 recordings were made on each sampling date. Means and 95% confidence intervals were calculated from the proportion of each species in each of the samples (Snedecor & Cochran 1967, pp. 511–516). Both normal and arcsine-transformed data were used in the calculation but only the estimates from the normal data are illustrated because both showed the same seasonal patterns. Moreover the mean proportions calculated from normal data add up to

Downloaded from rstb.royalsocietypublishing.org

unity whereas those from arcsine-transformed data do not. As many species occurred in low numbers this discrepancy was frequently considerable (*ca.* 20%). No account was taken of differences in biomass between samples so that bias is introduced in this method.

Diatoms were examined after dispersion in dilute HCl (Tippet 1970), which also served to dissolve $CaCO_3$ present with the algae in the original samples. In many cases, identification could only be made at the specific level from cleaned frustules. Numbers of individual species were then related to estimates of groups of species obtained from the preserved samples. Volumes of species were estimated from the linear dimensions at approximately monthly intervals. At least 10–20 individuals of each species had to be measured to obtain 95% confidence intervals of the linear dimensions of *ca.* 10%. The soluble $CaCl_2$ was removed by washing and centrifugation. The organic matter was oxidized by treatment with a hot 1:3 (by volume) mixture of concentrated HNO_3 and concentrated H_2SO_4. The frustules were washed with distilled H_2O and mounted in Naphrax. Means and 95% confidence intervals were estimated from logarithmically transformed data after the number of diatoms in each sample had been recalculated in terms of unit area of channel bed so that bias was not introduced by samples of different sizes.

2.6. *Cladophora biomass*

Cladophora was also estimated by a cropping technique. A quadrat 50 cm × 15 cm × 30 cm was pressed onto the gravel and the *Cladophora* was removed by hand from within the box. Samples were immediately dried at 105 °C and weighed; no attempt was made to remove the epiphytes. The dried material was milled and subsamples were ashed at 550 °C to estimate the organic weight. Surface water was removed from other samples with a domestic spin drier (Edwards & Owens 1960) and subsamples were used to determine chlorophyll *a*: fresh weight ratios and dry weight: fresh weight ratios.

2.7. *Sediment samples*

Sediment samples (Welton & Ladle 1979) were analysed for chlorophyll *a* and phaeopigments by extraction into methanol and transfer to 90% acetone before spectrophotometry (Marker 1972, 1976*a*).

2.8. *Suspended materials*

Suspended solids were examined, at least weekly, by taking 5 l of water from the surface at the outflow. No attempt was made to study the vertical profile in detail but preliminary studies suggested little difference over most of the column. Water was initially screened through a 0.5 mm sieve; 4 l were filtered through GF/C glass-fibre filters from which pigments were extracted by boiling in 100% methanol. The pigments were transferred quantitatively to 90% acetone before spectrophotometry (Marker 1972; Marker & Gunn 1977). Algae, from a further 100 ml of water, were concentrated with Lugol's iodine and numbers were estimated with the aid of a sedimentation chamber and inverted microscope (Lund *et al.* 1958; Marker & Gunn 1977). At least 100 individuals of each major species were counted on every occasion.

No attempt was made to estimate large particulate drifting organic matter recirculating round the channel, but a 1 mm screen fixed to the outflow trapped material leaving the channel. The screen was cleaned once every 24 h and twice a week the material removed was analysed for chlorophyll *a* and phaeopigments.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

2.9. *Waterston Stream*

For comparisons, analogous studies were done in a natural source water stream that ran within a few metres of the channel (Ladle & Bass 1981). On each sampling date 20 stones were removed at random. Pigments were extracted from ten of these stones and chlorophyll *a* was estimated. Algae were removed from the other ten stones and examined as before. The area projected by each stone was estimated from photographs and hence the densities of chlorophyll *a* and of algae were calculated.

This stream is usually dominated by macrophytes (*Ranunculus* spp., *Apium nodiflorum* (L.) Lag. and *Nasturtium officinale* R. Br.). These macrophytes were removed by hand from a 100 m reach of the stream, immediately before the dark covers were removed from the channel. Algal colonization of both of the exposed gravels could thus be followed simultaneously.

2.10. *Photosynthesis studies*

This type of channel, which is relatively deep and fast flowing, cannot be used to estimate photosynthetic rates from changes in oxygen concentration along the length of the channel because the total volume of water passes through the screw pump approximately once every $2\frac{1}{2}$ min, so that effectively the oxygen concentration is maintained in equilibrium with air. A recirculating channel 1.5 km long would have been required to give a period of contact between the flowing water body and the biota on the substratum sufficient for useful measurements on gas changes to be made.

Photosynthesis was therefore measured *in situ* during 1977 and 1978 in Perspex photosynthesis chambers (Marker 1976*b*). The uptake of ^{14}C, rather than the output of oxygen, was used to measure photosynthesis. The archimedean screw pump effectively kept the water saturated with oxygen and, because the biomass was higher than in natural streams, the dangers from oxygen bubble formation were much increased. Ampoules of $Na_2{}^{14}CO_3$ were prepared from material supplied by Radiochemical Centre, Amersham, code CFA2 (> 1.85 GBq mmol^{-1}) and buffered at pH 9.5 to prevent loss of $^{14}CO_2$.

Stones, taken at random, were placed in the base of each chamber which was then clamped to the upper half and filled with water from the channel; 0.59217 Bq (16 μCi) of $Na_2{}^{14}CO_3$ was injected and the chambers were incubated on the bed of the channel for the 2 h preceding midday G.M.T. At the same time photosynthetically available radiation was monitored continuously on the channel bed (Marker 1976*b*). The carbonate added from the ampoules was less than 0.1% of the total and the high pH of the ampoule did not affect the pH of the water in the chamber because of the buffering capacity of the calcium bicarbonate (more than 40 mg C as calcium bicarbonate).

After 2 h the chambers were brought to the surface, the water was drained off and the chambers were returned in the dark, to the laboratory within half an hour. The stones were quickly removed from the chamber and frozen. Metabolic processes, involving ^{14}C, were still taking place in the dark but these were assumed to be small compared with the processes that had taken place in the light. Moreover the use of preservatives immediately after removal from the channel was considered inadvisable because of possible interferences in subsequent analyses (particularly with chlorophyll). At each stage in the subsequent analysis ^{14}C was estimated on a Packard Tri-carb liquid scintillation spectrometer (C2425). Koch-Light Unisolve 1 was used as the scintillation cocktail and each vial was counted either for 100 min or up to 40 000 counts.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

Small quantities of water (0.05 ml) or methanol (2 ml) formed a clear liquid with the cocktail but 5 ml of water formed a stable gel. Quench curves were constructed for the different cocktail mixtures used, with chloroform as the primary quenching agent. Phaeopigments, present in the pigment extracts, caused some colour quenching. Tests with chloroform, phaeophytin and internal radiochemical standards showed that colour quenching differed by less than 1 % from assumed chemical quenching. ^{14}C analysis was done in four stages.

(i) The initial concentration of ^{14}C was estimated by adding 0.05 ml of the original chamber water to 10 ml of Unisolve 1 containing 0.5 ml of 2-phenylethylamine.

(ii) Pigments were extracted from the algae on the stones by immersion in methanol overnight in the dark at 4 °C (Marker 1976*a*). The pigment solution was filtered and made up to a known volume (100–250 ml). A small amount was used for chlorophyll *a* analysis. A further 50 ml were removed, acidified with HCl to 0.1 M and aerated for $1\frac{1}{2}$ h to remove residual $Ca^{14}CO_3$ and $Ca(H^{14}CO_3)_2$ and the volume was readjusted to 50 ml; 2 ml were mixed with 10 ml of Unisolve 1.

(iii) The stones and filter from the chlorophyll extraction were then covered with distilled water which was maintained at pH 2 with HCl during aeration for up to 2 h. This procedure was important because after a few months deposits of $CaCO_3$ built up on the stones. Moreover because of these deposits and the relatively small proportion of $^{14}CO_2$ fixed into the organic matter, it was felt that immersion in acidified water was preferable to exposing the stones to fumes of concentrated HCl (Wetzel 1964). After aeration, the water was filtered, the stones were rinsed and the water was made up to volume; 5 ml were mixed with 10 ml of Unisolve 1.

(iv) The organic residues on the stones and filters were oxidized by wet combustion and the CO_2 was trapped in 1.0 M NaOH solution. The carbonate was precipitated as $BaCO_3$, allowed to settle for 24 h, and then separated from the residual NaOH by repeated centrifugation and washing with distilled water. The $BaCO_3$ was centrifuged at only 300 *g* to provide a pellet that was sufficiently loose to be resuspended easily in water. After being washed the $BaCO_3$ was resuspended in 100 ml of water and 5 ml of the suspension were added to 10 ml of Unisolve 1. The gel formed kept the $BaCO_3$ in suspension.

Alkalinity, and hence total dissolved inorganic carbon in the water, was estimated by Gran titration (Mackereth *et al.* 1978). Estimates of total dissolved inorganic carbon by Gran titration differed by less than 0.5 % from infrared gas analysis of CO_2 released by acidification and by *ca.* 5 % from estimates by titration against 0.01 M acid with BDH 4.5 indicator, calculated from carbon dioxide–carbonate tables (Rebsdorf 1972).

3. Results

3.1. *Temperature*

The temperature of borehole water is relatively constant throughout the year and varies between 10.0 and 11.7 °C (Crisp 1970). However, the channel has a large volume (53.2 m^3) compared with the inflow rate (4.2 $m^3\ h^{-1}$). The temperature of the channel water, therefore, to some extent follows the diurnal changes in ambient temperature (figure 1). These changes are of the same magnitude as those found in local streams (Marker 1976*a*).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

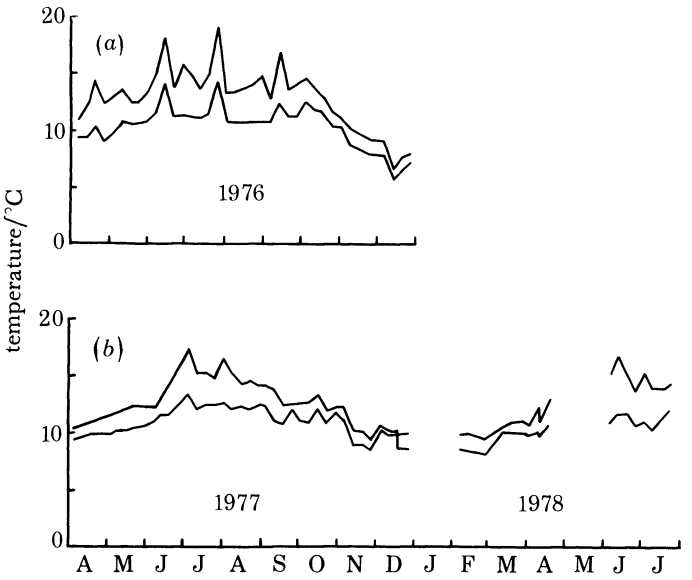

FIGURE 1. Seasonal variation in the weekly means of the daily maximum (upper curve) and minimum (lower curve) temperature. (*a*) April to December 1976; (*b*) April 1977 to July 1978.

TABLE 1. RANGE IN CHEMICAL COMPOSITION BETWEEN SIX WATER SAMPLES TAKEN CONSECUTIVELY FROM THE INFLOW PIPE AND THE RANGE BETWEEN SIX WATER SAMPLES TAKEN AT DIFFERENT POINTS AROUND THE CHANNEL

	inflow water	channel water
alkalinity/(mequiv l^{-1})	4.54–4.60	4.35–4.40
calcium/(mg l^{-1})	98–100	87.0–88.5
reactive phosphate/(μg l^{-1})	35.0–36.5	11–12
nitrate/(mg l^{-1})	5.20–5.35	5.15–5.25
silicon/(mg l^{-1})	3.65–3.70	3.15–3.16

TABLE 2. CHEMICAL COMPOSITION OF INFLOW WATER AND OUTFLOW WATER OF THE CHANNEL, EXPRESSED AS THE MEAN AND 95% CONFIDENCE LIMITS (c.l.)

year . . .	1976				1977			
source . . .	inflow		outflow		inflow		outflow	
	mean	c.l.	mean	c.l.	mean	c.l.	mean	c.l.
alkalinity/(mequiv l^{-1})	4.48	0.02	4.14	0.14	4.59	0.02	3.76	0.05
Ca/(mg l^{-1})	98.7	0.7	91.3	2.9	98.9	0.04	82.2	1.07
Mg/(mg l^{-1})	2.06	0.04	2.09	0.03	2.16	0.03	2.15	0.03
Na/(mg l^{-1})	8.7	0.1	8.7	0.1	8.60	0.06	8.50	0.05
K/(mg l^{-1})	1.32	0.07	1.28	0.04	1.25	0.02	1.21	0.02
NO_3-N/(mg l^{-1})	4.53	0.07	4.54	0.07	5.00	0.06	4.91	0.06
SiO_2-Si/(mg l^{-1})	4.27	0.06	3.97	0.22	3.70	0.02	3.35	0.19
reactive PO_4-P/(μg l^{-1})	35.2	1.4	19.4	3.3	37.3	0.7	10.4	1.27
total PO_4-P/(μg l^{-1})	38.8	2.3	22.1	3.3	39.2	0.8	14.9	2.43
pH	7.48	0.07	8.34	0.05	7.46	0.02	8.40	0.03

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

3.2. *Water chemistry*

The chemical composition of the input water from the borehole varied little between 1976 and 1978 and provided a stable base line from which to observe the effect of algae on nutrients in the water. Borehole water mixed in the channel rapidly because it entered just before the screw pump. The composition of the water varied little along the length of the channel (table 1).

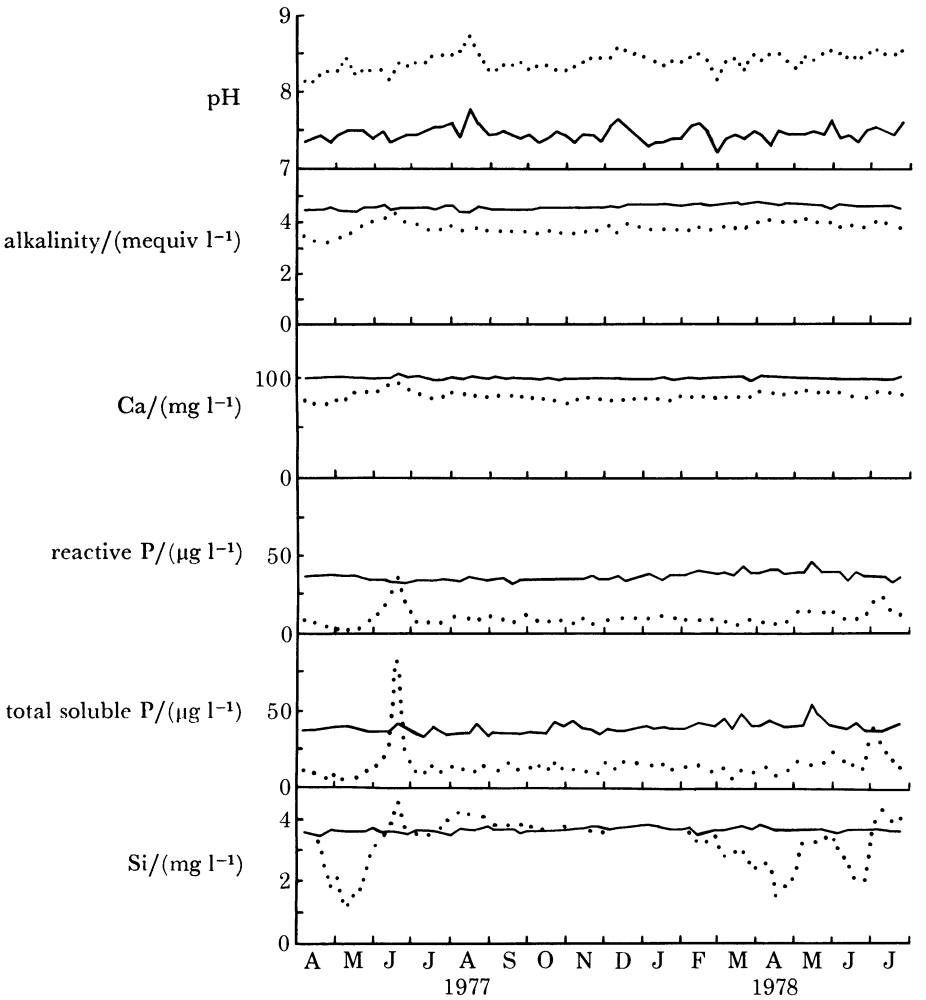

FIGURE 2. Seasonal variation in the concentration of the major chemical nutrients in inflow water (———) and outflow water (· · · · · ·).

Experiments in the dark were reported by Ladle *et al.* (1977) and a summary of the chemical changes between inflow and outflow in the light are shown in table 2. Substantial changes in the chemistry of the water during its residence in the channel were observed in 1976. These were monitored more closely during 1977 and 1978 and are shown in more detail in figure 2.

The calcium concentration in the outflow water was *ca.* 20 % lower than in the inflow water. Changes in alkalinity broadly followed the same pattern (figure 2) and both were due to loss of CO_2 and precipitation of $CaCO_3$ (Ladle *et al.* 1977; House 1981 *a*, *b*). However, outflow concentrations started to increase in May 1977, reached a maximum in June and then declined

Downloaded from rstb.royalsocietypublishing.org

again in July. They then remained *ca.* 20% lower than the inflow concentrations until the following spring, when a rise in concentration was again detected.

The pH of the outflow water was always substantially above that of the inflow due to a rapid loss of excess free CO_2. A loss of CO_2 and rise in pH occurs after water enters a natural stream from the borehole during passage downstream but is not usually associated with a marked change in calcium concentration (Casey 1969).

Silicon concentrations in the outflow water showed wide variations during 1977 and 1978, varying between 1.8 and 4.62 mg l^{-1}. Mean inflow concentrations were 3.70 mg l^{-1} with 95% confidence interval of ± 0.02. As the precision of the method is $\pm 2\%$ at 4 mg l^{-1} (American Public Health Association 1965) this means that for substantial periods of the year large amounts of silicon were either being taken up or released within the system. These variations in relation to diatom growth are discussed later on. Maximum periods of uptake (outflow concentration less than inflow concentration) were in April and May 1977 and April to June 1978. Periods of release (outflow concentration greater than inflow concentration) were June 1977, August to September 1977 and July 1978.

Soluble reactive phosphorus, as measured by the molybdate method, is largely inorganic phosphate but perhaps also small amounts of labile organic phosphorus. Total soluble phosphorus includes molybdate-unreactive phosphorus which is probably largely organic but may also contain polyphosphates. During experiments in the dark in February and March 1977, reactive phosphate in the outflow varied between 10 and 13 μg PO_4-P l^{-1}. Inflow concentrations were *ca.* 37 μg l^{-1} and the difference was probably due to coprecipitation with $CaCO_3$ (Ladle *et al.* 1977). When the dark covers were removed in April, the concentration fell further to 2.4 μg l^{-1} by 16 May, but then increased to approximately inflow levels (36.3 μg l^{-1} on 20 June), before settling down to between 7 and 12 μg l^{-1} for the remaining summer, autumn and winter. Concentrations fell in April 1978 to 5.7 μg l^{-1} before rising again in May and July 1978 (21.5 μg l^{-1}). Total phosphate (reactive and unreactive) followed a broadly similar pattern, reaching maxima in June 1977 (82.0 μg PO_4-P l^{-1}) and early July 1978 (39.6 μg PO_4-P l^{-1}). Both these concentrations were higher than that of the inflow.

Throughout the experiments concentrations of Na^+, K^+, Mg^{2+} and NO_3^- in the inflow differed little from the outflow.

3.3. *Silicon release from diatoms in laboratory experiments*

Twelve high-density polyethylene bottles were cleaned with chromic acid, washed out and left soaking in distilled water for 1 week, after which the bottles were rinsed out with water from the channel inflow and then 1 l of inflow water was added to each bottle. A suspension of benthic diatoms, which had been obtained by washing gently a few flints from the channel, was concentrated by centrifugation and added to eight of the bottles. Ten millilitres of chloroform were added to each of the bottles (Golterman 1960) which were then shaken for 5 min. A sample was then removed and the dissolved silicon was estimated. The bottles were divided into two sets, each set containing four diatom samples in inflow water and two bottles with inflow water alone (controls). Both sets were kept in the dark in the laboratory, one at 20 °C and the other at 10 °C. The release of silicon appeared to be temperature-dependent (figure 3). After 8 months silicon concentrations in samples that had been kept at 10 °C had only reached 8.6 mg l^{-1}, compared with 12.4 mg l^{-1} in samples at 20 °C. The concentration of silicon in the control samples remained constant throughout the experiment.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

In a second experiment samples were kept at room temperature in the dark for 5 months and the dissolved silicon was monitored in the water. Also initial and residual silica (insoluble) was estimated by the standard molybdate method after fusion with Na_2CO_3 at 950 °C (Allen *et al.* 1975). Approximately half the silicon had dissolved after 68 days and only 20% was left when the experiment ended after 135 days.

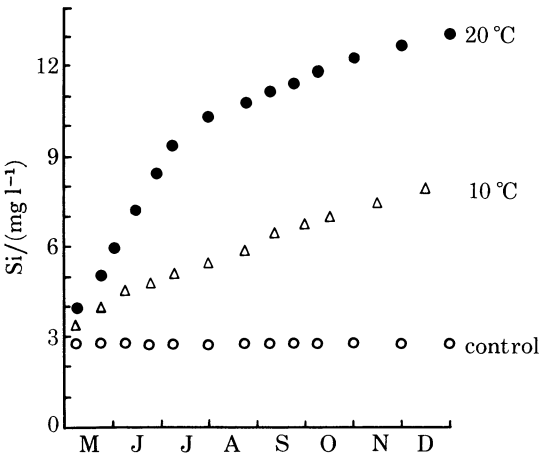

FIGURE 3. The release of molybdate-reactive silicon from diatoms.

3.4. *Chlorophyll a densities on the gravel*

Following the removal of dark covers in April 1976, there was a lag period of about 2 weeks, after which diatoms began to grow rapidly and reached a maximum of *ca.* 400 mg chl *a* m^{-2} after 7 weeks (figure 4*a*). The chlorophyll density then dropped to between 80 and 100 mg m^{-2}. Chlorophyll density rose again in the autumn to *ca.* 300 mg and fell only slightly in the early winter, remaining high at *ca.* 200 mg m^{-2}.

A similar pattern occurred after the removal of the dark covers in April 1977. Chlorophyll *a* increased very rapidly on the surface flints (0–50 mm) after an initial lag phase of 1 week (figure 4*b*). Densities increased from 1.2 to 33 mg chl *a* m^{-2} between 12 and 18 April and from 33 to 298 mg m^{-2} between 18 and 26 April. Thus over a period of 2 weeks densities increased by nearly 300-fold (over a similar 2 week period in 1976 densities increased 200-fold). For 3 days following 26 April the dark covers were replaced to estimate changes in silicon concentration in the dark (see § 3.18(iii)); during that week chlorophyll *a* densities decreased insignificantly by 13 mg m^{-2}. After the removal of the covers chlorophyll *a* increased again and reached a maximum of 518 mg m^{-2} on 16 May. Density remained static for 2 weeks between 9 and 25 May but then declined rapidly, reaching a minimum at the beginning of August. Densities gradually increased again until the end of October but then declined slowly to a minimum in mid-February. They increased again during the spring and reached a maximum in April 1978.

Samples from the 50–100 mm layer of gravel contained substantially less chlorophyll *a* with densities generally below 100 mg m^{-2} except in May 1977 and the spring of 1978. Maximum densities during the initial colonization phase and in the spring of 1978 occurred 1 week later than on the surface gravel (figure 4*b*). The decision to use 100 mm sampling units was justified by the analysis of units some 200 mm deep, introduced for invertebrate sampling. Less than

Downloaded from rstb.royalsocietypublishing.org

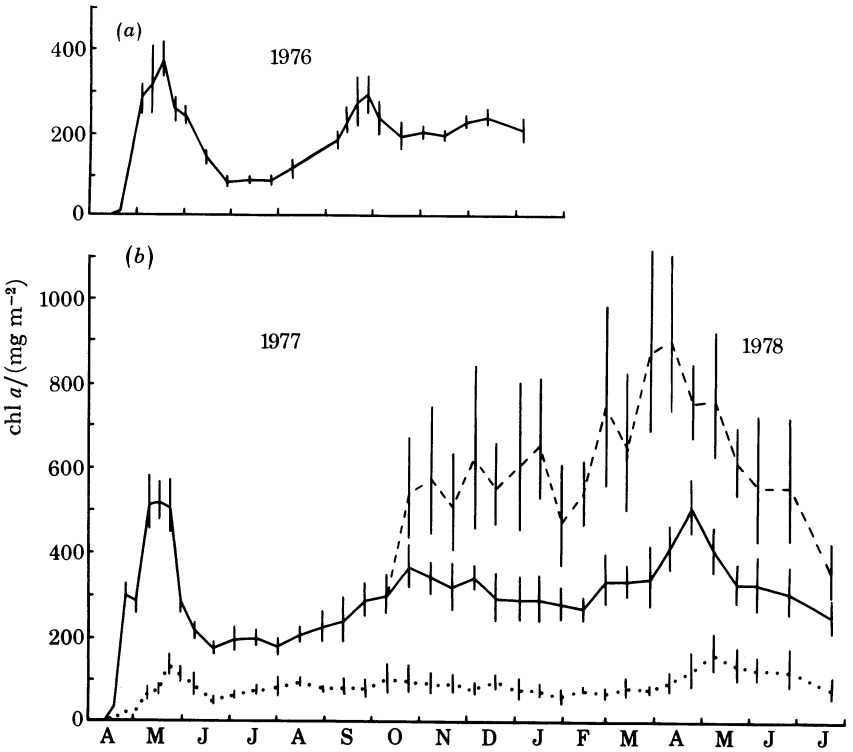

FIGURE 4. Seasonal variation in benthic chlorophyll *a*: (*a*) April to December 1976; (*b*) April 1977 to July 1978; ——— epilithic chlorophyll *a* between 0 and 50 mm depth, - - - - epilithic chlorophyll *a* and *Cladophora* between 0 and 5 mm depth, · · · · · · epilithic chlorophyll *a* between 50 and 100 mm depth. Vertical bars represent 95% confidence intervals.

TABLE 3. DISTRIBUTION OF CHLOROPHYLL *a* AND PHAEOPIGMENTS IN THE GRAVEL

(Errors expressed as 95% confidence limits.)

depth cm	biomass/(mg m^{-2}) chl *a*	biomass/(mg m^{-2}) phaeopigments	distribution (%) chl *a*	distribution (%) phaeopigments	degradation chl *a* (%)
0–5	163.4 ± 16.9	14.1 ± 2.0	79	44	8
5–10	29.2 ± 6.1	7.2 ± 1.1	14	22	20
10–15	8.2 ± 2.2	5.5 ± 1.4	4	17	40
15–20	6.3 ± 2.2	5.5 ± 2.1	3	17	47

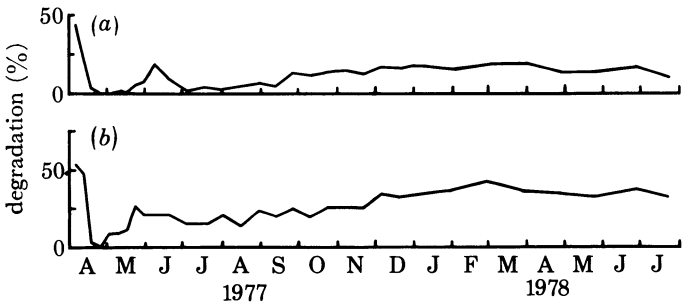

FIGURE 5. Seasonal variation in percentage degradation of the epilithic chlorophyll *a*: (*a*) 0–50 mm depth; (*b*) 50–100 mm depth.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

10% of the total chlorophyll occurred below 100 mm, although the proportion of degraded chlorophyll increased (table 3).

During the first 2 weeks of the initial colonization phase the amount of pigment extracted from the gravel was very small (less than 1.5 mg m^{-2}). The degree of degradation was high because the source of this pigment was old detritus on the surface of the gravel. The degree of degradation dropped rapidly as soon as the algae began to grow (figure 5). Apart from this initial period the pigment from the surface gravel was always less than 20% degraded whereas that from the subsurface gravel (50–100 mm) was between 20 and 40% degraded. The increase in degradation at the end of May corresponds to the decline in the algal biomass.

3.5. *Cladophora*: *chlorophyll a*

Cladophora appeared in small amounts during August 1977 and by the middle of October was present in sufficient quantities to appear in gravel samples. It was an essentially unbranched form, attached to the stones. *Cladophora* chlorophyll may have been underestimated on 10 October owing to poor extraction from fresh material but after this it was processed separately to ensure total extraction (figure 4*b*). During the autumn *Cladophora* contributed substantially to the algal biomass but declined in midwinter before appearing to increase again in the spring. In fact the *Cladophora* continued to decline in the spring and the increase was due to a massive growth in epiphytic diatoms. The *Cladophora* appeared to die very rapidly under the dense epiphyte cover. Live diatoms were therefore lost from the channel as they were carried away with the *Cladophora*. By July 1978 the *Cladophora* had virtually disappeared. Separate estimates are not available for *Cladophora* chlorophyll and epiphyte chlorophyll during the spring because it was impossible to separate the diatoms from the decaying *Cladophora*.

3.6. *Cladophora biomass*

Cladophora was also estimated by cropping from a large quadrat (750 cm^2) each month but errors were still large with this method (figure 6). Organic weights were high in December 1977 (12.2 g m^{-2}), declined during the winter but then increased in the spring as the epiphytes grew. Maximum biomass was reached in early March 1978 (14.9 g m^{-2}) owing to heavy epiphyte cover. After then the decline in *Cladophora* was faster than the increase in epiphyte cover. There was insufficient *Cladophora* to crop after May.

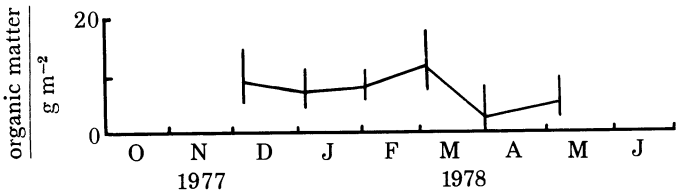

FIGURE 6. Biomass of *Cladophora glomerata*. Vertical bars represent 95% confidence intervals.

3.7. *Sedimentation of algae*

The loss of algae from the surface gravel into the lower layers was measured by means of sedimentation traps during the initial colonization phase in 1977 (figure 7). Daily losses were calculated from the sediment accumulating in traps over 14 days. Both chlorophyll *a* and

Downloaded from rstb.royalsocietypublishing.org

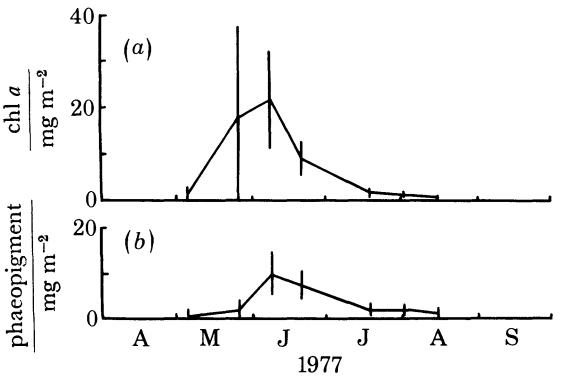

FIGURE 7. Sedimentation of diatoms, expressed in terms of (*a*) chlorophyll *a* and (*b*) phaeopigments, during the initial colonization phase (1977). Vertical bars represent 95% confidence intervals.

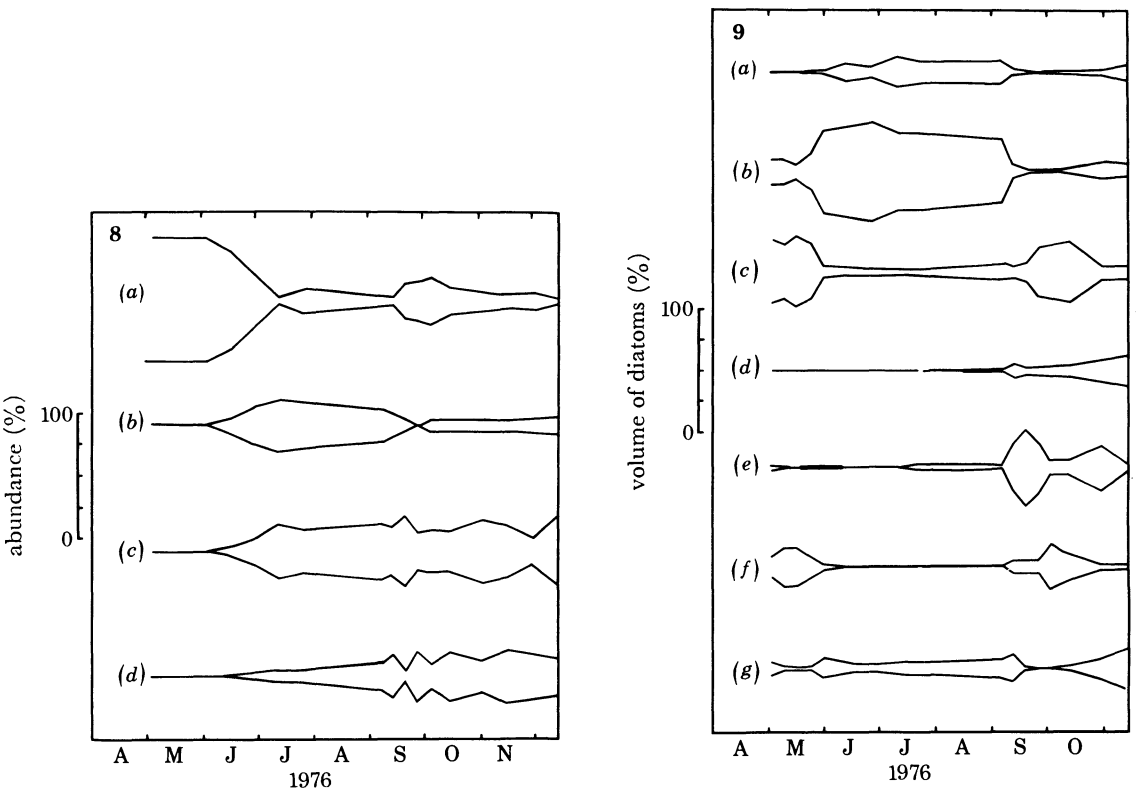

FIGURE 8. Seasonal variation in 1976 of the major groups of epilithic algae, expressed as percentage occurrence: (*a*) diatoms; (*b*) Chlorophyceae; (*c*) Chamaesiphonales; (*d*) Hormogoniales.

FIGURE 9. Seasonal variation in 1976 in the proportion of epilithic diatoms (based on volumes): (*a*) *Achnanthes lanceolata*; (*b*) *Achnanthes minutissima*; (*c*) *Meridion circulare*; (*d*) *Nitzschia fonticola*; (*e*) *N. palacea*; (*f*) *Synedra ulna*; (*g*) miscellaneous.

phaeopigments reached their maximum sedimentation during the 14 days ending on 8 June, which is 1–3 weeks after the maximum surface biomass. These pigments were only 31% degraded, suggesting a substantial loss of living algae. Chlorophyll *a* degradation gradually increased as total sedimentation decreased. Between 21 April and 20 June 0.690 g chl *a* m^{-2} and 0.268 g of phaeopigment per square metre were sedimented.

Downloaded from rstb.royalsocietypublishing.org

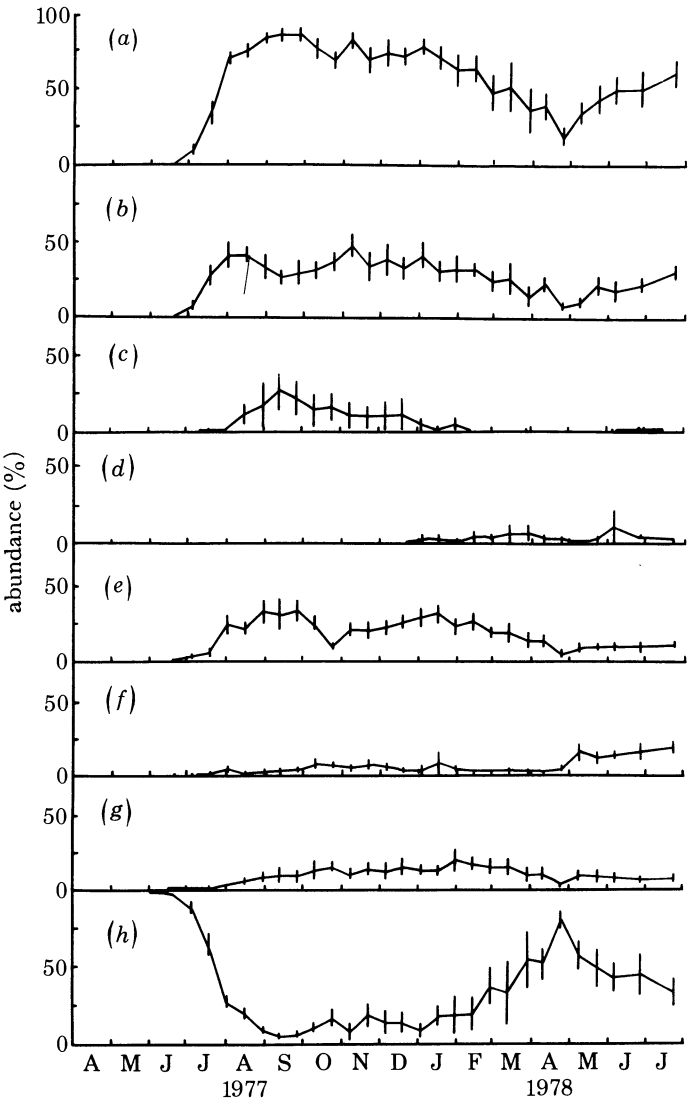

FIGURE 10. Seasonal variation in 1977 and 1978 in the epilithic algae, expressed as a percentage of the abundance of the whole epilithic flora: (*a*) total Cyanophyceae; (*b*) *Lyngbya kützingii*; (*c*) *Phormidium autumnale*. (*d*) *Phormidium incrustans*; (*e*) *Chamaesiphon polymorphus*; (*f*) miscellaneous Cyanophyceae; (*g*) *Gongrosira incrustans*; (*h*) total diatoms. Vertical bars represent 95% confidence intervals.

3.8. *Preliminary examination of the flora in* 1976

The initial colonization phase in May was dominated by diatoms, with green and blue-green algae (*Phormidium foveolarum* Gom. and *Lyngbya kützingii* (Schmidle)) developing during the summer (figure 8). Although the May chlorophyll peak was dominated by large numbers of *Achnanthes minutissima* (Kütz.), *Meridion circulare* Agardh and *Synedra ulna* (Nitzsch) Ehr. were more important in terms of volume (figure 9). The autumn chlorophyll peak arose through a further growth of diatoms covering the encrusting green and blue-green algae, with *Nitzschia palacea* Grun. and *Nitzschia fonticola* Grun. becoming particularly significant. During this preliminary examination, estimates were based on the mean of three samples.

Downloaded from rstb.royalsocietypublishing.org

3.9. *Seasonal variation in flora during* 1977 *and* 1978

During this period estimates were based on 15 samples on each occasion. Similar seasonal variations were observed during 1977 and 1978. Diatoms dominated the flora exclusively during the initial colonization phase between April and July (figure 10). A marked increase in the proportions of Cyanophyta and Chlorophyta occurred from August onwards and Cyanophyta dominated the flora throughout the autumn and winter. Diatoms started to increase again in February 1978 and reached a maximum in April before declining again. The relative decline in the Cyanophyta was largely due to an increased growth of diatoms overlying the crust of Cyanophyta.

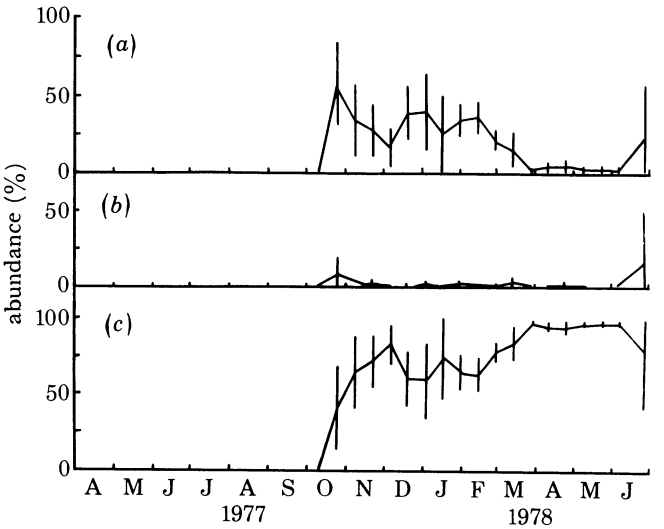

FIGURE 11. Seasonal variation in 1977 and 1978 in the epiphytic algae, growing on *Cladophora*, expressed as a percentage of the abundance of the whole epiphytic flora. Vertical bars represent 95% confidence intervals: (*a*) *Chamaesiphon* spp.; (*b*) miscellaneous Cyanophyceae and Chlorophyceae; (*c*) total diatoms.

The Cyanophyta that developed during the late summer of 1977 were largely lime encrusted (figure 10). *Lyngbya kützingii* Schmidle and *Chamaesiphon polymorphus* Geitler dominated the blue-green flora and rapidly developed into a hard calcareous crust. *Phormidium incrustatum* (Näg.) Gom. came in later in small amounts. *Phormidium autumnale* (Näg.) Gom. appeared in July, developed rapidly in August, reached a maximum in September and gradually disappeared in the autumn; it occurred as a patchy, greenish black gelatinous mass on the stones and was not encrusted with lime. *Pleurocapsa minor* Hansg., *Homoeothrix* spp., *Chamaesiphon polonicus* (Rostof.) Hansg., *Calothrix parietina* Thuret. and *Pseudochantransia* spp. (possibly a juvenile form of *Batrachaspermum*, a genus that is widespread in chalk streams) occurred in small amounts only in the epilithon. *Gongrosira incrustans* Schmidle was the dominant green alga.

The *Cladophora* epiphytes contained a much higher proportion of diatoms. Filamentous Cyanophyta and Chlorophyta were largely absent (figure 11). *Chamaesiphon incrustans* Grun. was present but most of the forms were substantially smaller (2–3 μm diameter) and were probably *Ch. regularis* (F. E. Fritsch). *Ch. polymorphus*, which occurred on the gravel, was absent.

Downloaded from rstb.royalsocietypublishing.org

3.10. *Seasonal variation in the diatom flora during* 1977 *and* 1978

Diatoms showed a very clear seasonal periodicity with principal maxima in May 1977 and April 1978 (figure 12). Minor growths occurred at the beginning of July 1977, at the end of November 1977 and in June 1978. There was a marked reduction in silicon concentration during each period of diatom growth (figures 2, 28) and a significant net release of silicon occurred after each decline in diatom numbers. During May 1978, however, the decline in numbers was not reflected in a net release in silicon because there was a surge in growth during June.

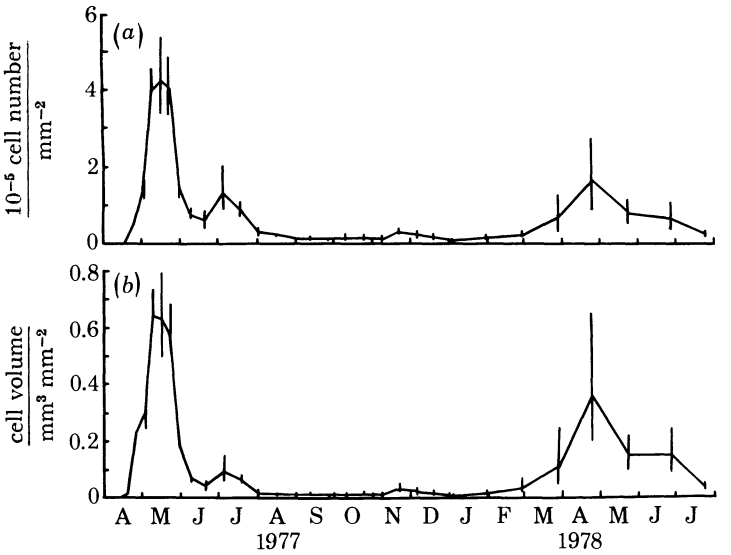

FIGURE 12. Seasonal variation in total epilithic and epiphytic diatoms: (*a*) numbers; (*b*) volumes. Vertical bars represent 95 % confidence intervals.

Total numbers were underestimated 1 week after the removal of the dark covers (12 April 1977) because the very low biomass (less than 2 mg chl *a* m^{-2}) made quantitative removal from rough flint surfaces difficult (Karlström 1978). However, 1 week later removal was relatively easy and between 18 and 25 April 1977 numbers increased 20-fold. Estimated generation time was substantially less than 2 days for four species and less than 3 days for the fifth (table 4). These five species dominated the initial colonization phase. Over the 16 months of study the diatom flora became more complex but the community was still relatively simple. Four different seasonal patterns were found (figure 13).

(i) *Synedra ulna*, *Meridion circulare* and *Nitzschia fonticola* showed maximum numbers in May 1977 and April 1978.

(ii) *Achnanthes minutissima* Kütz. colonized the gravel very rapidly and occurred in large numbers throughout the summer and autumn.

(iii) *Achnanthes pyrenaica* Hust., *Navicula tantula* Hust. and *Amphora ovalis* Kütz. var. *pediculus* Kütz. appeared after the initial colonization phase and remained relatively constant through the late summer and winter.

(iv) *Fragilaria virescens* Rolfs. and *Gomphonema rhombicum* Fricke appeared in the late summer and autumn and then became important the following spring.

Downloaded from rstb.royalsocietypublishing.org

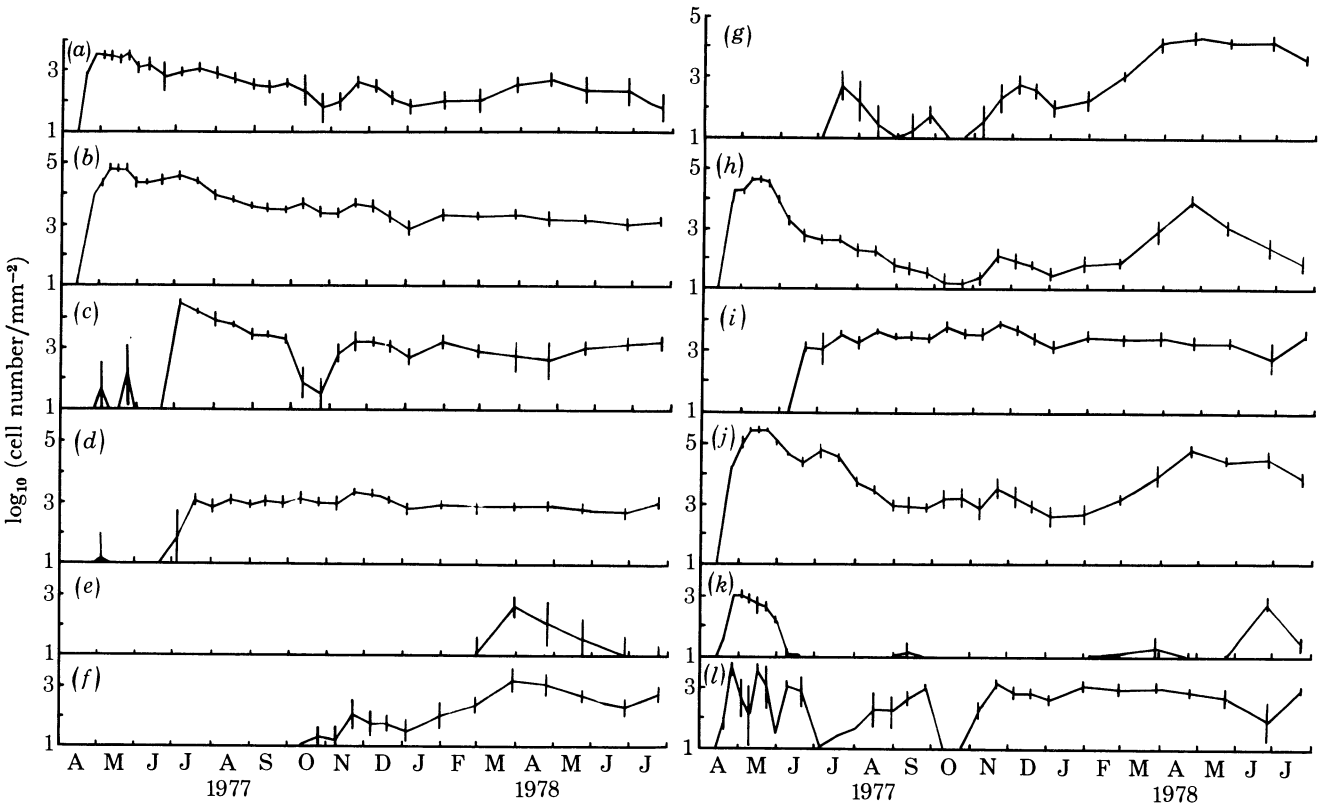

FIGURE 13. Seasonal variation in epilithic diatom flora in 1977 and 1978, expressed in terms of numbers of cells per unit area: (*a*) *Achnanthes lanceolata*; (*b*) *Achnanthes minutissima*; (*c*) *Achnanthes pyrenaica*; (*d*) *Amphora ovalis* var. *pediculus*; (*e*) *Cocconeis placentula*; (*f*) *Fragilaria virescens*; (*g*) *Gomphonema rhombicum*; (*h*) *Meridion circulare*; (*i*) *Navicula tantula*; (*j*) *Nitzschia fonticola*; (*k*) *Synedra ulna*; (*l*) miscellaneous diatoms. Vertical bars represent 95 % confidence intervals.

TABLE 4. DENSITY OF DIATOMS IN SUCCESSIVE WEEKS DURING THE INITIAL COLONIZATION PHASE IN 1977 AND THE ESTIMATED GENERATION TIME

	cell density/mm^{-2} 18 April	25 April	estimated generation time/day
Synedra ulna	42	915	1–2
Meridion circulare	520	15115	1–2
Achnanthes minutissima	221	7997	1–2
Achnanthes lanceolata	576	3601	2–3
Nitzschia fonticola	946	19664	1–2

Diatom volumes, which are illustrated here as proportions of the diatom flora (figure 14), are more useful than cell numbers for comparisons with chlorophyll *a* (figure 4) when diatoms are a major proportion of the algae. The initial colonization phase was clearly dominated by *Meridion circulare*, *Nitzschia fonticola* and *Synedra ulna*, which were again important the following spring (1978), together with *Fragilaria virescens* and *Gomphonema rhombicum*. Note that only these five species contributed significantly to the algal biomass. *Achnanthes minutissima*, *Ach. pyrenaica*, *Amphora ovalis* var. *pediculus* and *Navicula tentula* were only significant contributors to the diatom flora in the intervening months when diatoms, taken together, generally comprised less than 20 % of the total algal flora.

Downloaded from rstb.royalsocietypublishing.org

3.11. *Comparison between the epiphytic and epilithic floras*

Figure 15 illustrates the relative abundance of diatoms, based on cell volumes, epiphytic on *Cladophora*. A comparison with figure 14 illustrates the marked difference from the epilithic diatoms. *Synedra ulna* and *Nitzschia fonticola* colonized the *Cladophora* initially in the autumn and *N. fonticola* was again important the following spring. *Meridion circulare* appeared slightly later

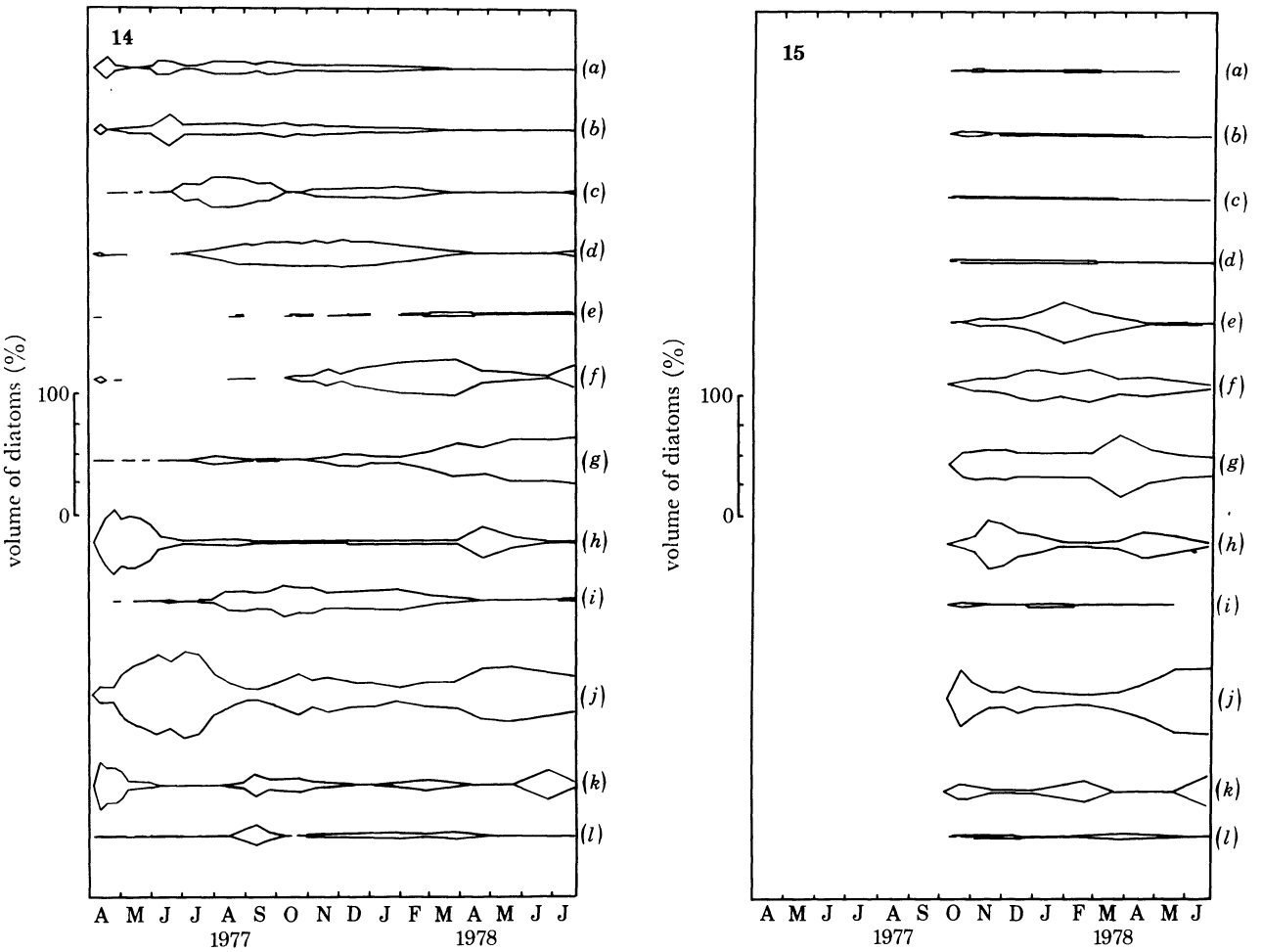

FIGURE 14. Seasonal variation in the proportions of epilithic diatoms in 1977 and 1978, expressed as percentages of the total epilithic diatom volume; (*a*)–(*l*) as in figure 13.

FIGURE 15. Seasonal variation in the proportions of epiphytic diatoms (on *Cladophora*) in 1977 and 1978, expressed as percentages of the total epiphytic diatom volume; (*a*)–(*l*) as in figure 13.

in the autumn and then again in April. *Gomphonema rhombicum* and *Fragilaria virescens* dominated the winter flora. *Cocconeis placentula* (Ehr.), which is a typical epiphyte in chalk streams, comprised over 30 % of the diatoms in mid-January but was virtually absent from the gravel. *Achnanthes pyrenaica*, *Navicula tantula* and *Amphora ovalis*, which were important components of the epilithon during the autumn and winter, were virtually absent from the epiphytic diatom flora. The difference between the two floras was confirmed with a three-way analysis of variance. The first factor was the substrates (gravel and *Cladophora*), the second was sampling dates (11), the third factor included the most abundant species (12). Only 11 dates were used because

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

there was insufficient *Cladophora* in June and July 1978. The comparison was made between the proportions of species because of the difficulties of relating numbers to a comparable unit area of both substrates. Consequently, both substrates and dates showed no differences at all in the analysis of variance because the cumulative total in these directions was always the same (table 5). However, it is the interactions that were of real interest. There was a highly significant

TABLE 5. ANALYSIS OF VARIANCE COMPARING THE EPIPHYTIC AND EPILITHIC DIATOM FLORA ON *CLADOPHORA* AND FLINTS

	degrees of freedom	sum of squares	mean square	variance ratio	probability
A, substrates	1	0	0	0	—
B, dates	10	0	0	0	—
C, species	11	12.62	1.15	370	$<<<0.001$
1st-order interaction					
AB	10	0	0	0	—
AC	11	1.73	0.157	51	<0.001
BC	110	5.45	0.050	16	<0.001
2nd-order interaction					
ABC	110	1.82	1.652	5.33	<0.001
error	1320	4.14	0.0031		
total	1583	25.75			

TABLE 6. ANALYSIS OF VARIANCE COMPARING THE ALGAL FLORA OF *CLADOPHORA* AND FLINTS

	degrees of freedom	sum of squares	mean square	variance ratio	probability
A, substrates	1	0	0	0	—
B, dates	10	0	0	0	—
C, species/groups	10	32.60	3.26	553	$<<<0.001$
1st-order interaction					
AB	10	0	0	0	—
AC	10	10.09	1.01	171	$<<<0.001$
BC	100	7.43	0.0744	12.6	$<<0.001$
2nd-order interaction					
ABC	100	1.92	0.0192	3.25	0.001
error	1210	7.12	0.0059		
total	1451	59.16			

interaction between species and sampling dates, confirming the seasonal variation of species. The third order interaction was also significant, confirming that the floristic difference between substrates itself differed between dates. A second analysis was done on the whole algal flora in which the diatom species were classed as one group. This analysis showed similar differences (table 6).

3.12. *Fine suspended matter*

Concentrations of chlorophyll *a* and phaeopigments in the water above the gravel were measured at least weekly (and sometimes more frequently) between April 1977 and July 1978. Suspended chlorophyll *a* concentrations showed maxima in May 1977, late April 1978 and June 1978 (figure 16). They reflected most clearly changes in the benthic diatom populations (figure 12) rather than changes in the general benthic flora (figure 4). The similarity with the silicon uptake data (figures 2, 28) is very striking. The activity of diatoms in July 1977 and

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

November–December 1977, however, barely showed above background chlorophyll levels. The seasonal variation in phaeopigment concentrations showed a similar pattern to chlorophyll *a* but with the maxima less well emphasized. The initial colonization phase was represented by a phaeopigment maximum that occurred 2 to 3 weeks after the suspended chlorophyll *a* and benthic chlorophyll *a* maxima.

Diatoms showed a seasonal variation in the suspended solids that was quantitatively very similar to that of the benthic flora. The noticeable periods of diatom activity (May 1977, July 1977, November 1977, April 1978 and June 1978) were not always represented by the same

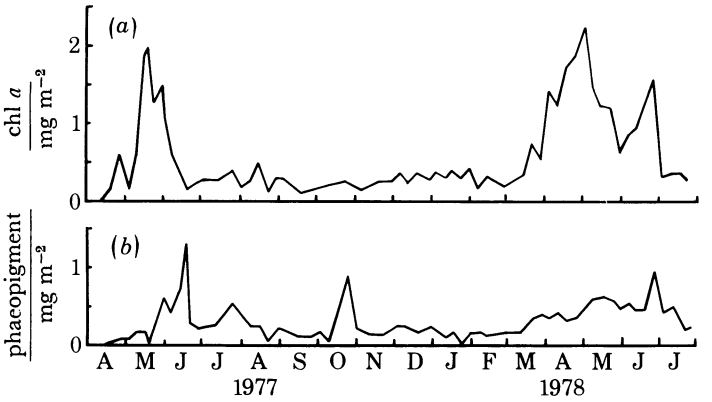

FIGURE 16. Seasonal variation in suspended chlorophyll *a* (*a*) and phaeopigment (*b*) in 1977 and 1978.

species but the composition and seasonal variation broadly followed that of the benthos (figure 17). Note, in particular, the similarity shown by *Cocconeis placentula*, *Fragilaria virescens*, *Gomphonema rhombicum*, *Meridion circulare* and *Nitzschia fonticola* (figures 13, 17); differences were shown by *Achnanthes* spp. which were most important in the spring and summer in the suspended solids and by *Navicula* and *Amphora* which were relatively unimportant.

Phormidium spp. (trichome *ca.* 5 μm diameter) had maxima between August and October 1977 and in May–June 1978 which corresponded with maxima in the benthic biomass (figure 17). Filaments of *Lyngbya kützingii* were present in maximum numbers in autumn 1977 when *Cyanophyta* were replacing diatoms in the benthos and again the following summer. Their numbers decreased sharply in midwinter, although the benthic biomass showed no similar reduction.

Gongrosira incrustans and species of *Chamaesiphon* were barely represented in the suspended solids, although present in substantial amounts in the benthos. Flagellates were present sporadically throughout the year but were more abundant and consistent in the winter. Many appeared to be zoospores of *Gongrosira incrustans*.

To examine the relation between the benthic algae and suspended algae, a number of variables were compared. Suspended chlorophyll *a* and dissolved silicon concentrations were regressed against benthic diatom volume and benthic chlorophyll *a* densities. No significant relation exists between benthic chlorophyll *a* and either silicon or suspended chlorophyll *a* concentrations (table 7). In the first case 90.6% of the variation remains unexplained by the regression and in the second case 88.8%. However, a relation, significant at the 0.001 level, exists between benthic diatom volume and suspended chlorophyll *a* concentrations; in this case

Downloaded from rstb.royalsocietypublishing.org

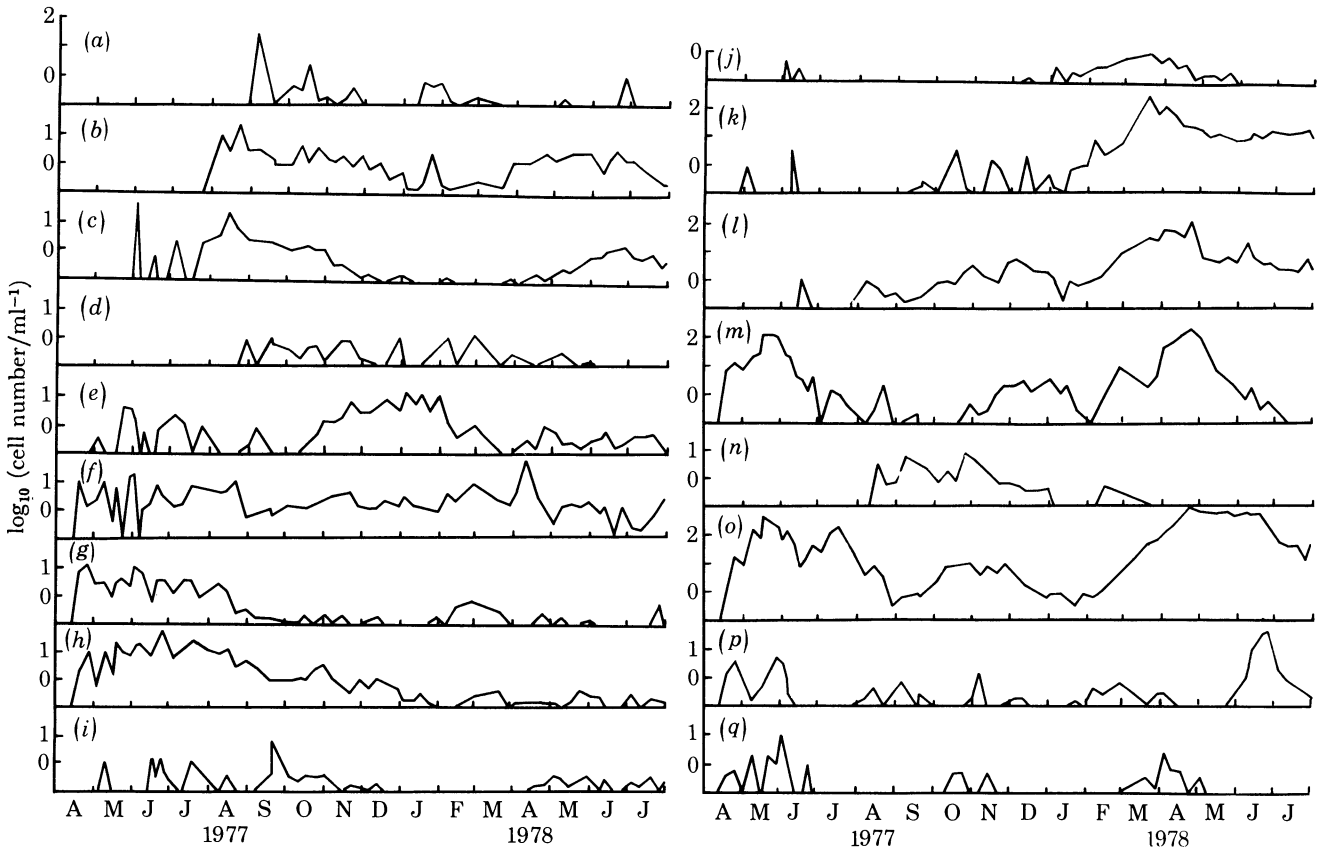

FIGURE 17. Seasonal variation in suspended algae during 1977 and 1978: (*a*) *Chamaesiphon* spp.; (*b*) *Lyngbya kützingii*; (*c*) *Phormidium* sp. (5 μm); (*d*) *Gongrosira incrustans*; (*e*) flagellates; (*f*) miscellaneous algae; (*g*) *Achnanthes lanceolata*; (*h*) *Achnanthes* spp.; (*i*) *Amphora ovalis* var. *pediculus*; (*j*) *Cocconeis placentula*; (*k*) *Fragilaria virescens*; (*l*) *Gomphonema rhombicum*; (*m*) *Meridion circulare*; (*n*) *Navicula* spp.; (*o*) *Nitzschia fonticola*; (*p*) *Synedra ulna*; (*q*) miscellaneous diatoms.

TABLE 7. LINEAR REGRESSION RELATIONS OF THE FORM $y = a + bx$ BETWEEN THE DENSITY OF BENTHIC ALGAE AND THE CONCENTRATION OF DISSOLVED OR SUSPENDED MATERIALS

x	*y*	*a*	*b*	S_b	*p*	prop. varn expl.
benthic chl *a*/(mg m^{-2})	silicon/(g m^{-3})	3.940	−0.00204	0.00119	n.s.	0.094
benthic chl *a*/(mg m^{-2})	susp. chl *a*/(mg m^{-3})	0.211	+0.000831	0.000442	n.s.	0.112
benthic diatom vol./(mm^3 m^{-2})	susp. chl *a*/(mg m^{-3})	0.325	+0.181	0.039	<0.001	0.435
silicon/(g m^{-3})	susp. chl *a*/(mg m^{-3})	1.33	−0.251	0.0525	<0.001	0.449
benthic diatom vol./(mm^3 m^{-2})	silicon/(g m^{-3})	3.95	−0.672	0.0562	$\ll 0.001$	0.836

Explanation of symbols and abbreviations: *b*, regression coefficient; S_b, standard deviation of *b*; *p*, probability; prop. varn expl., proportion of the variation explained by the regression; n.s. not significant.

43.5% of the variation is explained by the regression. An inverse relation of similar significance exists between dissolved silicon and suspended chlorophyll *a*, but there is a much closer inverse relation between dissolved silicon concentration and benthic diatom volume, with 83.6% of the variation being explained.

Suspended chlorophyll *a* concentrations showed a diel variation only during the initial

Downloaded from rstb.royalsocietypublishing.org

colonization phase by diatoms (figure 18). Outside this period variations were small. This is partly because the channel water has a 50% retention time of 8 h which substantially obscures much of the diurnal variation.

3.13. *Large suspended matter*

Substantial losses of large particulate material only occurred after November 1977 and reached their maximum in early March 1978 at over 25 mg chl a^{-1}. Phaeopigment levels were substantially lower. In September and October material was largely composed of *Phormidium autumnale*, which also occurred in the fine particulate matter. In the winter the material was

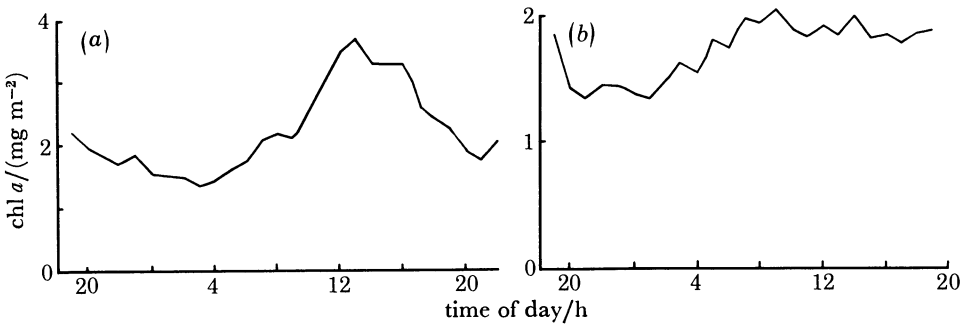

FIGURE 18. Diel variation in suspended chlorophyll *a*: (*a*) 12–13 May 1977; (*b*) 25–26 May 1977.

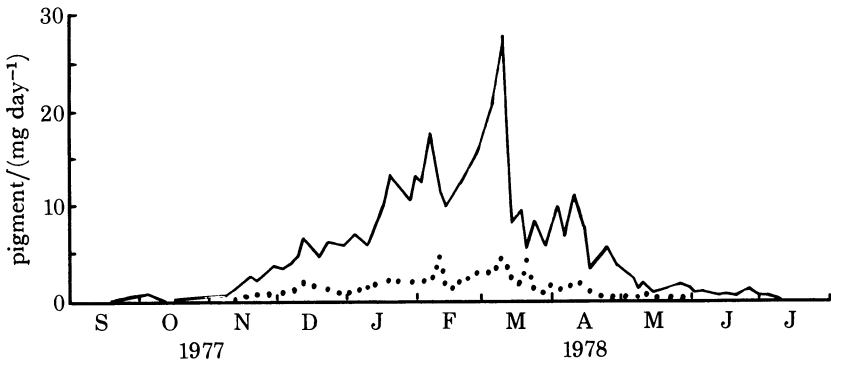

FIGURE 19. Losses of large particulate organic material (greater than 1.0 mm) through the outflow of the channel: ——— chlorophyll *a*; · · · · · · phaeopigment.

largely *Cladophora glomerata* which was virtually absent from the fine suspended solids. From February onwards the *Cladophora* contained increasing quantities of epiphytic diatoms but no attempt was made to estimate the proportions of the species present.

Comparisons between fine suspended chlorophyll *a* (figure 16) and large particulate chlorophyll *a* (figure 19) are complicated by the units used. However the concentrations (mg m^{-3}) given in figure 16 may be converted to losses from the channel (mg day^{-1}) by a multiplication factor of approximately 100 (4.2 $m^3 h^{-1} \times 24$). It can then be seen that during May 1977 and April–May 1978 losses of fine particulate chlorophyll *a* reached *ca* 200 mg chl *a* day^{-1}, which is nearly ten times greater than the losses of *Cladophora* chlorophyll.

Downloaded from rstb.royalsocietypublishing.org

3.14. *Algal colonization of gravel in Waterston stream*

The colonization of exposed gravel was studied in the neighbouring stream after emergent and submerged macrophytes had been removed from a 100 m reach at the same time as the dark covers were removed from the channel (5 April 1977). Chlorophyll *a* densities increased rapidly, reached a maximum in early May (more than 200 mg m^{-2}) and then decreased rapidly (figure 20). During June macrophytes started to grow rapidly and by the end of July

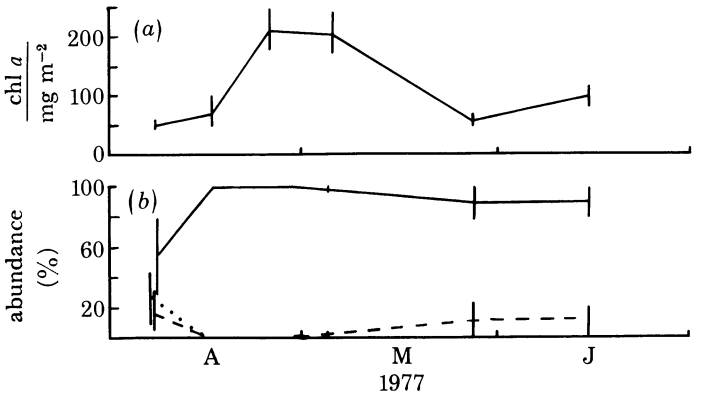

FIGURE 20. The initial colonization phase of gravel in Waterston Stream between April and June 1977. (*a*) Epilithic chlorophyll *a*. (*b*) Percentage abundance of the major algal groups: —— diatoms; – – – – Chlorophyceae; · · · · · · Cyanophyceae.

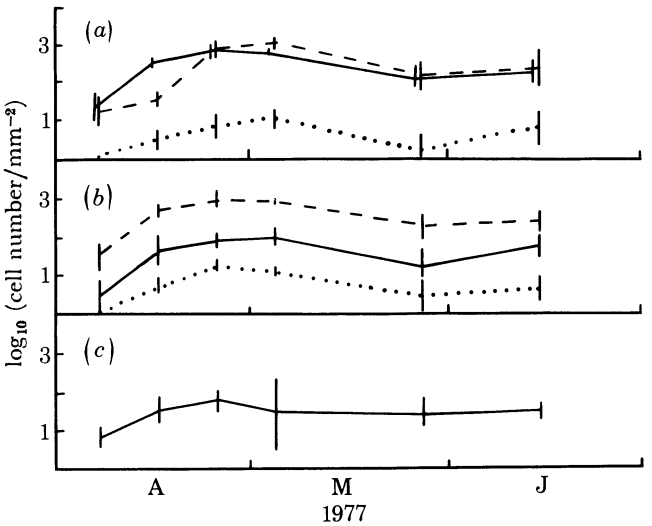

FIGURE 21. The initial colonization of gravel by diatoms in Waterston Stream, April–June 1977: (*a*) ———— *Achnanthes lanceolata*, – – – *Achnanthes minutissima*, · · · · · · *Melosira varians*; (*b*) ———— *Fragilaria virescens*, – – – *Meridion circulare*, · · · · · · *Synedra ulna*; (*c*) miscellaneous diatoms. Vertical bars represent 95 % confidence intervals. Some points have been moved by the equivalent of 3 days to distinguish overlapping 95 % limits.

the gravel was completely covered and so sampling was stopped. Through this phase diatoms dominated the flora, and most of the time there were only small quantities of green and blue-green algae (figure 20). Numerically the most significant diatoms were *Meridion circulare*, *Achnanthes minutissima* and *Achnanthes lanceolata*. *Fragilaria virescens*, *Melosira varians* and *Synedra ulna* were less important but, because of their size, they contributed significantly to the biomass

Downloaded from rstb.royalsocietypublishing.org

(figure 21). Cell number and cell volume per unit mass of chlorophyll *a* were considerably lower in Waterston Stream than in the channel. On 25 April and 4 May cell numbers were 9.86×10^7 and 2.22×10^8 (mg chl *a*)$^{-1}$ respectively and cell volumes were 11.3 and 22.2 mm^3 (mg chl *a*)$^{-1}$ respectively.

Nutrient concentrations in Waterston Stream were close to concentrations in the inflow water of the channel. The pH, however, was generally between 7.5 and 7.8. Silicon concentrations varied between 2.9 and 3.28 mg l^{-1} in April and May and between 3.43 and 3.75 mg l^{-1} in June and July. Reactive phosphate concentrations were *ca.* 20 μg PO_4-P l^{-1} at the beginning of April, fell to 8–9 μg PO_4-P l^{-1} in mid-May but rose above 10 μg l^{-1} in June.

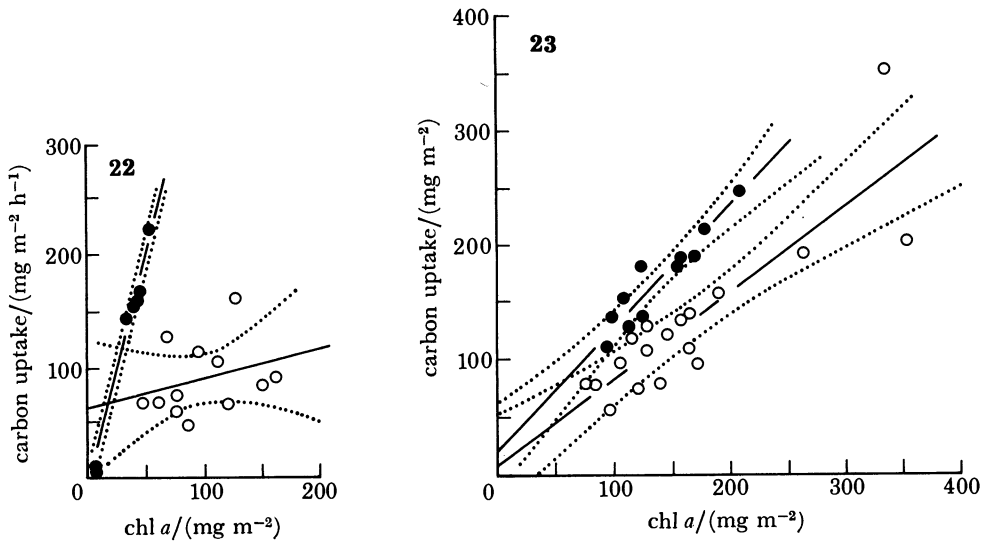

FIGURE 22. The relation between photosynthetic uptake of inorganic carbon (mg m^{-2} h^{-1}) and biomass (mg chl *a* m^{-2}) during the early colonization phase by diatoms in April 1977 (●) and during the decline in diatoms in June 1977 (○); ····· 95% confidence belts. For regression statistics see table 8.

FIGURE 23. The relation between the photosynthetic uptake of inorganic carbon (mg m^{-2} h^{-1}) and biomass (mg chl *a* m^{-2}) during July 1977 (●) and September 1977 (○); ····· 95% confidence belts. For regression statistics see table 8.

3.15. *The specific rate of photosynthesis* (mg C (mg chl *a*)$^{-1}$ h^{-1})

The photosynthesis of epilithic algae was measured at fortnightly intervals or sometimes more frequently from April 1977 until May 1978 and expressed as milligrams of carbon per square metre per hour. Data were combined each month for comparison by linear regression analysis. Most of the data did not require transformation and a summary of the analyses is shown in table 8 with examples illustrated in figures 22–25. The regression line intercepts did not differ significantly from zero. Consequently the regression coefficient is the average specific rate of photosynthesis. This can only be an approximation because the specific rate is expected to fall with increasing biomass (Marker 1976*b*). However for most of this study there was no such clear inverse relation between the specific rate and biomass because variation in the specific rate is relatively small at the high biomass densities that prevailed in the channel. The exception to this was the initial colonization phase, when diatom biomass varied between 0 and more than 500 mg chl *a* m^{-2}, and the specific rate dropped from 4.00 ± 0.41 on 21 April 1977 to

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

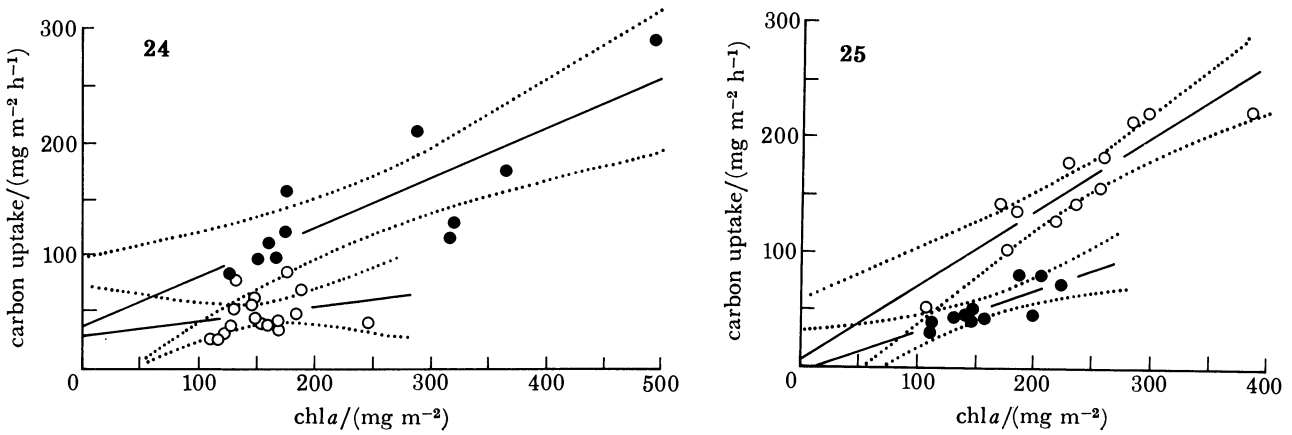

FIGURE 24. The relation between the photosynthetic uptake of inorganic carbon (mg m^{-2} h^{-1}) and biomass (mg chl *a* m^{-2}) during October 1977 (●) and December and January 1977–1978 (○); · · · · · · 95% confidence belts. For regression statistics see table 8.

FIGURE 25. The relation between the photosynthetic uptake of inorganic carbon (mg m^{-2} h^{-1}) and biomass (mg chl *a* m^{-2}) during February 1978 (●) and April 1978 (○); · · · · · · 95% confidence belts. For regression statistics see table 8.

TABLE 8. REGRESSION ANALYSIS OF PHOTOSYNTHESIS OF EPILITHIC ALGAE, WHERE x IS THE BIOMASS (mg chl *a* m^{-2}) AND y IS THE PHOTOSYNTHESIS (mg C m^{-2} h^{-1})

								geom. mean regn	
month	n	a†	S_a	b	S_b	p	prop. var. expl.	b	S_b
Apr.	11	−9.1	4.3	4.204	0.146	<<0.001	0.989	4.226	0.146
June	12	62.4	29.0	0.278	0.277	n.s.	0.0915	0.919	0.277
July	12	21.5	17.2	1.060	0.121	<0.001	0.884	1.127	0.121
Aug.	12	38.6	18.5	0.691	0.166	0.002–0.001	0.634	0.868	0.166
Sept.	18	7.9	19.6	0.752	0.109	<0.001	0.750	0.868	0.109
Oct.	11	34.2	27.2	0.445	0.0995	0.002–0.001	0.689	0.536	0.0995
Nov.	12	−28.1	16.3	0.554	0.0708	<0.001	0.859	0.597	0.0708
Dec.–Jan.	17	26.3	20.9	0.134	0.132	n.s.	0.064	0.480	0.474
Feb.	11	−5.07	15.2	0.365	0.092	0.01–0.002	0.636	0.458	0.09204
Mar.	17	−14.5	16.3	0.533	0.0783	<0.001	0.755	0.614	0.0783
Apr.	12	5.97	24.09	0.655	0.0988	<0.001	0.815	0.725	0.0988
May	18	16.8	12.0	0.548	0.0472	<0.001	0.894	0.579	0.0472

For explanation of symbols and abbreviations used see table 7. In addition: n, number; Sa, standard deviation of a; geom. mean regn, geometric mean regression.

† No value of a given here is significantly different from zero.

1.26 ± 0.37 on 1 June 1977. It was not in fact possible to combine all the May data for regression analysis, owing to these rapidly fluctuating specific rates. By June the mean specific rate was much lower and there was no significant correlation between the 'area-based' photosynthetic rate and biomass (table 8). Specific rates increased again during July and August when there was a small increase in the numbers of diatoms and the population structure was changing to Cyanophyceae and Chlorophyceae. Scattered mats of *Phormidium autumnale* in September and October affected the statistical distribution and a logarithm–logarithm transformation could have been more appropriate. However, the proportions of the error that were explained by the two regressions were not significantly different (74.5% compared with 75.0%). The specific rate fell throughout the autumn and winter and by December and January there was no

Downloaded from rstb.royalsocietypublishing.org

significant relation between the 'area-based' rate of photosynthesis and biomass (table 8; figure 24). Specific rates increased in the spring.

3.16. *The effect of irradiance and temperature*

The most important physical factors affecting photosynthesis are irradiance and temperature. The effect of flow is not so relevant to this study because velocity was constant throughout the year in the channel. The relation between photosynthesis, biomass, irradiance, temperature and

TABLE 9. MULTIPLE REGRESSION ANALYSIS STATISTICS BETWEEN THE DEPENDENT VARIABLE, PHOTOSYNTHESIS ($mg\,C\,m^{-2}\,h^{-1}$) AND THE INDEPENDENT VARIABLES, BIOMASS ($mg\,chl\,a\,m^{-2}$) (x_1), IRRADIANCE ($J\,m^{-2}\,s^{-1}$) (x_2) AND TEMPERATURE (°C) (x_3)

	$\log_e x_1$	$\log_e x_2$	$\log_e x_3$	$\log_e x_1$	$\log_e x_2$	$\log_e x_3$
			July–Sep. 1977			
n		36			36	
r^2		0.7856			0.7832	
a		−3.0381			−0.5994	
b	0.9182	−0.0422	1.4457	0.9138	−0.0462	0.1013
S_b	0.0871	0.0617	0.3954	0.0874	0.0619	0.0282
p	<0.001	0.5–0.4	<0.001	<0.001	0.4–0.5	0.02–0.001
			Oct.–Jan. 1977–1978			
n		46			46	
r^2		0.879			0.876	
a		−6.0568			−4.5963	
b	0.8948	0.5592	1.1245	0.8937	0.5600	0.1118
S_b	0.0957	0.1083	0.3115	0.0971	0.1115	0.0327
p	<0.001	<0.001	<0.001	<0.001	<0.001	0.02–0.001
			Jan.–Mar. 1978			
n		39			39	
r^2		0.856			0.8578	
a		−3.4356			−2.5885	
b	0.7240	0.3591	0.7700	0.7300	0.3505	0.0955
S_b	0.1343	0.0571	0.3023	0.1334	0.0577	0.0364
p	<0.001	<0.001	0.02–0.01	<0.001	<0.001	0.02–0.01
			Apr.–May 1978			
n		30			30	
r^2		0.884			0.884	
a		0.6658			0.440	
b	0.9696	−0.0793	−0.1601	0.9695	−0.0787	−0.0145
S_b	0.0774	0.0499	0.2347	0.0773	0.0500	0.0208
p	<<0.001	0.2–0.1	0.6–0.5	<<0.001	0.2–0.1	0.5–0.4

For explanation of symbols used see tables 7 and 8.

water velocity is complex (Talling 1957; McIntire *et al.* 1964; McIntire 1966; Fee 1973*a*, *b*) and there are insufficient data here available to establish detailed relation for each month. However, the period from July 1977 to May 1978 was split up into four:

(i) midsummer to early autumn 1977
(ii) autumn to midwinter 1977–1978
(iii) midwinter to spring 1978
} dominated by Cyanophyceae and Chlorophyceae

(iv) April–May 1978 — diatoms overlying Cyanophyceae and Chlorophyceae.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

A series of transformations were used successively in multiple regression analysis to find the minimum error sum of squares. Two transformations appeared equally appropriate:

$$y = a + \log_e(b_1x_1) + \log_e(b_2x_2) + \log_e(b_3x_3), \quad (1)$$

$$y = a + \log_e(b_1x_1) + \log_e(b_2x_2) + b_3x_3, \quad (2)$$

where y is the rate of photosynthesis (mg C m^{-2} h^{-1}), x_1, x_2 and x_3 are the biomass (mg chl a m^{-2}) irradiance (J m^{-2} s^{-1}) and temperature (°C) respectively, and b_1, b_2 and b_3 are the respective partial regression coefficients.

During periods (ii) and (iii) less than 15% of the variation remained unexplained by the analysis and between July and September the variation explained exceeded 88% (table 9). During periods (ii) and (iii) biomass, irradiance and temperature all had highly significant effects on the rate of photosynthesis. During periods (i) and (iv), the effect of irradiance was relatively less important because rates were measured at midday, when irradiance was frequently at or near saturation levels.

3.17. *Hourly rates of photosynthesis*

Hourly rates of photosynthesis for the whole channel were calculated from the regression statistics on photosynthesis and the separately estimated biomass data where $y = a + bx_2$, y being the hourly rate of photosynthesis for the whole channel, x_2 the estimated chlorophyll density for the whole channel, and a and b regression constants derived from the monthly photosynthesis data.

As the regression statistics were based on untransformed data (table 8) the biomass data were also used untransformed to simplify the calculation of approximate 95% confidence intervals.

The variance (V_y) of the estimated hourly rate of photosynthesis for the whole channel is (R. T. Clarke, personal communication)

$$V_y = s\left[\frac{1}{N} + \frac{1}{n} + \frac{\bar{x}_2 - \bar{x}_1}{\Sigma s} + V_x\left(b^2 + \frac{s^2}{\Sigma s}\right)\right],$$

where n is the number of samples on which photosynthesis was estimated, $\bar{x}_1$ is the mean biomass (mg chl a m^{-2}) of those samples, b is the regression coefficient relating photosynthesis to biomass, s^2 is the error mean square of the regression analysis, Σs is the sum of squares of the biomass of those samples used in the regression analysis, N is the number of samples taken to estimate the biomass of the surface stones of the whole channel, $\bar{x}_2$ is the mean biomass of those samples, and V_x is the variance of $\bar{x}$.

Since y is not normally distributed an approximation to the 95% confidence interval may be obtained from $2V_y^{\frac{1}{2}}$. Hourly rates of photosynthesis varied from a maximum of 354 mg C m^{-2} h^{-1} in May 1977 to a minimum of 50 mg C m^{-2} h^{-1} in midwinter (figure 26). Following the diatom maximum in May, photosynthesis crashed to 90 mg C m^{-2} h^{-1} in June. Summer rates varied between 100 and 140 mg C m^{-2} h^{-1} and a second maximum of 230 mg C m^{-2} h^{-1} was reached the following April.

Production per 24 h was calculated from these short-term exposures with use of conversion factors derived from earlier diel studies (Marker 1976*b*). Monthly estimates are shown in a histogram (figure 27) with maximum carbon fixation occurring in May 1977 (115 g C m^{-2}) and

Downloaded from rstb.royalsocietypublishing.org

late spring 1978 (64 g C m^{-2}). During the summer of 1977 monthly carbon fixation varied between 30 and 50 g C m^{-2} but between December and January it fell to between 9 and 10 g C m^{-2}. Total carbon fixation between April 1977 and June 1978 was estimated to be 590 g m^{-2} for the epilithic flora and 105 g m^{-2} for *Cladophora* and epiphytes. For the period April 1977 to December 1977 carbon fixation was estimated to be 350 g m^{-2} for the epilithon and 32 g m^{-2} for *Cladophora* and epiphytes.

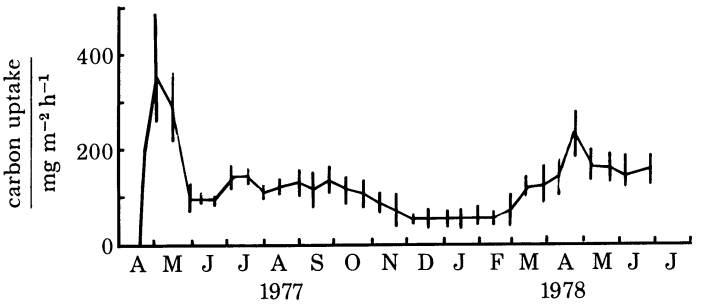

FIGURE 26. The seasonal variation in the hourly rates of photosynthetic carbon uptake, calculated from photosynthesis and biomass data. Vertical bars represent approximate 95 % confidence intervals because y is not normally distributed (see text).

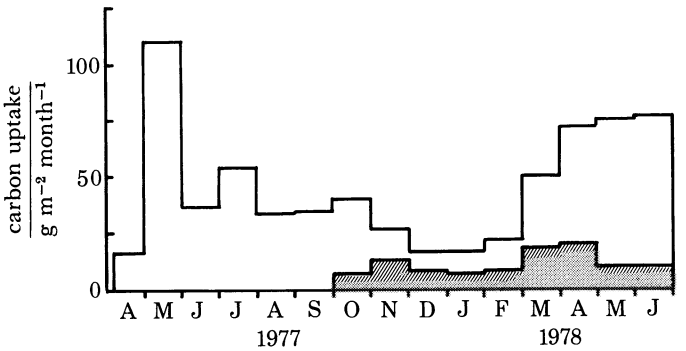

FIGURE 27. Estimated monthly production by epilithic algae and *Cladophora* with associated epiphytes (open histogram) and by *Cladophora* and associated epiphytes alone (hatched histogram).

3.18. *The dynamics of the initial colonization phase by diatoms*

The change in concentration of silicon in the water could provide one estimate of algal production, during the initial colonization phase, because the benthic flora was composed exclusively of diatoms. A number of conditions must be met.

(i) The discharge of water and the area of channel bed must be known. The channel was specifically designed for this type of experiment and has an area of *ca.* 100 m^2. The small pump delivered 103.2 m^3 day^{-1} from 5 April to 12 May and from 28 May to 4 June and the large pump delivered 252.8 m^3 day^{-1} from 12 to 28 May 1977.

(ii) Uptake of silicon must be diurnally constant. No diel variation in silicon uptake was detected during May. The inflow concentration of silicon over one 24 h period was 3.7 mg l^{-1}, with a coefficient of variation (c.v.) of 1.4 %. Outflow concentrations were

Downloaded from rstb.royalsocietypublishing.org

lower during May, with proportionately higher c.v. (11 May 1977, $\bar{x} = 1.0$, c.v. 5.4 %; 25 May 1977, $\bar{x} = 2.4$, c.v. 2.6 %).

(iii) The dissolution of biogenic silica must be small compared with uptake and non-biological precipitation must be insignificant compared with uptake by diatoms. During the initial experiments (largely abiotic) in the dark during March 1977 silicon was precipitated on average at a rate of less than 0.2 mg l^{-1} day^{-1} whereas uptake rates were between 1.0 and 5 mg l^{-1} day^{-1} during May. During the first week of experiments in the light there was no detectable difference between inflow and outflow silicon concentrations (less than 0.1 mg l^{-1}); after 3 weeks the difference in concentration between inflow and outflow was 2 mg l^{-1}. The channel was then covered with black polyethylene (25 April) and after 3 days in the dark the inflow was switched off. There was no detectable change in concentration over 24 h. However, by mid-June dissolution of silica was substantial and reached a maximum of 1.5 g m^{-2} day^{-1}.

TABLE 10. PARTIAL BUDGET FOR THE INITIAL COLONIZATION PHASE IN 1977, 0–60 DAYS (12 APRIL TO 8 JUNE)

(For details see biomass (figure 4), sedimentation (figure 7), suspended materials (figures 16, 19), photosynthetic carbon uptake (figures 22–27) and silicon uptake (figure 28).)

	biomass		Δ biomass	Si uptake	chl *a* equiv.	sedimentation per 14 days		suspended solids in outflow	
	mg chl *a* m^{-2}		(mg chl *a*	(g m^{-2}	calc. from	mg		mg wk^{-1}	
	0–5 cm	5–10 cm	m^{-2} wk^{-1})	wk^{-1})	Si uptake	chl *a*	phaeo-pigment	chl *a*	phaeo-pigment
12 Apr.	1.2	0.5							
18 Apr.	32.5	5.9	+36.7	1.203	26–51				
26 Apr.	297.9	21.0	+280.5	7.928	170–339				
2 May	285.7	25.4	−7.8	7.260	155–311				
9 May	514.6	65.9	+269.4	16.108	345–690	15.82	6.58	1.282	0.733
16 May	518.5	72.8	+10.8	21.386	458–916			4.250	1.319
23 May	507.5	133.2	+49.4	30.505	653–1306			14.105	0.733
30 May	286.9	110.3	−243.5	18.324	392–784	249.2	25.2	9.380	1.905
8 June	213.7	91.0	−92.5	4.291	92–184			9.415	4.361
						301.0	137.2	5.278	3.003
Σ60 days	518.5†	133.2†		107.0	2291–4581	566	169	43.7	12.1

† Maximum observed.

A detailed budget was attempted for the initial colonization phase (6 April to 5 June 1977) when sampling was more frequent and when dissolution of biogenic silica was minimal (table 10). Over a period of 60 days carbon uptake, estimated from photosynthesis studies, amounted to 132 g m^{-2}. During the same period silicon uptake was 107 g m^{-2}. The proportion of silica (SiO_2) in the diatoms was unknown but as several species were involved it was assumed to be *ca.* 50 % (i.e. 24 % Si + 26 % O_2 together with 50 % organic matter). Therefore the C: Si ratio of diatoms would be near 1.0 but was in fact 1.23. If it is further assumed that 1–2 % of the organic weight of diatoms is chlorophyll *a*, an uptake of 107 g of silicon would be equivalent to 2300–4600 mg chl *a* m^{-2}. The maximum algal biomass was 519 mg chl *a* m^{-2} in mid-May. Between 9 and 23 May the biomass hardly changed (less than 10 %) but over the same period silicon uptake was *ca.* 52 g m^{-2} (~ 1100–2200 mg chl *a* m^{-2}). During the period of rapidly declining biomass (23 May to 8 June) there was still a very substantial uptake of silicon (figure

Downloaded from rstb.royalsocietypublishing.org

28). Over the 60 days total sedimentation in the gravel was 735 mg of pigment per square metre and the loss of suspended solids from the channel outflow was only 55.8 mg of pigment per square metre (figures 16, 19; table 10).

For the 16 months of these experiments *net uptake* of silicon was 252 g m^{-2} and *net release* was 46.6 g m^{-2}. A more realistic period, however, is from April to December 1977 because only the spring period is avialable in 1978. During 1977 net silicon uptake was 119.0 g m^{-2} and net

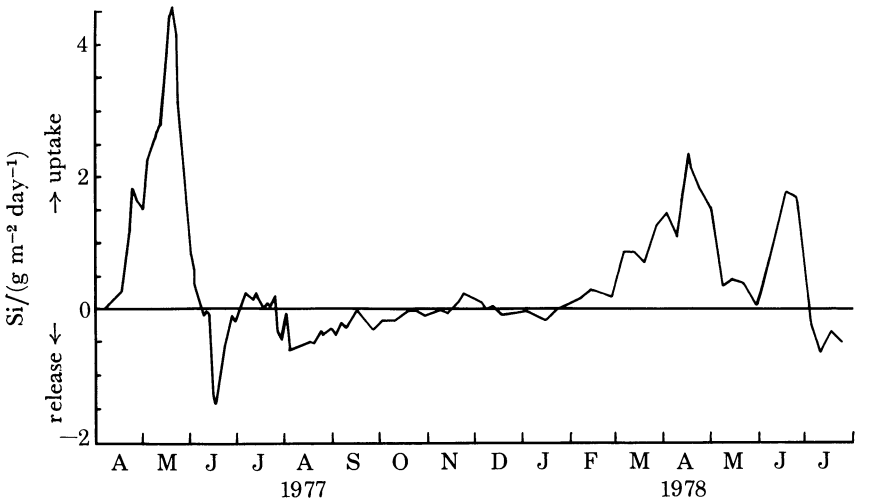

FIGURE 28. Uptake and release of silicon, estimated from changes in concentration between the inflow and outflow water of the channel.

release was 34.5 g m^{-2}. Release was, therefore, 29% of net uptake. Net production by diatoms would have been at least 250 g of organic matter per square metre in 1977 and 500 g m^{-2} for the whole 16 months. Concurrent dissolution of biogenic silica suggests that this may have been a substantial underestimate.

4. Discussion

In this section we discuss the production ecology and the population dynamics of hard-water benthic stream algae growing under constant flow conditions. In the first part we discuss the seasonal changes in biomass (based on chlorophyll *a*) in relation to changes in water chemistry. In the second part we discuss the population dynamics of the benthic algae and compare epilithic, epiphytic and suspended algae. In the third part we discuss the relation between production estimated from ^{14}C uptake with changes in biomass and finally draw conclusions from a budget study of the initial colonization phase by diatoms.

During the initial colonization phase and in the spring, algal densities in the channel were about twice those in Waterston Stream (figures 4, 20) and Bere Stream (Marker 1976*a*). Differences between the channel and Bere Stream were even greater in the summer, autumn and winter. However, variations between streams can be large and local densities of the order found in the channel can easily be found. The decline in biomass in natural streams during winter is much larger than in the channel and the following factors probably contribute to the difference.

Downloaded from rstb.royalsocietypublishing.org

(i) Macrophytes are present in streams, where they compete with benthic algae for light. They were excluded from the channel.
(ii) Rapid changes in discharge and water velocity, during winter, scour the stream bed.
(iii) Irradiance reaching the stream bed in winter is much lower in natural streams away from the source, due to turbidity.

The seasonal succession of algae in the channel was remarkably similar to that in other hard-water streams (Blum 1957; Marker 1976*a*). Rapidly fluctuating flow during winter in chalk streams washes out much weed and silt, exposing areas of clean gravel which are colonized by diatoms the following spring. The initial colonization phases by diatoms in 1976 and 1977 in the channel were remarkably similar to the spring outburst of benthic diatoms that occurs regularly each spring in local streams. The colonization of bare gravel in the neighbouring stream followed an almost identical pattern to the channel, although the biomass was lower and the species composition slightly different. Despite the absence of a winter wash out in the channel, diatoms reappeared in large numbers in April 1978, overlying the overwintering flora. Blum (1957) describes a similar phenomenon in the Saline River, with diatoms overgrowing an encrusted flora in the spring. The silicon concentration started to drop in the channel in January and February, which suggests that diatoms began to appear there in significant numbers rather earlier than in local streams. In chalk streams a change in silicon concentration is generally not apparent until late February or March. However, a combination of clear water more stable temperatures and the absence of winter spates could have allowed the growth cycle to start a few weeks earlier in the channel. Algae frequently grow rapidly after flood waters subside (Gumtow 1955; Bombowna 1972; Ertl *et al.* 1972) but this could be due to a change in subsurface irradiance as turbidity drops and a change in water velocity. Floodwaters also remove substantial amounts of benthic algae (Douglas 1958; Backhaus 1968; Moore 1977) but this cannot explain the drop in biomass in the late spring of 1976 and 1977 in the channel where the water velocity was constant.

The timing of the spring maximum is not directly affected by changes in mineral nutrients which remained in excess in the channel throughout the winter. During May 1977 the phosphate concentration dropped to *ca.* 1 $\mu g PO_4$-P l^{-1} but the rate at which it was being replenished should have prevented limitation. Phosphate was available to the benthos at a rate of 35–40 mg PO_4-P m^{-2} day^{-1} because 4.2 m^3 of water, containing 35–40 μg PO_4-P l^{-1} was entering the channel each hour.

During June the concentration of both molybdate-reactive phosphate (assumed to be largely inorganic phosphate) and molybdate-unreactive phosphate (probably largely organic phosphorus compounds) increased. The former approached inflow concentrations while the latter vastly exceeded inflow levels. The change is assumed to be release from the decaying diatom populations. At the same time the alkalinity and calcium concentration of the channel water approached those of the inflow water for the first time in this series of experiments. One of the initial problems of this recirculatory system had been the rapid precipitation of $CaCO_3$ and consequent drop in alkalinity (Ladle *et al.* 1977). Chalk streams maintain a much higher concentration of calcium bicabonate than might be expected from studies of calcite solubility at concentrations of CO_2 occurring in rivers. The differences between natural chalk streams and the channel may have been due to the more gentle flow régime (Jacobson & Usdowski 1975), CO_2 release from the sediments and possibly also the presence of inorganic and organic colloids. The decay of the diatom population in the channel may have helped to meet some of these criteria temporarily in June 1977.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

Substantial release of dissolved silicate occurred at the same time as that of the phosphate. Dissolution of biogenic silica has been widely reported from lakes and oceans (Lewin 1961; Calvert 1966; Schrader 1971; Conway *et al.* 1977), where the sediment can act as an important source of recycled dissolved silicate (Krauskopf 1956; Ohle 1964; Bailey-Watts 1976) and even sedimentation through a deep water column may allow enough time for some dissolution to take place (Berger 1968; Lerman & Lal 1977; Nelson & Goering 1977; Parker *et al.* 1978). Extensive dissolution has not been reported from rivers for a number of reasons. In most cases diatom maxima in rivers tend to be smaller than those observed in the channel and natural variation due to changes in discharge and water velocity will obscure trends. In addition river systems probably favour wash out rather than sedimentation of algae, so that dissolution will tend to take place in the estuary or ocean rather than in the headwaters. It is clear, however, that, under the stable conditions provided by the channel, substantial release of dissolved silicate was observed. High bicarbonate concentrations and high pH may favour dissolution (Jorgensen 1955; Golterman 1960) and both these conditions occur in chalk streams. However, the observation of MacKenzie & Carrels (1966*a*, *b*) that dissolved silicate entering the oceans from rivers reacts with bicarbonate and cations to form reconstituted clay minerals appears to have no counterpart in chalk streams, where high bicarbonate and silicate concentrations can coexist.

Diatom activity was irregular outside the spring and initial colonization phases. There were less pronounced periods of diatom activity 2 months after the major peaks (i.e. July 1977 and June 1978) and a similar pattern occurred in July 1976 although only proportions are shown in figure 9. Diatoms also recurred in late September 1976 and accounted for the increase in benthic chlorophyll *a* then, but in 1977 there was only a small increase in the late autumn. Marker (1976*a*) and Marker & Gunn (1977) reported that diatom growth was transitory and unpredictable in chalk streams outside the spring period and the evidence from the channel tends to support this view. Casey *et al.* (1981) also illustrated this variability but with data gathered over many years. A small but statistically significant depression in silicon concentration could be discerned in the late summer. Late summer diatom activity is far less well documented than the spring outburst although Edwards (1974) has shown the existence of more than one period of diatom activity in streams.

Diatom species showed a variety of seasonal patterns and the flora became progressively more diverse (see p. 283), although the initial experiments without gravel (Ladle *et al.* 1981) involved a benthic flora almost exclusively dominated by *Achnanthes minutissima*. *A. minutissima*, *M. circulare* and *S. ulna* are abundant at all chalk stream sources (see figure 21). *Amphora ovalis* var. *pediculari*s is a characteristic component of the lime-encrusted algae further downstream (unpublished results, see also Moore 1978). Both Eichenberger (1967*a*) and McIntire (1968) referred to *N. fonticola* in their channels. Other species were less common locally but apparently established themselves in the experimental conditions of the channel.

Very high numbers of diatoms observed during the middle of May 1977 were due to the high biomass (518 mg chl *a* m^{-2}) and the small size of many of the species. Maximum cell densities were 4.13×10^{11} m^{-2}, which corresponded to an estimated cell volume of 6.1×10^4 mm^3 m^{-2}. Moore (1978) recorded numbers of this order from a eutrophic tributary of the River Wylye and volumes of this order (and more) from the same stream and a larger, slower flowing river (Moore 1976). Maximum cell volumes observed in the channel corresponded to 118 mm^3 (mg chl *a*)$^{-1}$ and were broadly similar to that of *Asterionella* in Crose Mere of 357 mm^3 (mg chl *a*)$^{-1}$ (C. S. Reynolds, personal communication). Values quoted by Tolstoy (1979) and Javornicky

Downloaded from rstb.royalsocietypublishing.org

(1980) were of the same order. Close comparisons, however, are undesirable because substantial errors are associated with the estimation of cell volume due to assumed geometric shapes and large variations in size within species.

The hard calcareous crust of green and blue-green algae, which developed over the flints in the channel in the late summer, is typical of hard-water streams of southern England and northern France (Fritsch 1949; Adolphe & Rofes 1973; Marker 1976*a*) and hard-water streams in other parts of the world (Blum 1957; Golubic & Fischer 1975). Although higher temperatures favour the development of blue-green algae (Patrick *et al.* 1969) this is unlikely to be a satisfactory explanation for the succession observed in the channel, where temperature changes were small. Moreover Cattaneo *et al.* (1975) observed a similar succession occurring on glass slides over only 4 weeks. Within the channel these calcareous deposits gradually developed into a layer 3–4 mm thick and by July 1978 the sampling units were becoming quite difficult to remove due to the developing $CaCO_3$ concretions. Some physically induced precipitation certainly occurred (Ladle *et al.* 1977) but much was undoubtedly biologically induced (Fritsch & Pantin 1946). In chalk streams crusts do not usually have time to develop extensively, due to the destabilizing effects of macrophyte growth and winter spates. Generally crusts will only develop on the larger stones in riffles during the summer and in partially shaded and protected positions (i.e. by bridges or under north facing banks). Fritsch & Pantin (1946), Fritsch (1949) and Blum (1957) described similar crusts dominated by *Phormidium incrustatum*, whereas in the channel this species only developed during 1978. In addition species of *Schizothrix* were described by those authors as significant contributors but were not found in the channel or local streams. The dominant alga in the calcareous crusts of the channel showed no tapering of the filaments and was identified as *Lyngbya kützingii*, rather than *Homoeothrix varians*, which appears to be widespread in local chalk streams. *Ph. foveolarum* was recorded by Moore (1978) as a constituent of the epilithic algae of the Wylye, another chalk stream. Fritsch (1929) also described this species as part of the '*Chamaesiphon* community' but in his case *Ch. pseudo-polymorphus* was involved. The material in the channel more closely resembles the description of *Ch. polymorphus* by Kann (1973) although some *Ch. regularis* was probably present as well. Golubic & Fischer (1975) described calcareous nodules from streams with *Ch. polymorphus* and *Pleurocapsa minor*; chalk streams contain both *Pl. minor* and *Pl. fluviatilis* and the former was a minor component of the channel flora. *Ph. autumnale* is also present in many local chalk streams and was described by Fritsch (1929) as occurring 'on the bigger boulders of the most rapidly flowing streams'. The only green alga to form a major component of the lime crusts was *Gongrosira incrustatum*, which was also described by Fritsch & Pantin (1946) as a major component of the encrusted flora of a hard-water English stream.

Cladophora formed a significant part of the biomass during the autumn and winter of 1977–1978. One biomass estimate late in the autumn of 1978, after the sampling programme was complete, yielded 285 g of organic matter per square metre. This is a high biomass for clean water drawn directly from the aquifer, whose mean phosphate concentration is only *ca.* 30 μg PO_4-P l^{-1}. Moreover the water within the channel rarely had a phosphate concentration above 10 μg PO_4-P l^{-1}. Although there is considerable evidence that *Cladophora* biomass is in some way correlated to the phosphate concentration in natural water courses (Pitcairn & Hawkes 1973; Bolas & Lund 1974), our findings tend to agree with Wuhrmann & Eichenberger (1975) that phosphate alone may not always be the most important controlling factor. It is possible that *Cladophora* may be quite capable of producing extensive growths in headwaters,

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

although it does not generally do so, and that other factors, which are absent from the channel and eutrophic streams, may normally control its growth.

The epiphytic algae, growing on *Cladophora*, were significantly different from the epilithic algae. The positive third-order interaction in the analysis of variance showed that the differences were also time-dependent. Lime-encrusted algae were not found on the *Cladophora*, possibly because they require a firm substrate. Different species of *Chamaesiphon* were present on the two substrates.

These studies confirmed that suspended chlorophyll *a* concentrations were more closely related to benthic diatom densities than to benthic chlorophyll *a* concentrations (Casey *et al.* 1981). Both benthic diatom volume and dissolved silicon concentration were correlated with suspended chlorophyll *a* concentration ($p < 0.001$) and the proportions of the variation explained by the two regressions were similar. Only the latter relation was examined by Casey *et al.* (1981) in natural streams because benthic data were not available. The relation between benthic diatom volume and silicon concentration (in this case with silicon concentration as the dependent variable) in the channel was very close, with over 80% of the variation explained by the regression. However, the retention time of the water in the channel is relatively long for a headwater stream (8 h half life). Under natural conditions the relation would not be clear-cut due to the shorter retention time and the natural variation in silicon concentration. It therefore follows that changes in silicon concentrations could only be used to monitor changes in benthic diatoms at some considerable distance from the source and then only under special conditions (Casey *et al.* 1981). In headwaters variations in suspended chlorophyll concentration may be just as effective.

Diurnal variations in suspended chlorophyll *a* concentration were only observed during periods of diatom growth and were similar to, but not as marked as, those reported by Blum (1954) and Müller-Haeckel (1966). There is no simple way of estimating how long algae remain in suspension so that a half life retention time of *ca.* 8 h could obscure some diurnal variation.

The initial colonization phase in the channel confirmed the high growth rates suggested by *in situ* photosynthesis experiments in earlier studies (Marker 1976*b*). Difficulties arising in natural streams by colonization from algae drifting down from upstream were avoided in this study and, as grazing, wash out and sedimentation were minimal during the first few weeks, biomass accumulation will have approximated to net primary production. Benthic chlorophyll *a* increased over 200-fold during the second and third week, which corresponded to a generation time of less than 2 days. This is faster than those reported by Boylen & Brock (1973) at comparable biomass and temperature levels. Changes in cell numbers for several species confirmed this rate of growth for the third week (see table 4). These relative growth rates applied to small and large diatoms.

High initial rates of photosynthesis occurred in late April when diatoms were growing actively over the stone surfaces (figure 22, table 8). By June the specific rate of photosynthesis had fallen, as algal material and associated detritus began to sediment out and much could be found temporarily on the underside of the surface stones. The low photosynthetic rates will have been due to a combination of living algae being overlain by detritus and decaying material, algae on the underside of the stones still containing apparently undegraded chlorophyll, and possibly a general deterioration in the physiological state of the algae. The low rates are unlikely to have been due to light inhibition because there was little change in irradiance during May and early June. Although the specific photosynthetic rates recovered in July, they

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

were still lower than the April rates. Specific rates in the spring of 1978 were not as high as in the early part of the initial colonization phase, probably because the actively growing diatoms were covering a much less active encrusted population which had overwintered. It is possible that actively growing populations always occur on the surface because Tominaga & Ichimura (1966) have shown that algae from the surface of mats have a much higher specific rate of photosynthesis than have subsurface algae. Koboyasi (1961*b*, 1972) has shown that algae grown at high irradiance have a higher maximum specific photosynthetic rate than have algae grown at low irradiance. Overall rates of photosynthesis were towards the upper range quoted for artificial and natural streams (McIntire *et al.* 1964; Stockner 1968; Sperling 1975) and well above those of unstable environments (Stanley 1976; Marshall *et al.* 1971; Van Raalte *et al.* 1976).

The rate of photosynthesis (per unit area) is influenced by a wide variety of factors peculiar to benthic environments (McIntire *et al.* 1964; Kevern & Ball 1965; Pieczynska & Straskraba 1969; Naiman & Gerking 1975; Wong *et al.* 1976). Our evidence supports the view that irradiance is an important factor controlling the rate of photosynthesis, and hence primary production, during the autumn, winter and spring; this suggests that the onset of diatom growth in streams during the spring may be controlled both by the intensity of irradiance and by the duration of daylight (Marker 1976*b*; Moore 1978). Temperature also affects the rate of photosynthesis (Phinney & McIntire 1965; McIntire 1966) but this is probably not as relevant in the channel because temperature variations were smaller than in natural streams. During the summer, rates of photosynthesis were not significantly correlated with irradiance, possibly because irradiance was approaching optimal levels for much of the incubation time near midday (McIntire *et al.* 1964; Pieczynska & Straskraba 1969). Flow is known to have a profound effect on the metabolic rate of lotic algae (Odum & Hoskin 1957; Hoskin 1959; Whitford & Schumacher 1961; McIntire 1966) and, although the water was recirculated adequately in the chambers, thick compact crusts of algae developed on the stones and diffusion may well have limited the photosynthetic rate in the summer. The complex mosaic and high concentration of plants growing over the irregular stone surfaces make adaptation of the phytoplankton photosynthesis models (Talling 1957; Fee 1973*a*, *b*) difficult. Primary production had to be calculated from limited studies in enclosures (see also: Fraleigh & Wiegert 1975; Sumner & Fisher 1979) because the recirculating channel was not long enough for production to be calculated directly from changes in oxygen concentration (Gallegos *et al.* 1977; Edelmann & Wuhrmann 1978).

The difficulties and drawbacks of using ^{14}C to estimate algal production have been discussed at length elsewhere (Wetzel 1964; Harris 1978; Dring & Jewson 1979; Marker & Westlake 1980). Even if it is assumed that photosynthetic uptake of ^{14}C by a thick algal crust measures something approaching net photosynthesis, this still leaves the problem of night-time respiration in calculating 24 h net production rates. It has already been established that respiration can be considerable (McIntire *et al.* 1964; Stockner 1968; Van Raalte *et al.* 1976) and is temperature- and flow-dependent (Whitford & Schumacher 1961; McIntire 1966). Our carbon uptake figures will therefore be an overestimate of the 24 h net production. Figures for production based on changes in oxygen are also subject to overestimation (gross photosynthesis) or potentially serious underestimation (net community production). Our estimate of carbon uptake by algae (300 g C m^{-2} between April and December 1977) is not far above the upper ranges quoted for other streams (200 g C m^{-2} a^{-1} (Pomeroy 1959); 250 g C m^{-2} a^{-1} (Wetzel 1964); 200 g C m^{-2} a^{-1}

Downloaded from rstb.royalsocietypublishing.org

(Pamatmat 1968)) and reflects the greater biomass that developed in the more stable environment of the channel.

The use of silicon content as an estimate of net diatom production has many drawbacks. The silicon content of diatoms can be a function of silicate concentration (Paasche 1973*b*; Harrison *et al.* 1977) which ranged between 3.6 and 0.8 mg Si l^{-1} in the channel during the initial colonization phase. When the rate of water replenishment was increased 2.5-fold the concentration in the channel only increased from 0.8 to 1.6 mg l^{-1}. Part of this difference may have been due to a concurrent increase in the overall growth rate, but part, however, may have been due to the rate of silicon uptake changing independently of the photosynthetic rate. The silica content of diatoms can be a function of size and species (Parsons *et al.* 1961; Paasche 1973*a*; Durbin 1977) or a function of temperature (Hart 1942; Hasle & Smayda 1960; Furnas 1978), and silicate may be released from living cells (Nelson *et al.* 1976). Silicate may also be stored in the cell sap, although not to the same extent as phosphate, and Paasche (1980) considered this to be less than 10% of the total cell silicon. However, the errors in using silicon to estimate diatom production are quite different from the errors involved with ^{14}C and the results from the two methods actually agreed quite closely. Over the first 60 days uptake of silicon (by weight) was only *ca.* 30% less (by weight) than uptake of carbon (by weight). Maximum uptake rates of 4–5 g Si m^{-2} day^{-1} confirmed that the population of diatoms was in fact producing very rapidly in mid-May. If it is assumed that the diatoms were 50% SiO_2, the production of organic matter would have been 8–10 g m^{-2} day^{-1}. Changes in biomass and cell number during April broadly matched production estimated from silicon or carbon uptake, whereas the theoretical increments of chlorophyll *a* based on silicon or carbon uptake were far in excess of the changes in biomass observed from 10 May onwards (table 10). During late May and June there was still measurable carbon uptake (more than 1 g C m^{-2} day^{-1}). Losses of algae in the suspended solids through the outflow were small (less than 10% maximum biomass and 1–2.5% of the estimated production over the initial 60 days). Even allowing for errors due to diel variations the loss from this sink is still small compared with total production and also small compared with loss from natural streams (Marker & Gunn 1977). Losses through sedimentation were tenfold greater and about the same as the maximum biomass. Sedimentation measured every 14 days in this way must underestimate true losses because some of the pigment will have been photoxidized before sedimenting out of the light. It is possible that part of this material may be chlorophyllide *a* or oxidized derivatives of chlorophyll *a* (Hallegraeff & Jeffrey 1982; Jacobsen 1982), which are not distinguished by the spectrophotometric acidification technique. In the headwaters of streams water rapidly passes through the system whereas in the channel it is largely recirculated. Moreover in streams suspended solids are caught up in weed beds or pass through the system but are prevented from sedimenting into the gravel by fine sediment in the spaces between the flints. The balance between losses due to sedimentation or through suspended solids is affected as much by the physical environment of the ecosystem as by the biological components. There remains a substantial gap between the two independent estimates of primary production on the one hand and the biomass and measured losses on the other. The grazing impact of chironomid larvae during the initial colonization phase, which will be examined in other papers (M. Ladle, J. S. Welton & J. A. B. Bass, personal communication) is substantial and partially explains the crash in diatom populations after the initial colonization phases in 1976 and 1977 and late in the spring of 1978. Preliminary studies have already been described for 1976 (Ladle *et al.* 1980) and during 1977 chironomid numbers were about 30%

Downloaded from rstb.royalsocietypublishing.org

higher than in 1976, reaching their maximum in the first 2 weeks of June, the same time as the diatom population collapsed. Substantial effects by grazing invertebrates on diatom populations have been suggested elsewhere (Mason & Bryant 1975; Eichenberger & Schlatter 1978). This is clearly more relevant here than nutrient depletion which can frequently explain the cessation of phytoplankton growth in lakes (Lund *et al.* 1963; Moed 1973).

The costs of research on which this paper is based were borne by the Natural Environment Research Council and the Department of the Environment (contract number DGR/480/467).

The authors wish to thank the many members of the River Laboratory staff who helped and worked on this project. We also thank Professor W. D. P. Stewart, F.R.S., Dr J. F. Talling, Mr R. T. Clarke, Dr M. Ladle and Mr D. F. Westlake for useful discussions, and Mr J. Carter, Dr E. Haworth and Dr B. A. Whitton for advice on algal taxonomy.

References

Adolphe, J.-P. & Rofes, G. 1973 Les concrétionnements calcaires de la Levriere. *Bull. Ass. fr. Étude Quatern.* pp. 79–87.

Allen, S. E., Grimshaw, H. M., Parkinson, S. A. & Quarmby, C. 1975 *Chemical analysis of ecological materials.* Oxford: Blackwell Scientific Publications.

American Public Health Association 1965 *Standard methods for the examination of water and waste water* (12th edn). New York: American Public Health Association.

Backhaus, D. 1968 Ökologische Untersuchungen an den Aufwuchsalgen der obersten Donau und ihre Quellflüsse. II. Die raumliche und zeitliche Verteilung der algen. *Arch. Hydrobiol. Suppl.* **34**, 24–73.

Bailey-Watts, A. E. 1976 Planktonic diatoms and some diatom silica relations in a shallow eutrophic Scottish loch. *Freshwat. Biol.* **6**, 203–213.

Berger, W. H. 1968 Radiolarian skeletons: solution at depths. *Science, N.Y.* **159**, 1237–1238.

Blum, J. L. 1954 Evidence of a diurnal pulse in stream phytoplankton. *Science, N.Y.* **119**, 732–734.

Blum, J. L. 1956 The ecology of river algae. *Bot. Rev.* **22**, 291–341.

Blum, J. L. 1957 An ecological study of the algae of the Saline River, Michigan. *Hydrobiologia* **9**, 361–408.

Bolas, P. M. & Lund, J. W. G. 1974 Some factors affecting the growth of *Cladophora glomerata* in the Kentish Stour. *Wat. Treat. Exam.* **23**, 25–51.

Bombowna, M. 1972 Primary production of a montane river. In *Productivity problems of freshwaters* (ed. Z. Kajak & A. Hillbricht-Ilkowska), *Proc. IBP–UNESCO Symp. Productivity Problems of Freshwaters, Kazimierz-Dolny*, 1970, pp. 661–671. Warsaw and Krakow: Polish Scientific Publishers.

Boylen, C. W. & Brock, T. D. 1973 Effects of thermal additions from the Yellowstone geyser basins on the benthic algae of the Firehole River. *Ecology* **54**, 1282–1291.

Butcher, R. W. 1932 Studies on the ecology of rivers. II. The microflora of rivers with special reference to the algae on the river bed. *Ann. Bot.* **46**, 813–861.

Butcher, R. W. 1949 Problems of distribution of sessile algae in running water. *Verh. int. Verein. theor. angew. Limnol.* **10**, 98–103.

Calvert, S. E. 1966 The accumulation of diatomaceous silica in the sediments of the Gulf of California. *Bull. geol. Soc. Am.* **77**, 569–596.

Casey, H. 1969 The chemical composition of some southern chalk streams and its relation to discharge. *River Auth. Ass. Yb.* pp. 103–113.

Casey, H., Clarke, R. T. & Marker, A. F. H. 1981 The seasonal variation in silicon concentration in chalk streams in relation to diatom growth. *Freshwat. Biol.* **11**, 335–344.

Casey, H. & Newton, P. V. R. 1973 The chemical composition and flow of the River Frome and its main tributaries. *Freshwat. Biol.* **3**, 317–333.

Cattaneo, A., Ghittori, S. & Vendegna, V. 1975 The development of benthonic phytocoenosis on artificial substrates in the Ticino River. *Oecologia* **19**, 315–327.

Conway, H. L., Parker, J. I., Yaguchii, E. M. & Mellinger, D. L. 1977 Biological utilization and regeneration of silicon in Lake Michigan. *J. Fish. Res. Bd Can.* **34**, 537–544.

Crisp, D. T. 1970 Input and output of minerals for a small watercress bed fed by chalk water. *J. appl. Ecol.* **7**, 117–140.

Dewhurst, F. 1976 Some pollutants of laboratory atmospheres. *Lab. News* **110**, 19.

Douglas, B. 1958 The ecology of the attached diatoms. *J. Ecol.* **46**, 295–322.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

Dring, M. J. & Jewson, D. H. 1979 What does ^{14}C-uptake by phytoplankton really measure? A fresh approach using a theoretical model. *Br. phycol. J.* **14**, 122–123.

Durbin, E. G. 1977 Studies on the autecology of the marine diatom *Thalassiosira nordenskiaddii*. 2. The influence of cell size on growth rate and carbon, nitrogen, chlorophyll *a* and silica content. *J. Phycol.* **13**, 150-155.

Edelmann, W. & Wuhrmann, K. 1978 Energy balance of running water systems. *Verh. int. Verein. theor. angew. Limnol.* **20**, 1800–1805.

Edwards, A. M. C. 1974 Silicon depletion in some Norfolk rivers. *Freshwat. Biol.* **4**, 267–274.

Edwards, R. W. & Owens, M. 1960 The effect of plants on river conditions. I. Summer crops and estimates of net productivity of macrophytes in a chalk stream. *J. Ecol.* **48**, 151–160.

Eichenberger, E. 1967*a* Ökologische Untersuchungen an Modellfliessgewassern. I. Die Jahreszeitliche Verteilung der bestandes-bilden den pflanzlichen Organismen bei verschiedener Abwasserbelastung. *Schweiz Z. Hydrol.* **29**, 1–31.

Eichenberger, E. 1967*b* Ökologische Untersuchungen an Modellfliessgewassern. II. Jahrezeitliche Veranderung der Biomassen – bildung bei veschiednen Abwasserbelastungen. *Schweiz Z. Hydrol.* **29**, 35–52.

Eichenberger, E. 1972*a* Ökologische Untersuchungen an Modellfliessgewassern. III. Die Jahreszeitlichen veranderungen im Verhaltnis von heterotrophen zu phototrophen Biomasse bei verscheidenen Abwasserbelastungen. *Schweiz Z. Hydrol.* **34**, 155–172.

Eichenberger, E. 1972*b* Ökologische Untersuchungen an Modellfliessgewassern. IV. Auswirkung der Selbstreinigung auf die Biomassbildung in einem Abwassergradienten. *Schweiz Z. Hydrol.* **34**, 173–189.

Eichenberger, E. & Schlatter, F. 1978 The effect of herbivorous insects on the production of benthic algal vegetation in outdoor channels. *Verh. int. Verein. theor. angew. Limnol.* **20**, 1806–1810.

Ertl, M., Juris, S. & Tomajka, J. 1972 Preliminary data about the seasonal changes and vertical stratification of periphyton from the middle reach of the River Danube. *Arch. Hydrobiol. Suppl.* **44**, 34–48.

Fee, E. J. 1973*a* A numerical model for determining integral primary production and its application to Lake Michigan. *J. Fish. Res. Bd Can.* **30**, 1447–1468.

Fee, E. J. 1973*b* Modelling primary production in water bodies. A numerical approach that allows vertical inhomogeneities. *J. Fish. Res. Bd Can.* **30**, 1469–1473.

Fraleigh, P. C. & Wiegert, R. G. 1975 A model explaining successional change in standing crop of thermal blue-green algae. *Ecology* **56**, 656–664.

Fritsch, F. E. 1929 The encrusting algal communities of certain fast flowing streams. *New Phytol.* **28**, 165–196.

Fritsch, F. E. 1949 The lime-encrusted *Phormidium*-community of British streams. *Verh. int. Verein. theor. angew. Limnol.* **10**, 141–144.

Fritsch, F. E. & Pantin, C. F. A. 1946 Calcareous concretions in a Cambridgeshire stream. *Nature, Lond.* **157**, 397–399.

Furnas, M. 1978 Influence of temperature and cell size on the division rate and chemical content of the diatom, *Chaetoceros curvisetum*. *J. exp. mar. Biol. Ecol.* **34**, 97–109.

Gallegos, C. L., Hornberger, G. M. & Kelly, M. G. 1977 A model of river benthic algal photosynthesis in response to rapid changes in light. *Limnol. Oceanogr.* **22**, 326–333.

Golterman, H. L. 1960 Studies on the cycle of elements in freshwater. *Acta bot. neerl.* **9**, 1–58.

Golubic, S. & Fischer, A. G. 1975 Ecology of calcareous nodules forming in Little Connestega Creek near Lancaster, Pennsylvania. *Verh. int. Verein. theor. angew. Limnol.* **19**, 2315–2323.

Gumtow, R. B. 1955 An investigation of the periphyton in a riffle of the West Gallatin River, Montana. *Trans. Am. microsc. Soc.* **74**, 278–292.

Hallegraeff, G. M. & Jeffrey, S. W. 1982 Profiles of photosynthetic pigments in the east Australian current using thin-layer chromatography. *Arch. Hydrobiol., Beih., Ergebn. Limnol.* (In the press.)

Harris, G. P. 1978 Photosynthesis, productivity and growth: the physiological ecology of phytoplankton. *Arch. Hydrobiol., Beih., Ergebn. Limnol.* **10**, 1–171.

Harrison, P. L., Conway, H. L., Holmes, R. W. & Davis, C. O. 1977 Marine diatoms in chemostats under silicate or ammonium limitation. 3. Cellular chemical composition and morphology of *Chaetoceros debilis*, *Skeletonema costatum* and *Thalassiosira gravida*. *Mar. Biol.* **43**, 19–31.

Hart, T. J. 1942 Phytoplankton periodicity in Antarctic surface waters. *Discovery Rep.* **21**, 261–356.

Hasle, G. R. & Smayda, T. J. 1960 The annual phytoplankton cycle at Drøbak, Oslofjord. *Nytt Mag. Bot.* **8**, 53–75.

Hoskin, C. M. 1959 Studies of oxygen metabolism of streams of North Carolina. *Publs Inst. mar. Sci. Univ. Tex.* **6**, 186–192.

House, W. A. 1981*a* Kinetics of crystallisation of calcite from calcium bicarbonate solutions. *J. chem. Soc. Faraday Trans.* I **77**, 341–359.

House, W. A. 1981*b* An experimental investigation of CO_2 adsorption during calcite precipitation. *Colloid. Surf.* **2**, 119–131.

Jacobsen, T. R. 1982 Comparison of chlorophyll *a* measurements by fluorometric, spectrophotometric and high pressure liquid chromatographic methods in aquatic environments. *Arch. Hydrobiol., Beih., Ergebn. Limnol.* (In the press.)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

Jacobson, R. L. & Usdowski, E. 1975 Geochemical controls on a calcite precipitating spring. *Contr. Miner. Petr.* **51**, 65–74.

Javornicky, P. 1980 Density-dependent effects – 5. Primary production. In *The functioning of freshwater ecosystems* (ed. E. D. Le Cren & R. H. Lowe-McConnell), §5.4.2.6, pp. 170–173. Cambridge University Press.

Jorgensen, E. G. 1955 Solubility of silica in diatoms. *Physiologia Pl.* **8**, 846–851.

Kann, E. 1973 Zur Systematik und Ökologie der Gattung *Chamaesiphon* (Cyanophyceae). 1. Systematik. *Arch. Hydrobiol. Suppl.* **41**, 117–171.

Karlström, V. 1978 Role of the organic layer on stones in detrital metabolism in streams. *Verh. int. Verein. theor. angew. Limnol.* **20**, 1463–1470.

Kevern, N. R. & Ball, R. C. 1965 Primary productivity and energy relationships in artificial streams. *Limnol. Oceanogr.* **10**, 74–87.

Koboyasi, H. 1961*a* Chlorophyll content in sessile algal community of Japanese mountain river. *Bot. Mag., Tokyo* **74**, 228–235.

Koboyasi, H. 1961*b* Productivity in sessile algal community of Japanese mountain river. *Bot. Mag., Tokyo* **74**, 331–341.

Koboyasi, H. 1972 Chlorophyll content and primary production of the sessile algal community in the mountain stream Chigonozawa running close to the Kiso Biological Station of the Kyoto University. *Mem. Fac. Sci. Kyoto Univ., Ser. Biol.* **5**, 89–107.

Krauskopf, K. B. 1956 Dissolution and precipitation of silica at low temperatures. *Geochim. cosmochim. Acta* **10**, 1–26.

Ladle, M., Baker, J. H., Casey, H. & Farr, I. S. 1977 Preliminary results from a recirculating experimental system: observations of interaction between chalk stream water and inorganic sediment. In *Interactions between sediments and freshwater* (ed. H. L. Golterman), pp. 252–257. The Hague: Junk.

Ladle, M. & Bass, J. A. B. 1981 The ecology of a small chalk stream and its responses to drying during drought conditions. *Arch. Hydrobiol.* **90**, 448–466.

Ladle, M. & Casey, H. 1971 Growth and nutrient relationships of *Ranunculus penicillatus* var *calcareus* in a small chalk stream. *Proc. Eur. Weed Res. Coun. 3rd Int. Symp. Aquatic Weeds, Oxford, England*, pp. 53–62.

Ladle, M., Casey, H., Marker, A. F. H. & Welton, J. S. 1981 The use of large experimental channels for ecological research. *Proc. Wld Symp. Aquaculture in Heated Effluents and Recirculation Systems, Stavanger, Norway* (1980) vol. 1, pp. 279–287.

Ladle, M., Welton, J. S. & Bass, J. A. B. 1980 Invertebrate colonisation of the gravel substratum of an experimental recirculating channel. *Holarct. Ecol.* **3**, 116–123.

Lerman, A. & Lal, D. 1977 Regeneration rates in the ocean. *Am. J. Sci.* **277**, 238–258.

Lewin, J. G. 1961 The dissolution of silica from diatom walls. *Geochim. cosmochim. Acta* **21**, 182–198.

Lund, J. W. G., Kipling, C. & Le Cren, E. D. 1958 The inverted microscope method of estimating algal numbers and the statistical basis of estimating by counting. *Hydrobiologia* **11**, 143–170.

Lund, J. W. G., Mackereth, F. J. H. & Mortimer, C. H. 1963 Changes in depth and time of certain chemical and physical conditions and of standing crop of *Asterionella formosa* Hass. in the north basin of Windermere in 1947. *Phil. Trans. R. Soc. Lond.* B **246**, 255–293.

McIntire, C. D. 1966 Some factors affecting respiration of periphyton communities in lotic environments. *Ecology* **47**, 918–930.

McIntire, C. D. 1968 Structural characteristics of benthic algal communities in laboratory streams. *Ecology* **49**, 520–537.

McIntire, C. D., Garrison, R., Phinney, H. K. & Warren, C. 1964 Primary production in laboratory streams. *Limnol. Oceanogr.* **9**, 92–102.

McIntire, C. D. & Phinney, H. K. 1965 Laboratory studies of periphyton production and community metabolism in lotic environments. *Ecol. Monogr.* **35**, 237–258.

MacKenzie, F. T. & Garrels, R. M. 1966*a* Chemical mass balance between rivers and oceans. *Am. J. Sci.* **264**, 507–525.

MacKenzie, F. T. & Garrels, R. M. 1966*b* Silica–bicarbonate balance in the ocean and early diagenesis. *J. sediment. Petr.* **36**, 1075–1084.

Mackereth, F. J. H., Heron, J. & Talling, J. F. 1978 Water analysis: some revised methods for limnologists. *FBA scient. Publ.* no. 36. Ambleside: Freshwater Biological Association.

Marker, A. F. H. 1972 The use of acetone and methanol in the estimation of chlorophyll in the presence of phaeophytin. *Freshwat. Biol.* **2**, 361–385.

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

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

Marker, A. F. H. 1980 A note on the extraction of chlorophyll from benthic algae using methanol. *Arch. Hydrobiol., Beih., Ergebn. Limnol.* **14**, 88–90.

Marker, A. F. H. & Gunn, R. J. M. 1977 The benthic algae of some streams in southern England. III. Seasonal variations in chlorophyll *a* in the seston. *J. Ecol.* **65**, 223–234.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

Marker, A. F. H. & Westlake, D. F. 1980 Primary production – introduction. In *The functioning of freshwater ecosystems* (ed. E. D. Le Cren & R. H. Lowe-McConnell), pp. 141–146. Cambridge University Press.
Marshall, N., Oviatt, C. A. & Skauen, D. M. 1971 Productivity of the benthic microflora of shoal estuarine environments in southern New England. *Int. Rev. ges. Hydrobiol. Hydrogr.* **56**, 947–956.
Mason, C. F. & Bryant, R. J. 1975 Periphyton production and grazing by chironomids in Alderfen Broad, Norfolk. *Freshwat. Biol.* **5**, 271–277.
Moed, J. R. 1973 Effect of combined action of light and silicon depletion on *Asterionella formosa* Hass. *Verh. int. Verein. theor. angew. Limnol.* **18**, 1367–1374.
Moore, J. W. 1976 Seasonal succession of algae in rivers. I. Examples from the Avon, a large slow-flowing river. *J. Phycol.* **12**, 342–349.
Moore, J. W. 1977 Seasonal succession of algae in a eutrophic stream in southern England. *Hydrobiologia* **53**, 181–192.
Moore, J. W. 1978 Seasonal succession of algae in rivers. III. Examples from the Wylye, a eutrophic farmland river. *Arch. Hydrobiol.* **83**, 367–376.
Müller-Haeckel, A. 1966 Tages – und Jahresperiodik von *Ceratoneis arcus* Kütz. *Oikos* **18**, 315–326.
Mullin, J. B. & Riley, J. P. 1955 The colorimetric determination of silicate with special reference to sea and natural waters. *Analytica chim. Acta* **27**, 31–36.
Naiman, R. J. & Gerking, S. D. 1975 Interrelationships of light, chlorophyll and primary production in a thermal stream. *Verh. int. Verein. theor. angew. Limnol.* **19**, 1659–1664.
Nelson, D. M. & Goering, J. J. 1977 Near surface silica dissolution in the upwelling region off northwest Africa. *Deep Sea Res.* **24**, 65–73.
Nelson, D. M., Goering, J. J., Kilham, S. S. & Guillard, R. R. L. 1976 Kinetics of silicic acid uptake and rates of silica dissolution in the marine diatom, *Thalassiosira pseudonana*. *J. Phycol.* **12**, 246–252.
Odum, H. T. & Hoskin, C. M. 1957 Metabolism of a laboratory stream microcosm. *Publs Inst. mar. Sci. Univ. Tex.* **4**, 115–133.
Ohle, W. 1964 Interstitiallosungen der Sediment. Mahrstaffgehalt des Wassers und Primarproduktion des Phytoplanktons im Seen. *Helgoländer. wiss. Meeresunters.* **10**, 441–429.
Paasche, E. 1973*a* The influence of cell size on growth rate, silica content, and some other properties of four marine diatom species. *Norw. J. Bot.* **20**, 197–204.
Paasche, E. 1973*b* Silicon and the ecology of marine plankton diatoms. 1. *Thalassiosira pseudonana* (Cyclotella nana) grown in a chemostat with silicate as limiting nutrient. *Mar. Biol.* **19**, 117–126.
Paasche, E. 1980 Silicon content of five marine plankton diatom species measured with a rapid filter method. *Limnol. Oceanogr.* **25**, 474–480.
Pamatmat, M. M. 1968 Ecology and metabolism of a benthic community of an intertidal sandflat. *Int. Revue ges. Hydrobiol. Hydrogr.* **53**, 221–298.
Parker, J. I., Conway, H. L., Yaguchi, E. M. & Edgington, D. N. 1978 Dissolution of diatom frustules and silicon cycling in Lake Michigan, U.S.A. *Verh. int. Verein. theor. angew. Limnol.* **20**, 336–340.
Parsons, T. R., Stephens, K. & Strickland, J. D. H. 1961 On the chemical composition of eleven species of marine phytoplankters. *J. Fish. Res. Bd Can.* **18**, 1001–1016.
Patrick, R., Crum, B. & Coles, J. 1969 Temperature and manganese as determining factors in the presence of diatom or blue-green algal floras in streams. *Proc. natn. Acad. Sci. U.S.A.* **64**, 472–478.
Phinney, H. K. & McIntire, C. D. 1965 Effect of temperature on metabolism of periphyton communities developed in laboratory streams. *Limnol. Oceanogr.* **10**, 341–344.
Pieczynska, E. & Straskraba, M. 1969 Field experiments on the effect of light conditions in Phragmites stands on the production of littoral algae. *Bull. Acad. pol. Sci. Cl. II Sér. Sci. biol.* **17**, 43–46.
Pitcairn, C. E. R. & Hawkes, H. A. 1973 The role of phosphorus in the growth of *Cladophora*. *Water Res.* **7**, 159–171.
Pomeroy, L. 1959 Algal productivity in salt marshes of Georgia. *Limnol. Oceanogr.* **4**, 386–397.
Rebsdorf, A. 1972 *The carbon dioxide system in freshwater*. Freshwater Biological Laboratory: Hillerød, Denmark.
Schrader, H. G. 1971 Faecal pellets: role in sedimentation of pelagic diatoms. *Science, N.Y.* **174**, 55–57.
Snedecor, G. W. & Cochran, W. G. 1967 *Statistical methods* (6th edn), pp. 511–516. Iowa State University Press.
Sperling, J. A. 1975 Algal ecology of southern Icelandic hot springs in winter. *Ecology* **56**, 183–190.
Stanley, D. W. 1976 A carbon flow model of epipelic algal productivity in Alaskan tundra ponds. *Ecology* **57**, 1034–1042.
Stockner, J. C. 1968 Algal growth and primary productivity in a thermal stream. *J. Fish. Res. Bd Can.* **25**, 2037–2058.
Sumner, W. T. & Fisher, S. G. 1979 Periphyton production in Fort River, Massachusetts. *Freshwat. Biol.* **9**, 205–212.
Talling, J. F. 1957 The phytoplankton population as a compound photosynthetic system. *New Phytol.* **56**, 133–149.
Tett, P., Gallegos, C., Kelly, M. G., Hornberger, G. M. & Grosby, B. J. 1978 Relationships among substrate, flow, and benthic microalgal pigment density in the Mechums River, Virginia. *Limnol. Oceanogr.* **23**, 785–797.
Tippett, R. 1970 Artificial surfaces as a method of studying populations of benthic micro-algae in freshwater. *Br. phycol. J.* **5**, 187–199.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

Tolstoy, A. 1979 Chlorophyll *a* in relation to phytoplankton volume in some Swedish lakes. *Arch. Hydrobiol.* **85**, 133–151.

Tominaga, K. & Ichimura, S. 1966 Ecological studies on the organic matter production in a mountain river. *Bot. Mag., Tokyo* **79**, 815–829.

Van Raalte, C. D., Valiela, I. & Teal, J. M. 1976 The effects of fertilization on the species composition of salt marsh diatoms. *Water Res.* **10**, 1–4.

Welton, J. S. & Ladle, M. 1979 Two sediment trap designs for use in small rivers and streams. *Limnol. Oceanogr.* **24**, 588–592.

Westlake, D. F., Casey, H., Dawson, F. H., Ladle, M., Mann, R. H. K. & Marker, A. F. H. 1972 The chalk-stream ecosystem. In *Productivity problems of freshwaters* (ed. by Z. Kajak & A. Hillbricht-Ilkowska), *Proc. IBP–UNESCO Symp. Productivity Problems of Freshwaters, Kazimierz-Dolny*, 1970, pp. 615–635. Warsaw and Krakow: Polish Scientific Publishers.

Wetzel, R. G. 1964 A comparative study of the primary productivity of higher aquatic plants, periphyton and phytoplankton in a large shallow lake. *Int. Rev. ges. Hydrobiol. Hydrogr.* **49**, 1–61.

Whitford, L. A. & Schumacher, G. F. 1961 Effect of current on mineral uptake and respiration by freshwater algae. *Limnol. Oceanogr.* **6**, 423–425.

Wiegert, R. G. & Fraleigh, P. C. 1972 Ecology of Yellowstone thermal effluent systems: net primary production and species diversity of a successional blue-green algal mat. *Limnol. Oceanogr.* **17**, 215–228.

Williams, R. S. 1981 The spatial distribution of chironomid larvae within stands of submerged macrophytes. Ph.D. thesis, University of Reading.

Wong, S. L., Clark, B. & Painter, D. S. 1976 Application of underwater light measurements in nutrient and production studies in shallow rivers. *Freshwat. Biol.* **6**, 543–550.

Wuhrmann, K. & Eichenberger, E. 1975 Experiments on the effects of inorganic enrichment of rivers on periphyton primary production. *Verh. int. Verein, theor. angew. Limnol.* **19**, 2028–2034.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES