Structural and functional characteristics of epiphyton and epipelon in relation to their distribution in Lake Vechten

Herman J. Gons
Limnological Institute, 'Vijverhof' Laboratory, Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands

Keywords: periphyton, submerged macrophytes, sediment, artificial substrates, oxygen exchange, production, decomposition, sedimentation

Abstract

Epiphyton and epipelon were quantitatively collected, respectively, from the submerged macrophytes and the sandy lake bottom of Lake Vechten (The Netherlands). On a weight basis, epiphyton was maximal in autumn and epipelon in summer. In winter the chemical composition of epiphyton and epipelon was similar. In summer the epiphyton had on a unit weight basis more organic matter and carbonate, and had per unit organic matter a higher algal number, nitrogen and energy content than the epipelon. Algae predominating the epiphyton were filamentous greens and pennate diatoms; those in the epipelon were pennate diatoms and blue-green algae. In both cases, species known to frequent the phytoplankton were abundant. The diatoms were quantified using paper chromatographic pigment analyses. Both the epiphyton and the epipelon exhibited maximal photosynthesis in mid summer. That light was generally the limiting factor was evident from periphyton developed on artificial substrates. This periphyton differed widely in its composition from that on the natural substrates, mainly because the latter collected much more sedimenting matter.

In dense *Ceratophyllum* stands light was severely attenuated and the significant gradients in oxygen and pH were caused by the differences with depth in the proportions of photosynthesis and respiration. The oxygen content and pH at the bottom decreased owing to epipelic respiration. The epiphytic composition depended greatly on the degree of light attenuation. The epiphytic and epipelic respiration, except during part of the early summer, exceeded photosynthesis on a 24 h basis; this included the macrophytic photosynthesis during the time the vegetation was maximally developed. During the growing season import of organic matter, i.e. deposited seston, greatly exceeded that due to the photosynthetic production. After the summer maximum, the epipelon decreased faster than predicted from its oxygen exchange. It was concluded that sedimentation and resuspension determined mainly the changes in epiphyton and epipelon. Especially when covered with vegetation, the lower littoral of Lake Vechten plays a large part in the aerobic decomposition of sestonic organic matter.

Introduction

The present study deals with particulate matter collected from defined substrates in Lake Vechten, which are: submerged macrophytes; the sandy lake bottom; and perspex plates. The matter is composed of live organisms, detritus, and includes compounds generated by biological activity, such as calcium carbonate, but also clay particles. For practical purposes the size limits were 125 and 0.2 μm (see Methods). The above collection of materials will be referred to as periphyton. Thus the definition of periphyton by Wetzel (1975), i.e. microfloral growth upon substrates, was broadened into an analogue of the seston of the open water.

Periphyton may be subdivided referring to the substrate; Round (1973) used the terms epipelic and epiphytic for the algal communities associated

Hydrobiologia 95, 79–114 (1982). 0018-8158/82/0951-0079/$07.20.
© Dr W. Junk Publishers, The Hague. Printed in The Netherlands.

with, respectively, sediments and macrophytes. As the species composition of the algal communities in the periphyton collected from the different substrates in the lake are comparable with Round's classification, the two kinds of periphyton are denoted as epipelon and epiphyton.

Traditionally, algae, being the more conspicuous component of periphyton, received more attention from limnologists. This has changed since studies revealed that functionally heterotrophic processes may often be important, and even predominant (Pieczyńska 1975; Mann 1975). A number of structural (Allanson 1973) and functional (Allen 1971; Wetzel & Allen 1972; Wetzel 1975) interrelationships within periphyton, and between periphyton and its substrate, have become apparent. However, much evidence is still circumstantial and scattered, especially if compared with that on planktonic communities.

For periphyton in lakes, as a rule, algae were regarded as the most important viable component. Consequently, attached organisms, considered to be the true periphyton, are distinguished from 'dependent' free-living organisms, or pseudo-periphyton (Sládečková 1962). The periphyton was, from the viewpoint of energetics, considered largely to be self-supporting, for which, at least during the growing season, algal photosynthesis provides the basis for the trophic dynamic structure. This was also the viewpoint at the start of the periphyton study (1977) on Lake Vechten, being aimed at periodicity and productivity of the epiphytic algae associated with the submerged macrophytes. The macrophytes covered most of the littoral zone down to 5 m depth, which comprises more than a third of the lake area. Floating-leaved and emergent macrophytes, in contrast, are less important substrates occupying about 5% of the lake area. Predominating submerged species were *Elodea* sp. and *Ceratophyllum demersum*, with *Myriophyllum spicatum* as a good third.

During the last few years, the submerged macrophytes declined; in 1980 there was nearly no growth below 3 m; *Ceratophyllum* predominated, while *Myriophyllum*, but for some isolated poorly developed individuals, had disappeared (for details, see Best 1982). These events led to an extension of the investigations on the epipelon. Seasonal changes could be studied quantitatively, which was allowed by the nature of the bottom: this is sandy, and has steep slopes, which prevents the accumulation of refractory matter over the years.

The periphyton research is a part of ecosystem studies on Lake Vechten with the main aim to quantify the pool sizes and fluxes of carbon. As a consequence the approach has been essentially non-taxonomic, but was directed towards characterization of the periphyton as an entity in the carbon cycle.

The following aspects have been investigated:

1. *Chemical composition:* The distinction between organic matter and other constituents was based on ignition losses. More information was obtained by elementary analyses. In this way, carbonate and ash content could be differentiated giving information on photosynthetic activity and degree of advance of mineralization. The latter may be further qualified by the elementary composition of the organic matter, from which the caloric equivalent and proximate molecular composition can also be derived (Spoehr & Milner 1949; Milner 1953); Hallegraeff (1976) applied this to seston of Dutch lakes. For other examples see Wetzel (1975) and Parsons *et al.* (1977).

2. *Composition of algal species and photosynthetic pigments:* The identification and counts of organisms were restricted to the algae, since their recognition is relatively simple, and their species composition provides information on functional aspects of the relevant biota (Cholnoky 1968; Hutchinson 1975; Round 1973). Also, this gave insight into interactions between the littoral and limnetic region. Chlorophyll *a*, of course, was measured to provide information on the autotrophic component of the periphyton. Paperchromatographic pigment analyses were carried out to supplement information on the importance of the taxa and the viability of the algae as demonstrated by Hallegraeff (1976).

3. *Oxygen exchange:* Since the environment of both epiphyton and epipelon is aerobic, oxygen measurements were used to establish material balances (Odum 1971; Parsons *et al.* 1977). The periphyton was characterized by the dark oxygen consumption, i.e. the potential community respiration (r), and the maximum gross oxygen production (p_g^{max}), which expresses the photosynthetic capacity. The ratio p_g^{max}/r is a measure of the relationship between the autotrophic and heterotrophic components. The *in situ* changes depended, of course, on the conditions of irradiation and on the depth distribution of light and periphyton.

During the first two years the studies involved average properties of epiphyton collected from plant shoots, or large sections, over which great differences might exist, in particular with respect to light. The subsequent research was focussed on the depth distribution of epiphyton within dense stands of *Ceratophyllum* and of epipelon. This included measurements on physico-chemical gradients in the field. From the summer of 1980 onwards, epiphyton and epipelon were studied along a fixed transect through the SE part of the lake (Fig. 1).

Materials and methods

Sampling procedures

For epiphyton plants, or their parts, were collected by SCUBA-diving. The epiphyton and macrophyte were separated using a Vibromixer (Chemap, Zürich), if necessary after cutting the macrophyte into sections. During the procedure the pH was lowered, using automatic titration with 0.1 N HCl, to 5 in order to dissociate carbonate encrustations. After this treatment (Fig. 2A) had been applied for 15–30 min, the epiphyton was quantitatively removed from its substrate, and the lake water's pH quickly returned to its pretreatment value. The method did not damage algal cells, filaments, or photosynthetic pigments. When applied with care, the macrophytic parts also remained intact. Possible interference of the lowered pH with respiratory and photosynthetic capacity was minimized by first removing the more loosely associated part by using the Vibromixer only: usually, this loose material comprised about three quarters or more of the total of epiphyton, also on the basis of chlorophyll.

Epipelon was collected using a specially designed stainless steel sampler (Fig. 2B). A known area of sediment can be isolated within the sharp-edged cylindrical chamber of this apparatus, which is forced into the sandy bottom by a weight, but prevented from penetrating too deeply by a wide rim. By applying suction through the butyl rubber tubing, water spurts through the narrow holes just above the rim into the chamber, thus eddying the

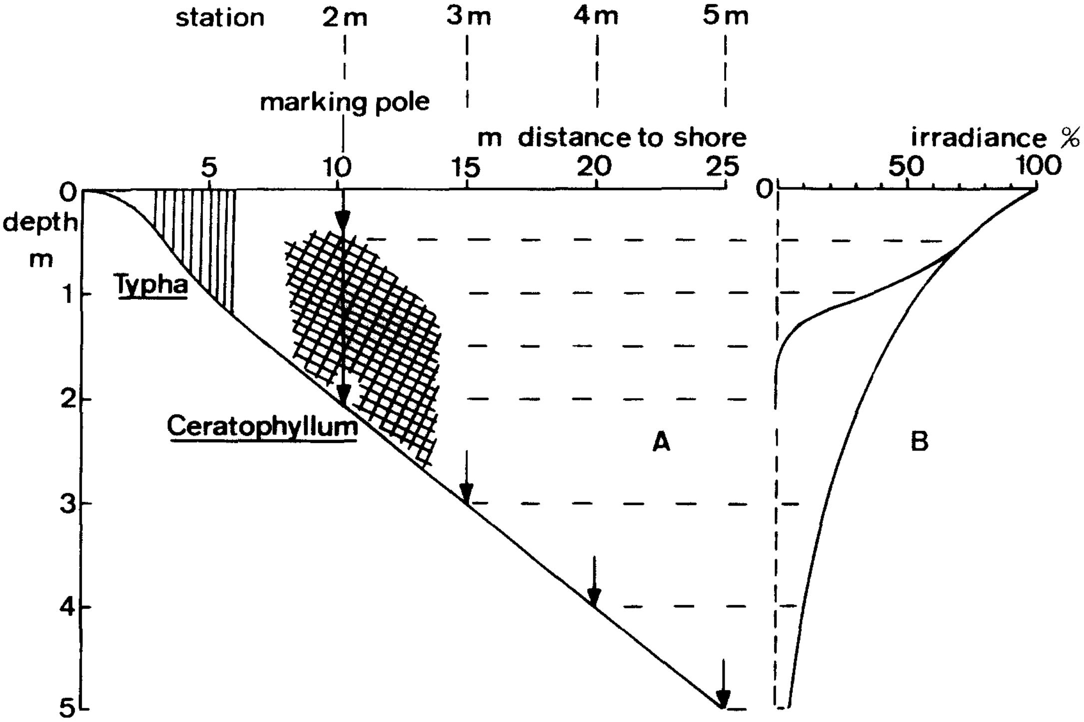


Fig. 1. Transect through the littoral zone of the SE part of the lake during 1980 and 1981. Conditions of light irradiance (B) as determined on 9 September 1980. The line on the left gives the light within the vegetation.

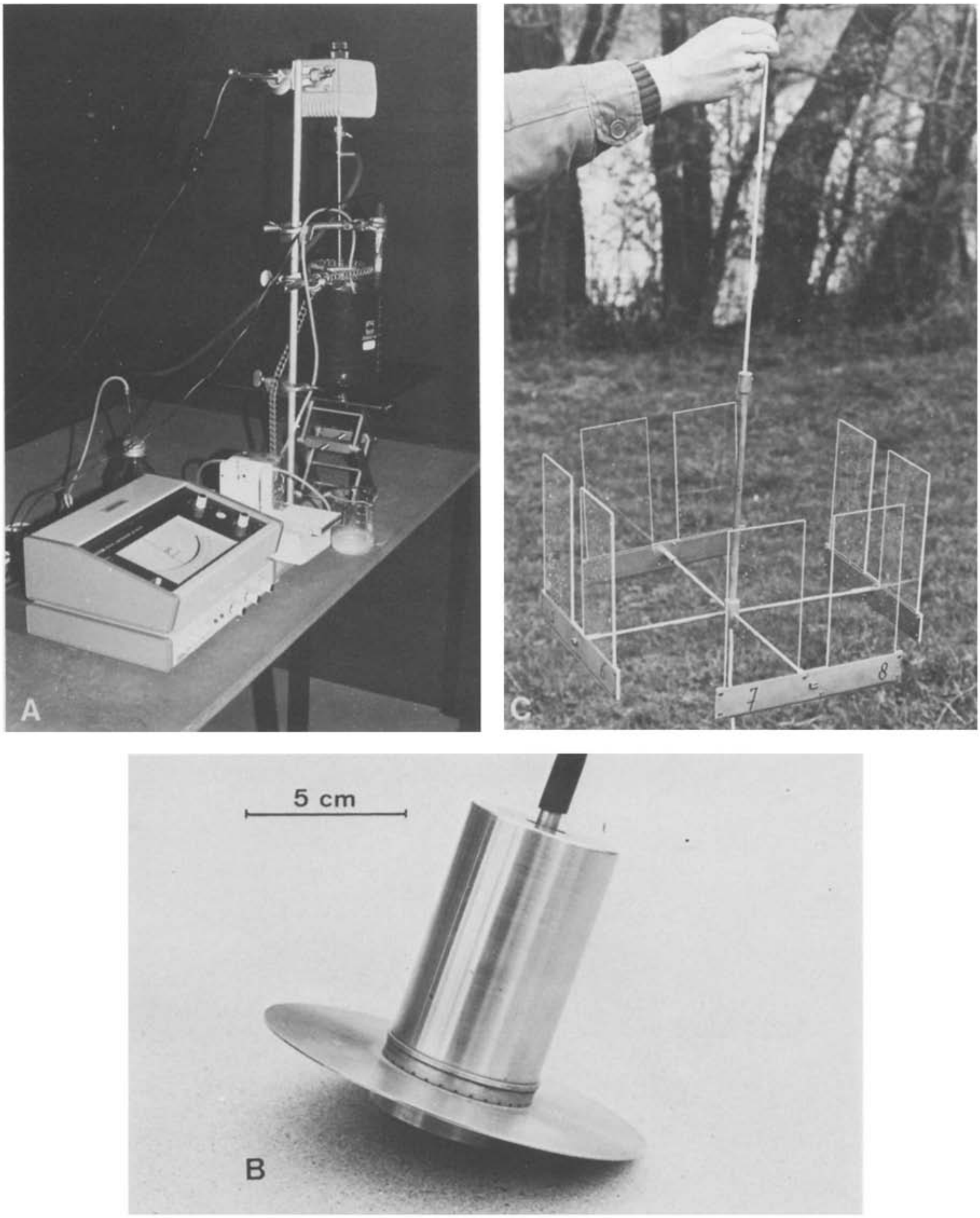


Fig. 2. The equipment used for the periphyton studies. A: Vibromixer combined with pH-stat for separating epiphyton from the macrophytes. B: Epipelon sampler. C: Assemblage for artificial substrates.

isolated volume of about 8 ml above the sand. The pumping was continued until all epipelic matter was removed from the sand, which involved a volume of about 0.7 l. The method is sufficiently powerful to bring up large sand grains. At each station (Fig. 1) five such samples were collected in one polyvinyl vessel.

Perspex plates used as artificial substrates (Fig. 2C) were exposed vertically so that 10 × 20 cm on either side could be colonized. At one particular depth eight such plates were hung. The first plate was removed and replaced by another after each interval. The others were removed one by one after subsequent intervals, in order to pursue the developments continuously. In the laboratory the periphyton was scraped off the sides and the edges.

All samples were treated with the Vibromixer, but the epipelon and 'perspex' periphyton were not exposed to the lowered pH. Thereafter, the suspensions were filtered over 125 μm mesh, to remove larger animals, leaf debris, etc. The 'perspex' periphyton sometimes clogged the filter due to abundance of filamentous green algae. The larger parts, notably snails and *Dreissena,* were then removed manually. Sand grains, present mainly in the epipelic samples, did not interfere with the subsequent analyses.

In general the suspensions were processed for analysis immediately. The samples for cell counts and pigment composition were conserved by, respectively, adding Lugol's solution and storage at -30 °C.

Water samples for physico-chemical analysis were collected using the sampler described or a similar apparatus (without wide rim) that could be lowered in dense *Ceratophyllum* stands without displacing plant shoots.

Gravimetric and elementary analyses

Aliquots of the suspensions were centrifuged and the pellets transferred into 25 ml glass vials. Dry weights were determined after freeze-drying and overnight storage in a desiccator.

After homogenizing, part of the dry matter was weighed into aluminium combustion boats (Perkin-Elmer, Oak Brook, Ill.) and ashed at 450 °C to determine the ignition loss. With this temperature it was safe to operate, since no decomposition of $CaCO_3$ occurs. Another part was used for elementary analysis using a Perkin-Elmer model 240 C-N-H analyzer.

For determining the contribution of $CaCO_3$ and the composition of the organic matter, elementary analysis was also carried out on the residue after ignition at 450 °C. The $CaCO_3$ as a percentage of the total was then computed according to:

$$\%\,CaCO_3 = (\%C_r \times \text{residue/total}) \times 100/12. \quad (1)$$

The carbon content of the organic matter was determined as:

$$\%\,C = \frac{\%\,C_t - (\%C_r \times \text{residue/total})}{\text{loss on ignition/total}} \quad (2)$$

where C_r = carbon contained in the residue, and
C_t = carbon contained in the total matter.

The hydrogen and nitrogen contents of the organic matter were computed in the same way as carbon (eq. 2).

All data on the contents and ratios of C, H and N are given on a weight basis.

Cell counts

The technique applied was the same as for the phytoplankton (see Blaauboer 1982). The data given in the Results are expressed as cell numbers, except for the blue-green algae, where the numbers refer to filaments.

Intactness of chloroplasts was used as a measure of viability of pennate diatoms.

Pigment analyses

Chlorophyll was extracted in methanol and computed according to Iwamura *et al.* (1970). Unless otherwise stated, the chl *a* values refer to 'total chl *a*', and may include considerable proportions of breakdown products.

The 2-dimensional paperchromatographical separation of the pigments (Fig. 3) essentially followed Hallegraeff (1976), but the extraction was in methanol. The pigments were concentrated by evaporation under nitrogen, and transferred in acetone prior to the separation. The yield of the procedure was fairly good: the integrated light absorption of the separated pigments was approximately 90% of that of the methanol extract. Not all pigments were

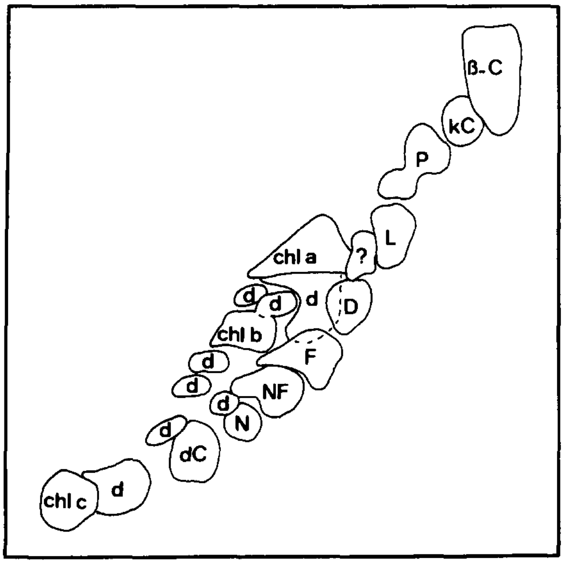


Fig. 3. 2-Dimensional paper chromatogram of epiphyton. chl *a, b, c* = chlorophyll *a, b, c*; *β*-C ≙ beta-carotene; dC = carotenoid derivative; kC = ketocarotenoid; ? = unidentified carotenoid; D = diadinoxanthin; F = fucoxanthin; NF = neofucoxanthin; N = neoxanthin; L = lutein; P = phaeophytin; d = chlorophyll derivatives.

completely isolated (Fig. 3), but in most cases the relevant pigments could be estimated accurately by applying spectrometric corrections. The results are expressed as percentage of total light absorption by the separated pigments.

Oxygen exchange

Two oblong glass containers, filled with water and maintained at *in situ* temperature under the control of a kryo-thermostat (Colora, Lorch/Württ.), served as the incubator. The containers received illumination (TL F 20 W/33 fluorescent lamps, Philips, Eindhoven) ranging from 3 to 5 $W.m^{-2}$ to saturating and often inhibiting values of 120 $W.m^{-2}$. For dark incubations the samples were wrapped in aluminium foil.

Oxygen consumption in the dark, i.e. the potential community respiration (r), was measured in duplicate in BOD-bottles containing approximately 260 ml of the suspension. During the incubation the suspension was not stirred, so the periphyton settled down on the bottom. The start and end concentrations of oxygen were measured using a YSI meter and self-stirring BOD-bottle probe (Yellow Springs, Ohio). In general the incubation time was about 4 h, excluding pre-incubation of 1–2 h, but the epipelic winter samples especially required overnight incubation for reliable results. Periodically, chemical oxygen consumption was checked. In general all oxygen consumption stopped on adding 10 ml of 37% formaldehyde.

For measuring the oxygen exchange vs. irradiance, the periphyton was incubated on filters. Depending on the concentration, 10–100 ml was filtered over 0.2 μm filter (Sartorius, Göttingen) with 5 cm diameter. Subsequently, the filter was cut into two equal halves, inserted into a glass vial containing on the average 26.4 ml of prefiltered (0.2 μm) lake water. The vials were tightly closed with screw caps, and inspected to ensure exclusion of air. The oxygen was measured using the YSI meter and probe, but the stirrer's boot was removed. After the incubation the filter half was first removed. Insertion of the probe isolated the content of the vial from exchange with air. The incubation time was similar to that of the BOD-bottles. For calculating net production the filtered lake water was incubated as blanks.

The results of the dark incubations in the BOD-bottles and of the filters were almost always comparable. The former, however, were used more often and the respiration values in the Results refer to these.

On one occasion the oxygen exchange vs. irradiance curve was determined for *Ceratophyllum*, when 4 plant tips of 15 cm length made free of the epiphyton were used. The plant tips were incubated in the above BOD-bottles, filled with lake water well below oxygen saturation. Each section was used for incubation at one irradiance and in the dark. Following a pre-incubation of 30 min, the sections were incubated for 1 h. Thereafter the four were transferred into the dark and, after 10 min pre-incubation, the respiration was measured over 90 min.

The irradiances were measured using R 3001 photometer equipped with an SD 101 photodiode detector with spectral range of 400–700 nm (Macam, Livingston, Scotland). The results were corrected for reflections by the glass of BOD-bottles and vials.

Physico-chemical parameters in situ

Light in stands of *Ceratophyllum* was measured with the laboratory equipment already mentioned. The sensor could be moved vertically without causing significant changes in the position of the macrophytes shoots.

Oxygen and temperature were measured in the field, using both the BOD-bottles and the YSI meter and probe.

For the remaining analyses the samples were surrounded with ice and transported to the laboratory. The pH and HCO_3^- were determined on arrival, the latter potentiometrically with a Quéré automatic titrator (Jouan, Paris).

Results and discussion

Epiphyton

Distribution of epiphytic matter. Due to the loose association of epiphyton to macrophytes, stirring resulted in loss of particles *in situ.* Consequently, the total epiphytic matter was underestimated, and the results tend to be biased in favour of the matter more firmly attached to the substrate.

By far the greater part of the epiphyton consisted of detrital matter (Fig. 4A). In the epiphyton associated with *Chara* studied by Allanson (1973), algae were far more important as a structural component. Also, relative to the seston in Lake Vechten, algae were scarce, but bacteria and microfauna, namely Protozoa, were abundant. The significance of mucoid substances in keeping in place the epiphytic matter is shown in Fig. 4B.

The amounts of epiphyton were surprisingly high, considering the appearance, and the epiphyton dry weight often exceeded that of its substrate. The ash content was high; typically, organic matter amounted only to about 20%. This was for a great part due to carbonates, probably precipitated during photosynthesis of macrophyte and epiphytic algae (Fig. 4C). Despite this, the organic matter of epiphyton was also at times more than that of the macrophyte.

In 1978, epiphyton was compared from five populations of submerged macrophytes: *Elodea* sp., *Myriophyllum spicatum,* and *Ceratophyllum demersum* at three different depths (Fig. 5). Early in the season the plants had been tagged (see Best 1982). The five associations differed considerably on various dates, but the proportions of epiphyton to macrophyte on a weight basis did not differ significantly depending either on macrophyte species or depth when the seasonal averages were compared.

Speaking in general, the proportions of epiphyton were low from May to July, but high in early spring and autumn. Per area unit of littoral, the greatest quantities of epiphyton occurred in September and October (Fig. 30), with high proportions (Fig. 5) at the time of the maximum macrophyte standing crop.

Chemical composition. For the same categories of samples, average chemical characteristics (April-September) are summarized in Table 1.

The percentage organic matter was low, close to 20% for all groups. The carbon content varied more widely. These data include the carbon contained in carbonates. Thus, the variations in both % carbon (Table 1) and the high values of C:N and C:H ratios are explained by the high contribution of carbonate. The latter differed from category to category, assuming the carbon content of the organic matter to be 50%.

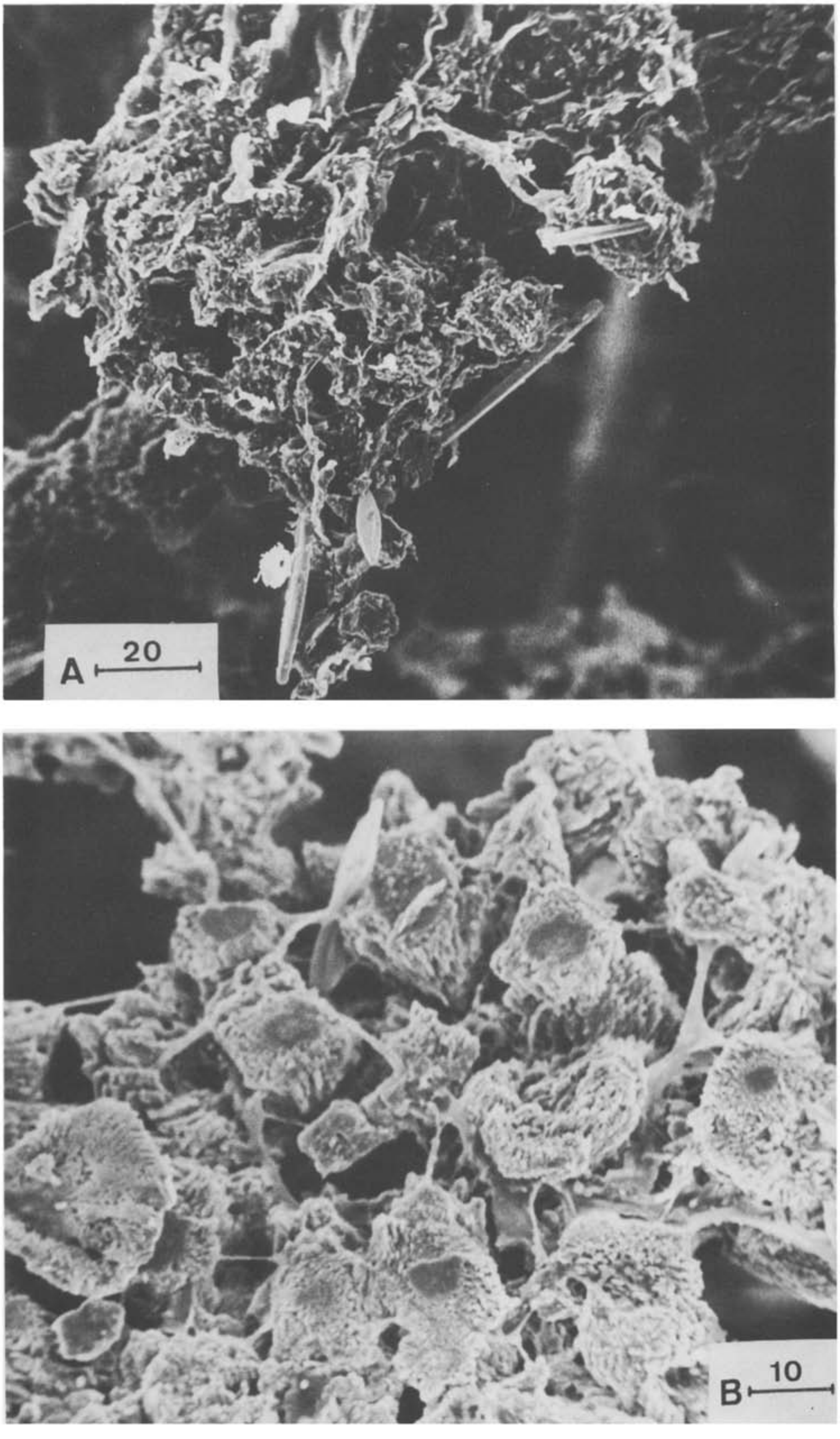
The % organic matter (Fig. 6) fluctuated seasonally, particularly when the macrophyte growth was fast; then the organic matter and carbon were maximal up to, respectively, 50 and 25%. This will have been due to comparatively low accumulation rates of both sediment and carbonates on the surfaces of the rapidly extending macrophytes, and to the development of epiphytic algae.

The decrease in organic matter and carbon content with depth of the epiphyton from the three *Ceratophyllum* stands (Table 1) is noteworthy, as are the great seasonal changes occurring with the epiphyton from the lesser depth (Fig. 6).

Large but unknown quantities of carbonate obscured the composition of the epiphytic organic

Table 1. Chemical characteristics of epiphyton during April-September 1978.

Substrate	Stratum (m)	% organic matter	% C	% H	% N
Ceratophyllum demersum	1–2	22.2	13.4	1.8	1.2
Ceratophyllum demersum	2–3	21.2	12.5	1.7	1.3
Ceratophyllum demersum	3–4	19.7	10.4	1.7	1.1
Elodea sp.		19.6	10.3	1.5	1.0
Myriophyllum spicatum		19.3	12.6	1.6	1.1


A
20
B
10

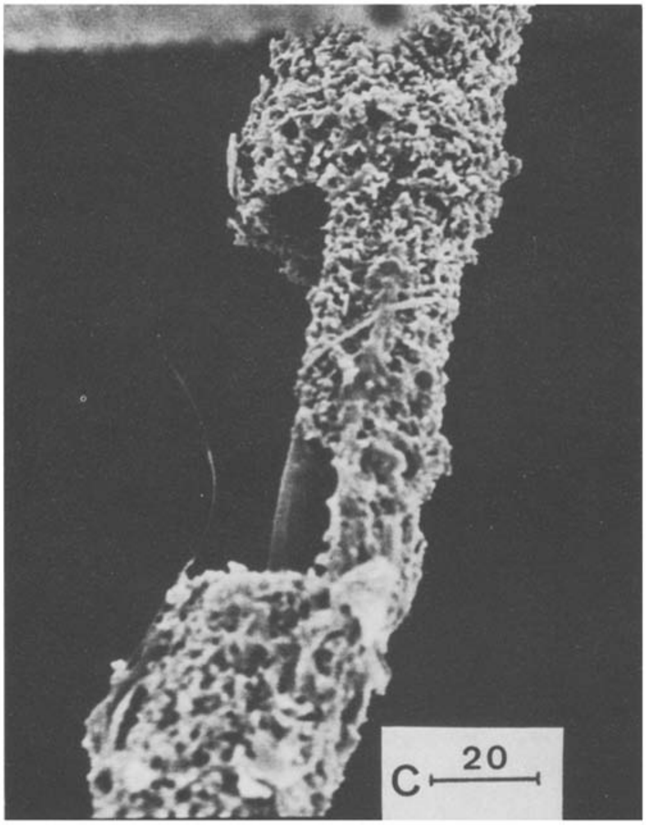


Fig. 4. Scanning electron photomicrographs of epiphyton. Scale in μm. A: Detrital aggregates with diatoms. B: Carbonate deposits and mucoid strands. C: Carbonate encrustation on filamentous green alga.

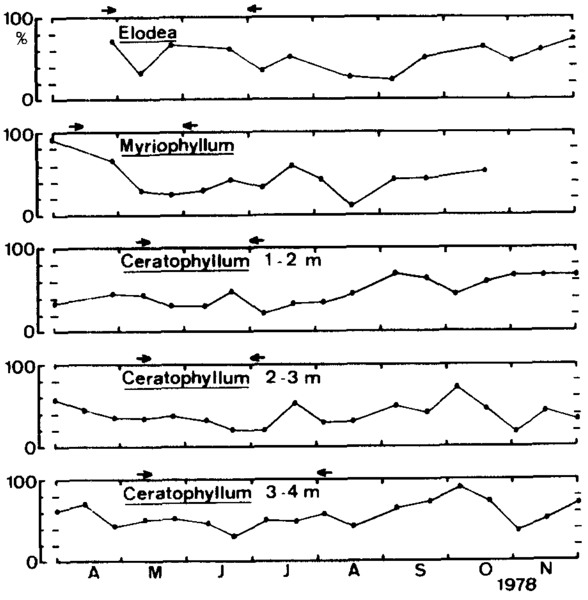


Fig. 5: Contribution of epiphyton on total dry weight basis to submerged vegetation. Arrows indicate the periods of main growth of the macrophytes.

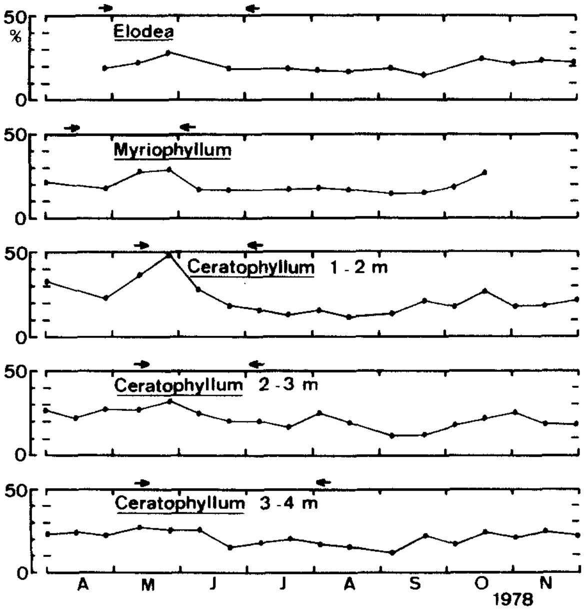


Fig. 6. Percentage organic matter of epiphyton from submerged vegetation. See also Fig. 5.

matter, until both total matter and the residue on ignition were analysed (see Methods) for the epiphyton collected from *Ceratophyllum* during 1980 and 1981 (Fig. 7A and Table 2).

Assuming all carbon in the residue came from $CaCO_3$, contributions of organic matter (i.e. the loss on ignition), $CaCO_3$ and ash (i.e. the residue minus $CaCO_3$), are given in Fig. 7. As in 1978 (Fig. 6), the organic matter was about 20%, but seasonal changes were less, notably during early summer. The $CaCO_3$ contributed the most in June and July and least in spring; this suggests a direct relation with photosynthetic activity. The decrease in $CaCO_3$ already in the second half of July is explained later.

The ash percentage indicated prevalence of the more viable epiphytic communities during summer, and increase in the detritus content during autumn and winter until spring next year. These changes were not substantiated by clear seasonal patterns in the carbon content of the organic matter, nor in organic C:N ratio.

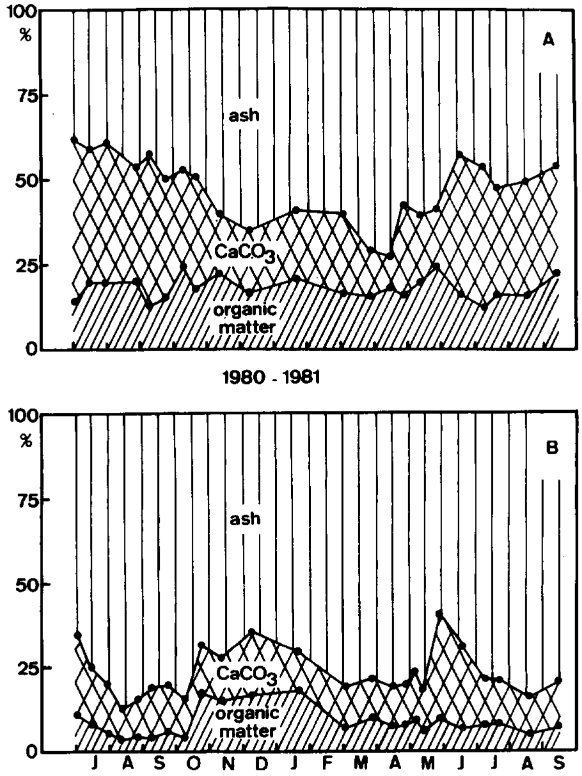


Fig. 7. Contribution of organic matter, calcium carbonate and ash to epiphyton (A) and epipelon at 4 m (B).

Table 2. Chemical characteristics of epiphyton and epipelon during July 1980–June 1981.

A. Composition of total matter

	% organic matter	% $CaCO_3$	% ash	% C	% H	% N
Epiphyton	18.4	28.3	53.3	12.0	1.6	1.0
Epipelon, 3 m	10.4	15.2	74.4	5.8	1.0	0.5
Epipelon, 4 m	8.9	15.2	75.9	5.4	0.9	0.4
Epipelon, 5 m	10.1	15.2	74.7	6.4	1.0	0.5

B. Composition and R-value of organic matter

	% C	% H	% N	R-value
Epiphyton	47.0	7.9	5.2	37.1
Epipelon, 3 m	42.0	7.7	4.2	31.8
Epipelon, 4 m	42.8	7.7	4.2	32.7
Epipelon, 5 m	45.2	8.1	4.6	35.7

The annual averages of the elementary composition of the epiphytic organic matter are given in Table 2B. The nitrogen percentages were fairly high, indicating a fair contribution of proteinaceous matter. For degree of reduction, the concept of the R-value (Spoehr & Milner 1949) was used. The R-value of carbon compounds ranges from zero, for carbon dioxide, to 100, for methane, and may be applied equally well to mixtures of organic compounds such as we find in plant materials (Milner 1953). Hallegraeff (1976) established the following equation for sestonic matter:

$$\text{cal. mg ash-free dry weight}^{-1} = -0.245 + 0.144\ .\ R.$$

Epiphytic algae. Detritus and carbonates were the major fractions in the epiphyton. Live algae were only a small part, smaller than the phytoplankton in the seston of Lake Vechten. This was evident from microscopical observations and pigment analyses.

During 1977 cell counts were made of the algae collected from 75 cm shoot lengths of *Ceratophyllum.* On the basis of numbers three categories of algae were most important (Fig. 8), and showed a marked periodicity. In spring small green algae predominated, mainly *Chlorella* and *Scenedesmus* species. As the growing season advanced, the frequency of these species decreased; abundant development of filamentous green algae was followed by predominance of pennate diatoms later on.

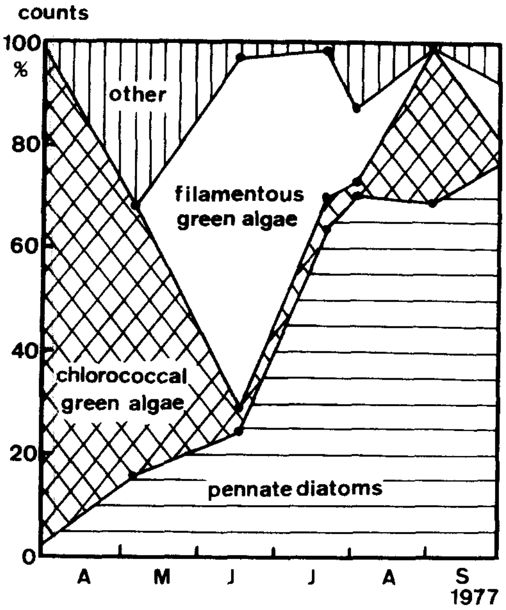


Fig. 8. Succession in the percentage composition of main algal groups of epiphyton from *Ceratophyllum.*

Important species of filamentous green algae belonged to the genera *Mougeotia, Spirogyra, Oedogonium* and *Bulbochaete.* Within this group *Oedogonium* filaments were most abundant all through summer and autumn, sometimes up to 100%.

Pennate diatom species are listed in Table 3. Most of the araphid diatoms have been encountered frequently in the phytoplankton (Blaauboer 1982), but the others were either absent or present in very low numbers. The biraphid species were especially abundant, notably of the genus *Nitzschia.* This makes the diatom association not typically epiphytic but rather epipelic; see Round (1973) and Hutchinson (1975).

The other algae (Fig. 8) are mainly species known to occur planktonically. In May high numbers of small unidentified flagellates occurred. During the months thereafter, blue-greens of the genera *Oscillatoria, Lyngbya* and *Anabaena* dominated the other algae.

In the following years similar patterns were found (see also Fig. 17). Also, in 1977 and 1978, the species composition of the epiphyton from *Ceratophyllum* was comparable with that from *Elodea* and *Myriophyllum.*

Table 3. Pennate diatom species in the epiphyton collected from submerged macrophytes.

Araphidineae
Asterionella formosa
Centronella reichelti
Diatoma elongatum
D. sp.
Fragilaria brevisstriata
F. capucina
F. construens var. *venter*
F. intermedia
F. sp.
Synedra acus
S. acus var. *angustissima*
S. pulchella
S. rumpens var. *familiaris*
S. ulna
S. vaucheriae

Raphidioidineae
Eunotia lunaris
E. spp.

Monoraphidineae
Achnanthes lanceolata
A. lanceolata var. *rostrata*
A. spp.
Cocconeis pediculus
C. placentula
C. sp.
Rhoicosphenia curvata

Biraphidineae
Amphipleura pellucida
Amphora ovalis
A. sp.
Cymatopleura elliptica
C. solea
Cymbella affinis
C. spp.
Epithemia zebra
E. sp.
Gomphonema acuminatum
G. constrictum
G. olivaceum
G. parvulum
G. sp.
Gyrosigma attenuatum
G. sp.
Navicula hungarica var. *capitata*
N. radiosa
N. viridula
N. spp.
Nitzschia acicularis
N. amphibia
N. dissipata
N. palea
N. sigma
N. sigmoidea
N. subrostrata
N. spp.
Pinnularia microstauron
P. viridis
Rhopalodia gibba
R. sp.

Relationships of species composition between epiphyton and phytoplankton are shown in Fig. 9, for three characteristic times in the year: A. late March, when *Ceratophyllum* was still stretched over the bottom; B. June, between the two periods of main phytoplankton development and with exponential growth of the macrophytes; C. late August, when the littoral development had reached its maximum.

In March (Fig. 9A) the first three taxa in the epiphyton had similar frequencies in the phytoplankton; except for the not-determined pennate diatoms, all taxa in the epiphyton were also present in the plankton. The phytoplankton was more diverse: several species with fairly high frequencies did not occur in the epiphyton.

In June (Fig. 9B) a completely different situation existed. The epiphyton was richer in species, with

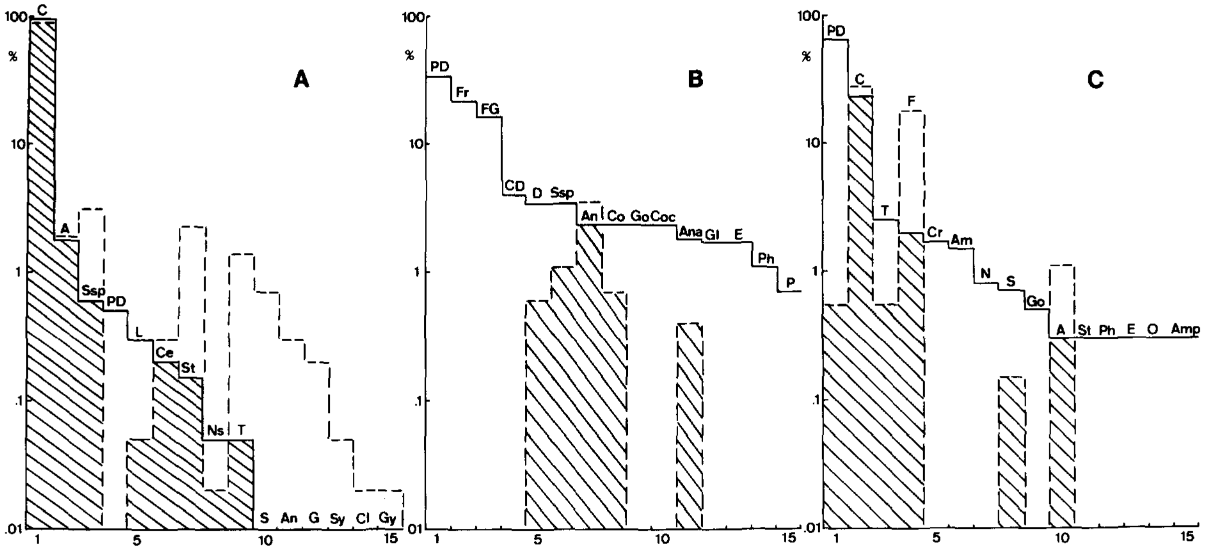


Fig. 9. Comparison of species composition of epiphyton with that of the phytoplankton. Hatched areas represent frequencies common to both groups. A: March. B: June. C: August 1977. See text for further explanation. A = *Asterionella formosa;* Am = *Amphipleura pellucida;* Amp = *Amphora* sp.; An = *Ankyra* sp.; Ana = *Anabaena* sp.; C = *Chlorella* sp.; CD = centric diatoms spp.; Ce = *Centronella reichelti; Cl* = *Closteriopsis* sp.; Co = *Coelastrum microporum;* Coc = *Cocconeis* sp.; Cr = *Crucigenia quadrata;* D = *Dinobryon divergens;* E = *Elakatothrix gelatinosa;* F = small flagellate spp.; FG = filamentous green algae spp.; Fr = *Fragilaria* sp.; G. = *Gloeocystis gigas;* Gl = *Gloeotrichia* sp.; Go = *Gomphonema* sp.; Gy = *Gyrosigma attenuatum;* L = *Lyngbya* sp.; N = *Navicula radiosa;* Ns = *Nitzschia sigma;* O = *Oocystis* sp.; P = *Peridinium willei;* PD = *pennate diatom* spp.; Ph = *Phacotus lenticularis;* S = *Scenedesmus* cf. *quadricauda;* Ssp = *Scenedesmus* spp.; St = *Stephanodiscus astraea;* Sy = *Synedra ulna;* T = *Tetraedron minimum.*

predominance of pennate diatoms and filamentous green algae, which groups were absent in the phytoplankton. Of the 15 epiphytic taxa listed, only five were also planktonic.

The situation found in August (Fig. 9C) was intermediate. The first four taxa were present in both epiphyton and phytoplankton. Of the remaining 11 taxa, only two were common in both habitats.

Principles underlying the above described differences and similarities in species composition will be discussed in the final section.

Photosynthetic pigments. The chlorophyll *a* in the epiphytic organic matter (Figs. 10 and 11) had about 5 mg . g^{-1} as the upper limit. Generally, two thirds of the chlorophyll was chromatographically pure (Fig. 12). Consequently, epiphytic algae cannot be expected to contribute much more than 50% to the epiphyton on an organic weight basis; see Sládeček & Sládečková (1964) and Weber (1973).

During the summer of 1978, the chlorophyll content was maximal in June, when the filamentous green algae predominated. The chlorophyll contents of the epiphyton from *Ceratophyllum* and *Myriophyllum* were similar, but that from *Elodea* tended to be lower than with the first two categories (Fig. 10).

Results of one year, 1980–1981, are given in Fig. 11. Between the summer maxima and spring minimum in these years, the chlorophyll content changed markedly. There is evidence that these were caused by variations in the contribution of species from the limnetic region rather than by specifically epiphytic forms. For example, in January, very high numbers of the centric diatom *Stephanodiscus* coincided with its massive growth in the open water.

It has been shown (Fig. 8) that three algal groups were most important numerically; with respect to pigmentation this involved only two types, i.e. diatoms and green algae. As these differ markedly in their auxiliary pigments (e.g. Round 1973 and Van den Hoek 1978), paper chromatography gave quantitative information on the contribution of the two types to the pigments in the epiphyton.

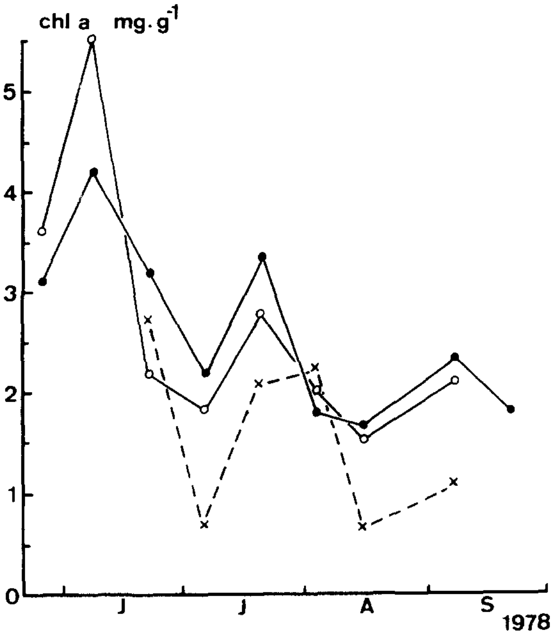


Fig. 10. Summer time changes in chlorophyll *a* content of epiphytic organic matter from *Ceratophyllum* at 1–2 m depth (dots), *Myriophyllum* (circles) and *Elodea* (crosses).

Neither pigment diversity nor pigment species composition changed substantially during the study, contrary to the results of seston (Steenbergen & Steketee, unpublished).

In Fig. 12 the course of six groups of pigments of the epiphyton collected from *Ceratophyllum* growing at 1–2 m depth is given.

About 20% of the total light absorption was by the chlorophyll degradation products. Similar percentages occurred also with seston, but in that case there was more fluctuation (Steenbergen & Steketee, unpublished; see also Hallegraeff 1976). Chlorophyll *a* varied between 35%, in August, and 45%, in June and autumn. The highest contribution of chlorophyll *b* + lutein was in June and autumn, while the diatom pigments were most important in the intervening period.

With the auxiliary pigments, chlorophyll *b* and fucoxanthin determinations allow the further quantification of the importance of the two groups of algae. In Fig. 13 the chlorophyll *b*: chlorophyll *a* ratio, which indicates the contribution of the green algae, has been plotted against the fucoxanthin: chlorophyll *a* ratio as an index for the diatoms.

For the epiphyton of the above depth category of *Ceratophyllum*, least-squares linear regression gave:

$$\text{chl } b/\text{chl } a = -0.47 \,.\, \text{fucoxanthin}/\text{chl } a + 0.44 \quad (r = 0.94).$$

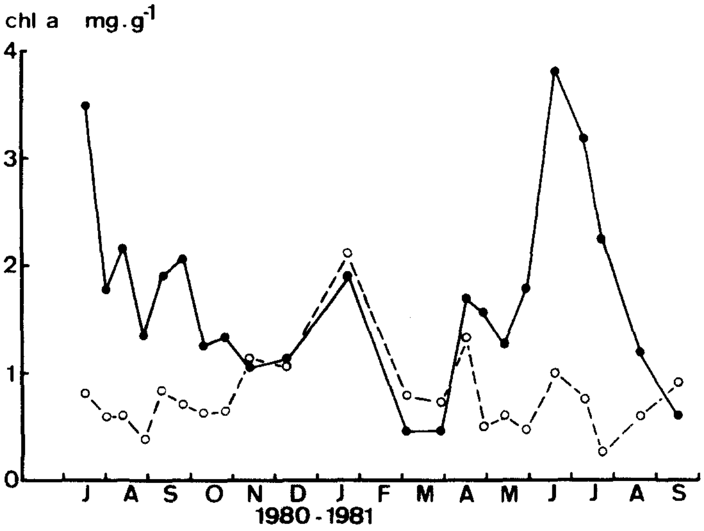


Fig. 11. Seasonal changes in chlorophyll *a* content of epiphytic organic matter from *Ceratophyllum* and epipelic organic matter at 4 m depth (broken lines).

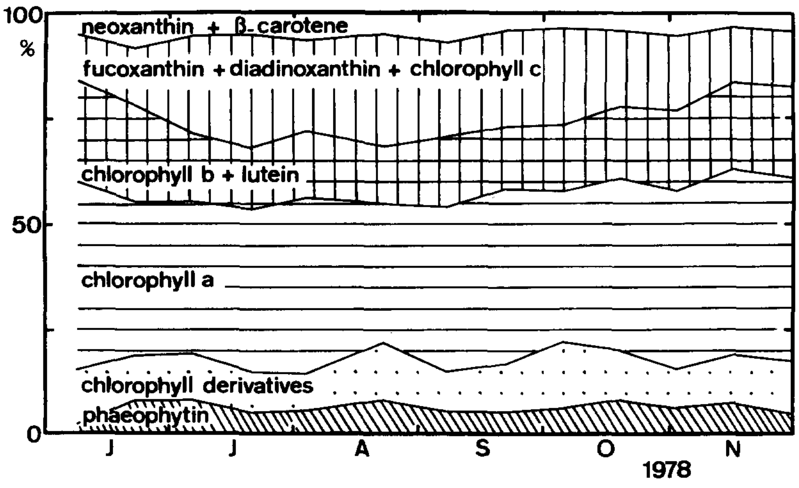


Fig. 12. Seasonal changes in pigment composition of epiphyton from *Ceratophyllum*. Chlorophyll *b* and lutein occur in green algae; fucoxanthin (sometimes including small amounts of neofucoxanthin), diadinoxanthin and chlorophyll *c* in diatoms; the remaining pigments in both groups of algae.

The intercept on the abscissa expresses the fucoxanthin: chl *a* ratio of a pure diatom chromatogram, which was 0.95 in this case. This is within the range of values for mono-algal diatom cultures and natural populations (Jeffrey 1968; Hager & Stransky 1970b; Jensen & Sakshaug 1973). We found that with light-limited cultures of *Nitzschia palea*, values ranged from 0.94 to 1.10 (Gons & Steketee, unpublished).

On the other hand the intercept, 0.44, on the ordinate represents exclusively green algae. Also, this chl *b*: chl *a* ratio is comparable to that for cultured green algae, both filamentous and chlorococcal species (e.g. Jeffrey 1961; Hager & Stransky 1970a).

The linear fit indicates that the epiphytic algae were not subject to marked changes owing to limiting factors; Jensen & Sakshaug (1973) reported that the fucoxanthin: chl *a* ratio of natural diatom communities may vary by a factor of 5.

If the ratios for epiphyton collected from *Elodea* and *Myriophyllum* are included in the regression, the relationship remains much the same. Yet, the values for the epiphyton from *Elodea* deviated in November (Fig. 13), while for epiphyton from *Myriophyllum* exceptional ratios occurred on one date in September, but those were in line with the given relationship.

The value of 0.95 was used to calculate the chlorophyll *a* associated with fucoxanthin. Further it was assumed that neoxanthin and β-carotene were distributed over the diatoms and green algae in the same proportion as chlorophyll *a*. Thus the contribution of the diatoms to the light absorption of the intact photosynthetic pigments was obtained for the epiphyton from *Ceratophyllum* (Fig. 14). This varied from about 25% in June and November to 62% in August. Similar high summer values for the diatoms also applied to the epiphyton from *Elodea* and *Myriophyllum;* for the latter the values were even higher, more than 80%, in September and October.

Epipelon

Distribution of epipelic matter. The study on the littoral sediments started after the submerged macrophytes stand area had become markedly reduced over recent years. The sediments are permanently aerobic down to about 5 m depth (Fig. 19). The material was collected along a fixed transect in the SE part of the lake (see Fig. 1 and Methods); here the bottom was sandy, and the thin layer of epipelon could be removed quantitatively by applying suction (see Methods).

The amounts of epipelon showed quite spectacular temporal changes (Fig. 15); the values for 5 m changed almost two orders of magnitude from a winter minimum of about 30 to a summer maximum of nearly 1 900 g. m^{-2}. The epipelon generally increased markedly with depth, especially in the

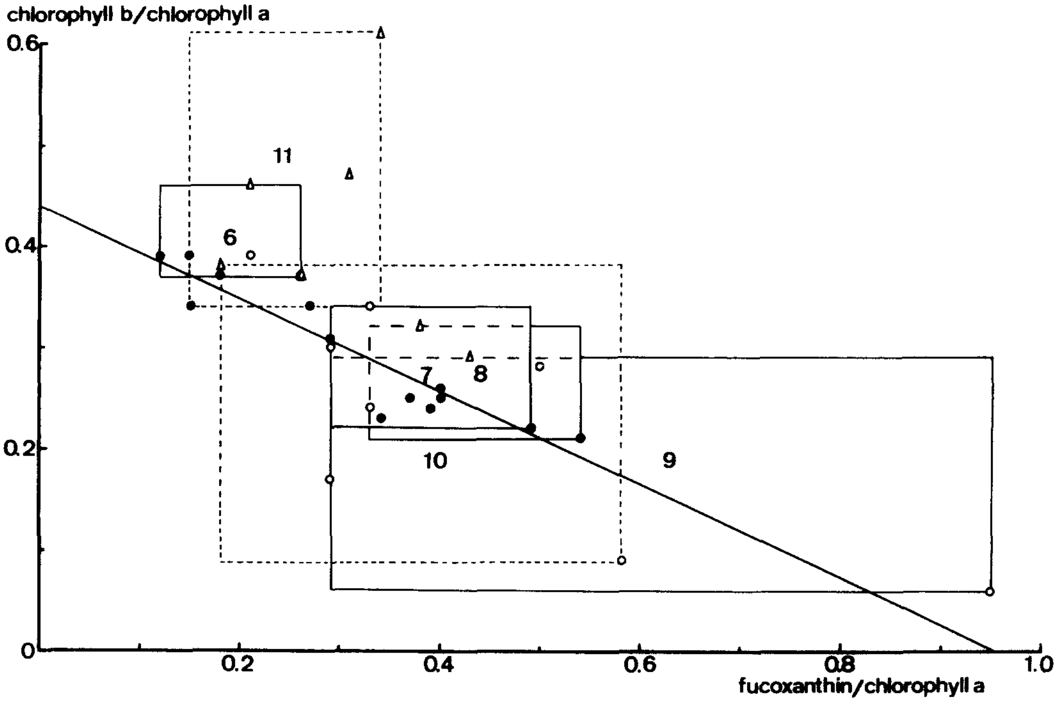


Fig. 13. Relationship between chlorophyll *b*/ chlorophyll *a* (index for green algae) and fucoxanthin/ chlorophyll *a* (index for diatoms) for epiphyton from *Ceratophyllum* (dots), *Myriophyllum* (circles) and *Elodea* (triangles) in 1978. The numbers refer to the months.

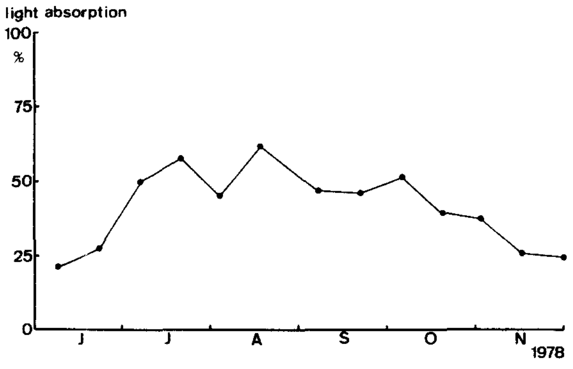


Fig. 14. Contribution of diatom pigments to the light absorption by the photosynthetic pigments in epiphyton from *Ceratophyllum*.

summer. Yet, the values were occasionally very close, notably following a rapid decrease, as in September both years.

As most changes in the epipelic densities cannot be explained by biological processes (see section on oxygen exchange), the dynamics are largely due to redistribution of matter within the lake.

So far, little is known about the densities and

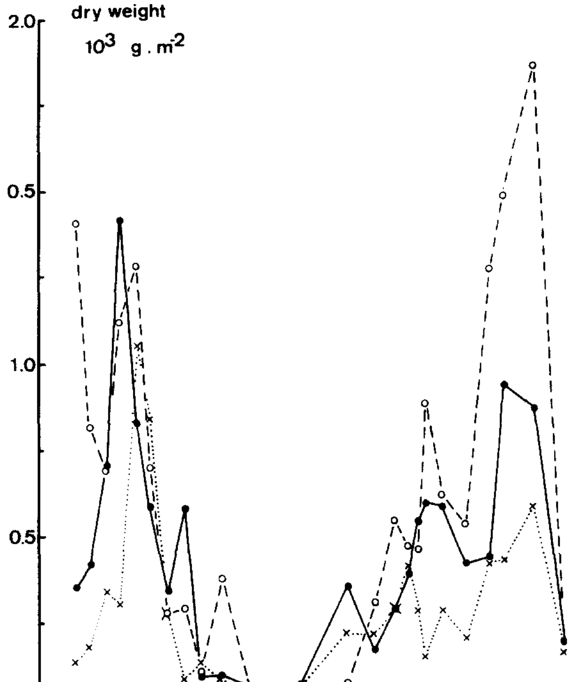


Fig. 15. Seasonal changes in epipelic dry weight at depths of 3 m (crosses), 4 m (dots) and 5 m (circles).

depth distribution of epipelon in the other lake parts. Some indications were obtained when the sampling was extended to the other side of the lake, and measurements were carried out at weekly intervals (Fig. 16).

The relative depth distributions showed a high degree of correspondence, indicating that redistribution patterns in both sides of the lake were similar. From 28 April to 12 May there was a general decrease at 2 and 3 m depths; excluding the high value at 5 m depth of 28 April along the North transect, the values increased especially at 5 m depth but also at 4 m. This suggests that the material lost from the lower depths was not resuspended, and thus mixed over the entire water column, but transported and redeposited along the bottom. It must be mentioned here that the bottom of Lake Vechten has steep slopes; along the South transect the slope is 11° and gradual; on the North side this is on the average 14°, and varies from 24° (between 1 and 2 m depth) to 10° (between 2 and 4 m).

For organic matter, the averages of all depths were not significantly different (Fig. 16), but the percentage organic matter was much higher on the North than on the South side (Table 4). From this it may be conceived that detritus in an advanced state of mineralization, having a small particle size and high ash content, tend to accumulate proportionally more on the South than on the North side of the lake.

The significance of the redistribution with respect to the development in the littoral and the lake's material cycles will be discussed in the final section.

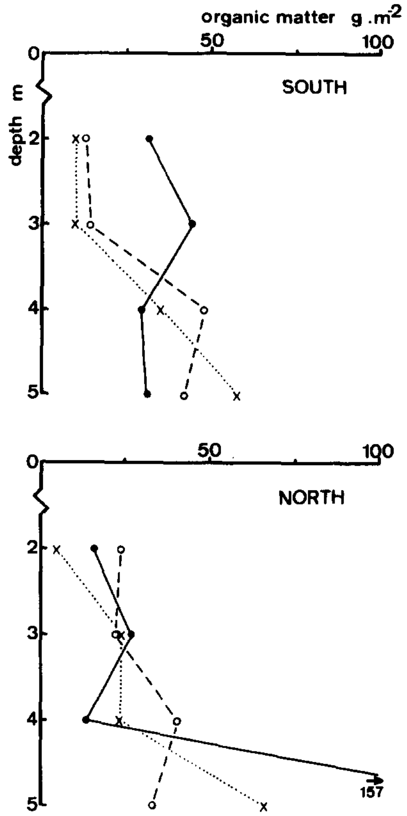


Fig. 16. Comparison of the distribution of epipelon at southern and northern sides of transect across the lake on 28 April (dots), 6 May (circles) and 12 May (crosses) in 1981.

Chemical composition. The study in 1980 and 1981 included that on epiphyton from *Ceratophyllum*, so the chemical compositions of epipelon and epiphyton can be compared (Table 2).

Table 4. Characteristics of epipelon on the southern and northern lake side. See text for further explanation.

	South transect			North transect		
Date	28 April	6 May	12 May	28 April	6 May	12 May
A. Total matter						
% organic matter	11.0	8.2	8.2	13.9	18.3	12.4
% $CaCO_3$	12.5	13.0	11.6	9.9	11.0	11.5
% ash	76.5	78.9	80.3	76.2	70.7	76.1
B. Organic matter						
% C	42.5	41.9	47.7	48.8	46.0	50.4
% N	4.1	4.3	5.6	4.3	4.1	4.7
C:N	10.3	9.6	8.5	11.4	11.2	10.8
chl *a* $mg.g^{-1}$	0.7	0.9	0.9	1.1	1.1	1.0

The proportion of organic matter in the dry weight of epipelon was on the average much lower than that of the epiphyton, resulting, of course, in the lower values for carbon, hydrogen and nitrogen (Table 2A). Elementary analysis of the residue on ignition demonstrated that the epipelon contained much less carbonate, but more ash than epiphyton; evidently the former included even more detritus than the epiphyton. This was demonstrated also by the elementary composition and R-value of the organic matter (Table 2B). The epipelon also differed qualitatively depending on the depth it came from, i.e. the energy content increased with depth. Nevertheless, for comparison with the epiphyton it is sufficient to deal with the data of the epipelon from 4 m (Fig. 7B).

The course of the percentages of the main constituents differed widely from that of the epiphyton. The minimum of organic matter, and the maximum of ash, occurred in August. After the fall recirculation, the increase in percentage organic matter was striking, which might be attributed to either input from the hypolimnion and deeper sediments, or differentially greater resuspension of detritus in an advanced state of mineralization. This change may also reflect input following decline of the macrophytes or leaf fall, but the former possibility was excluded by the low macrophytic biomass, and the latter by the exclusion of large fragments from the analyses. During the subsequent months the composition of the epiphyton and epipelon were similar, as were the chlorophyll contents (see below).

The carbonate content of epipelon changed less than that of epiphyton; only in May and June did the values increase, which may have been associated with photosynthetic activity in the epipelon itself: at 3 m depth calcium carbonate reached a maximum of 41%, but at 5 m it remained low (about 15%).

As mentioned above, the epipelon from opposite sides of the lake differed in organic matter and ash content. Depth averaged composition of the matter on the three dates are given in Table 4. Most characteristics support the conclusion that the epipelon from the North transect was in a less advanced state of decomposition, as was explained by differential redistribution over the lake of particulate matter, including $CaCO_3$. This was not apparent, however, from the percentage organic nitrogen: at the North side of the lake the organic C:N ratios were consistently higher.

Epipelic algae. For the greater part of the year the epipelon consisted almost exclusively of detrital associations, of which the components ranged from recently deposited plankton to fine-grained particles of undefined origin. In periods of clear water, however, conspicuous patches of algae developed upon the sediment surface, and a diver was able to distinguish between the various algal types, viz. filamentous green algae, diatoms and blue-green algae. Especially during the clear water phase of early summer, abundant, but temporary, growth of filamentous greens invariably occurred, sometimes down to depths over 4 m.

In relation to the total epipelic matter, the algae were considerably lower in number than in the epiphyton. Per unit organic matter the epipelon contained only a fifth, or less, of the numbers encountered in the epiphyton (Fig. 17).

Pennate diatoms and blue-green algae, as in case of epiphyton, occurred significantly more in the epipelon than in the epilimnetic phytoplankton. All pennate diatom genera listed in Table 3 also occurred in the epipelon. But in contrast with the epiphyton, filamentous green algae had very low frequencies or were absent. Proportionately, the epipelon contained less diatoms, but more blue-greens, than did the epiphyton. The greatest difference was in the contribution of the remaining taxa, i.e. mainly species which frequent the phytoplankton (see Blaauboer 1982). These, though similar in both epiphyton and epipelon, were relatively far more abundant in the latter.

The composition of epipelic algae did not differ consistently with depth.

Photosynthetic pigments. Year-round values for the chlorophyll *a* content of epipelic organic matter from 4 m depth are given in Fig. 11. From November to April the values were as good as equal to those of the epiphyton. This suggests that during these months the contribution of pigments of deposited seston was predominant in both associations, as was also apparent from microscopical observations. In summer, when the epiphytic communities thrived, the epipelic chlorophyll content remained low, although some increase did occur when the transparancy was high. Broadly speaking, the differences between epiphytic and epipelic chlorophyll content confirmed those in the algal numbers of the two associations during July-September 1980 (compare Fig. 17). The epipelic

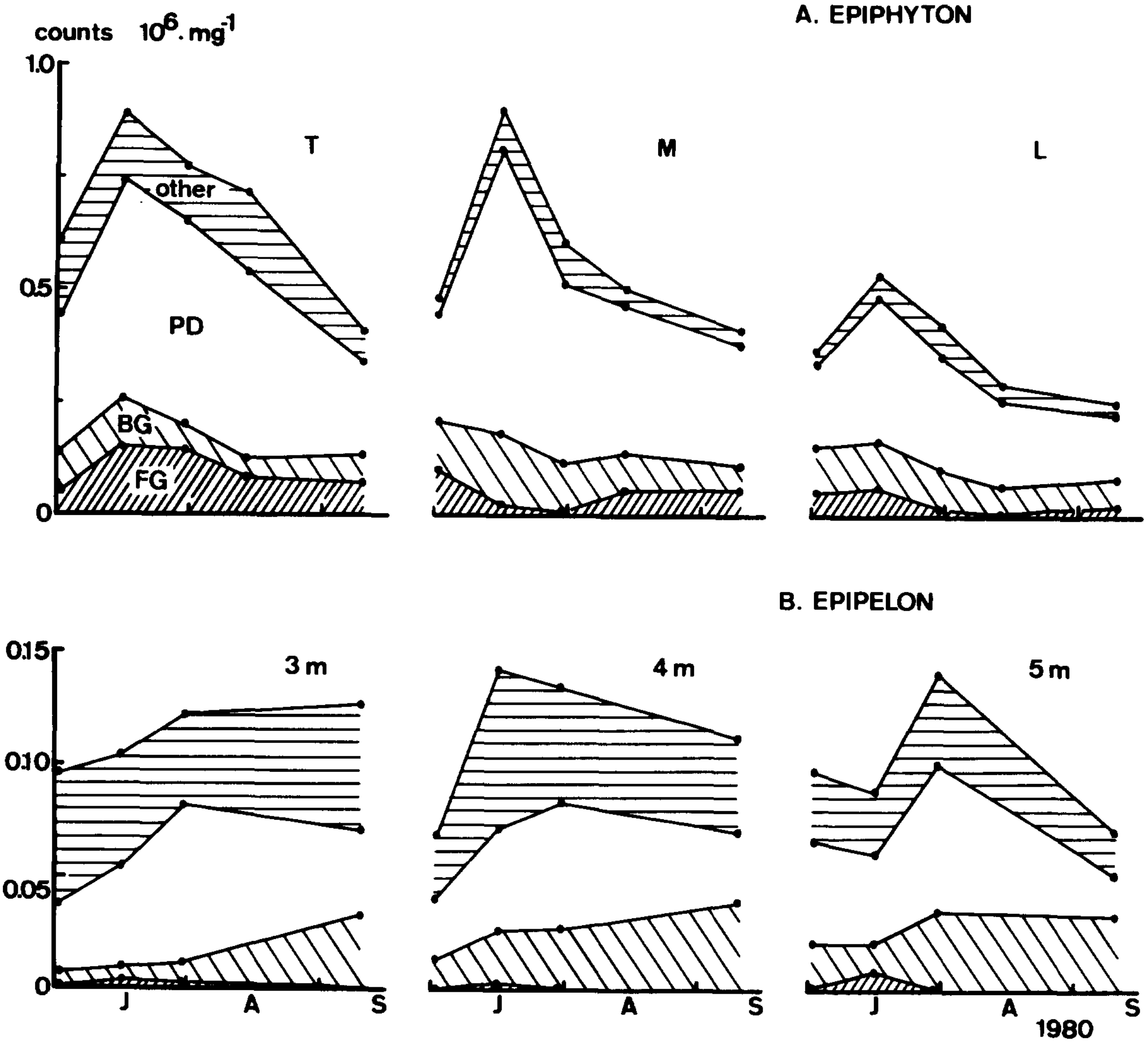


Fig. 17. Main algal groups in the epiphyton and epipelon during the summer of 1980. Abbreviations: T, M and L = top, middle and lower part of vegetation, see text; PD = pennate diatoms; BG = blue-green algae; FG = filamentous green algae.

chlorophyll content at the three depths did not differ consistently from one another.

With epipelon, paper chromatographical pigment analyses were carried out on the samples of 9 September 1980 only (Fig. 18). Generally, the percentage light absorption by chromatographically pure chlorophyll *a* of epiphytic and epipelic pigments was similar. The greatest difference was in chlorophyll *b*, reflecting the small proportion of filamentous green algae in the epipelon (Fig. 17). Other aspects of the distribution (Fig. 18) will be dealt with below.

Structure and function in relation to environmental conditions, with particular reference to light

Seasonal changes in physico-chemical characteristics of the lower littoral zone. For the growth of submerged macrophytes and the associated epiphytic algae and epipelic algae, the depth distribution of light is of foremost importance. Excluding those clear lakes where macrophytes may occur at such depths that hydrostatic pressure may inhibit their growth (Hutchinson 1975), the lower boundary up to which the macrophytes may occur un-

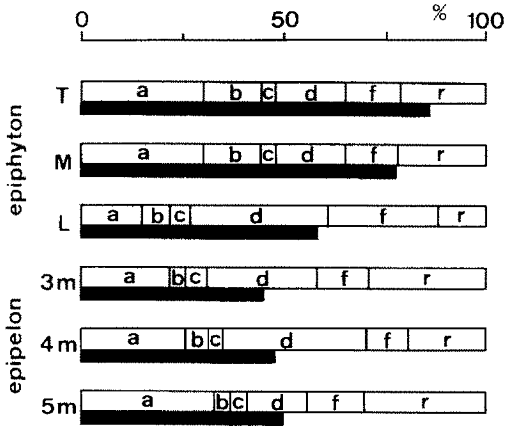


Fig. 18. Pigment composition and viability of pennate diatoms (black bars) on 9 September 1980. Abbreviations: T, M and L = top, middle and lower part of vegetation, see text; a, b, c, d = chlorophyll *a, b, c*, chlorophyllous breakdown products; f = fucoxanthin (including neofucoxanthin); r = remaining pigments.

doubtedly depends principally on the availability of light and water transparency. This, of course, also determines the distribution of the epiphytic and epipelic algae. Because of the generally poor conditions of irradiance in the lower littoral of lakes in the temperate regions, the growing season tends to be short (Kajak *et al* 1972) (see also the next sections).

The vertical extinction values in the littoral and the limnetic region (Steenbergen & Verdouw 1982) are generally similar. At the onset of the development of *Ceratophyllum* and of the associated epiphytic algae at 2 m depth, 15–30% of the surface light reached this depth. In early September 1980 the macrophytes apices reached up to 0.5 m below the surface, with about 75% of the surface irradiance, but a considerable part of the vegetation received no light owing to mutual shading (Fig. 1). The epipelon at 3, 4 and 5 m depth received, respectively, 5–20, 2–15 and 1–8% of the light at the surface. These values are of the incident light reaching the communities, but very little is known about the microdistribution of light within epiphyton and epipelon.

Oxygen content, temperature and pH were measured of the water above and within the *Ceratophyllum* stand and at the bottom along the transect. The isopleths are given in Figs. 19 and 20.

In 1980 the vegetation at station 2 m was well developed, but very poor in the next year: the decline of the macrophytes was continued and dramatic in 1981.

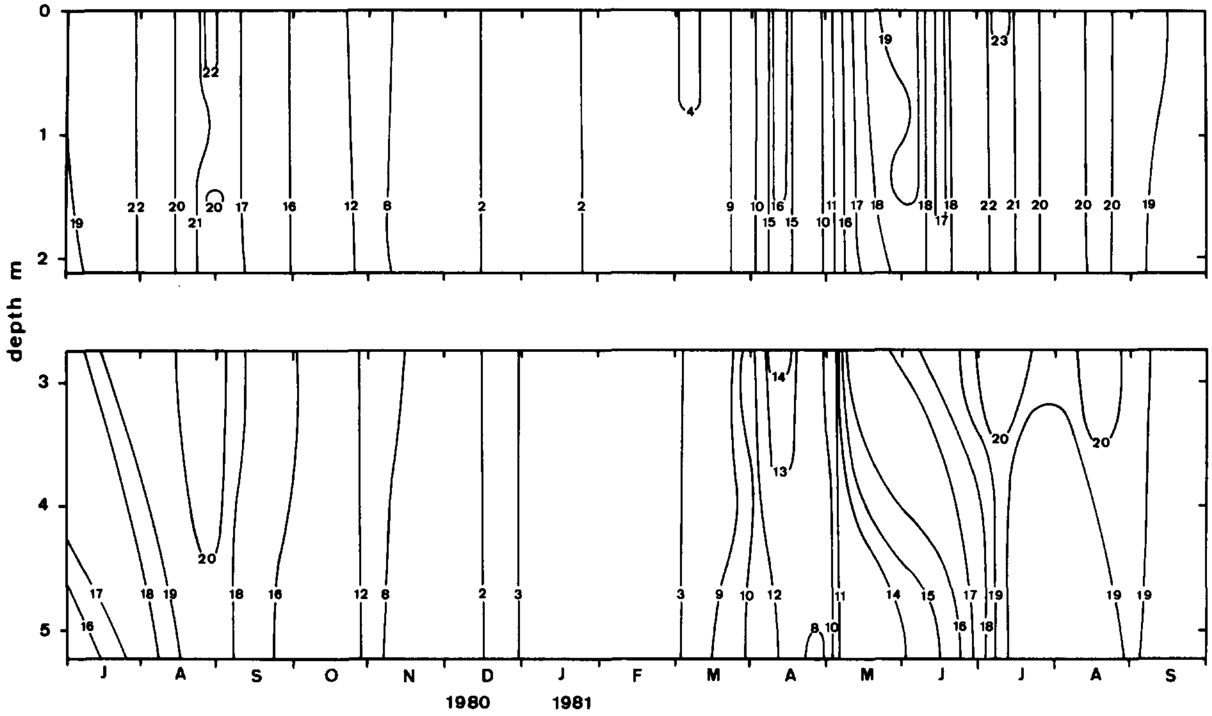
Since the thermocline was generally below 5 m (Steenbergen & Verdouw 1982), temperature variations with depth were slight, but from May to July a decrease of 3–5 °C might occur going from the surface (at station 2 m) to 5 m depth. In August and September the temperature somewhat increased with depth, possibly due to the initial cooling down. The gradients diappeared almost completely during the autumnal overturn. The icecover was insignificant and the mixing continued until April when the water was rapidly warmed and stratification started, but was terminated by a spell of cold weather. Early in May the stratification became stable, as is generally the case in the lake.

The oxygen gradients were more complicated (Fig. 19B). In July 1980 the oxygen concentration dropped by more than 9 mg. l^{-1} from station 2 m, above and within the upper part of the plant bed, down to 5 m. At 6 m the sediment was already anaerobic. The summer time concentrations at the bottom were lower than at the corresponding depths in the limnetic region (see Fig. 21B and Steenbergen & Verdouw 1982).

After July 1980, oxygen was minimal at the bottom between the plants. This was caused by the accumulation of sedimented matter, dissociated epiphyton and the macrophytes on the bottom where it was dark due to shading of the overlying vegetation. The oxygen concentrations at 3 m, i.e. outside the plant bed, were, however, considerably higher, although influenced by the water with low oxygen at 2 m: the highest values occurred between 3 and 4 m depth, where the oxygen concentration was even higher than that above the plants.

From mid September the macrophytes sank to the bottom and started to disintegrate in October; the oxygen gradients diminished, and the values became uniformly low due to the fall recirculation. On the bottom at station 2 m, however, the oxygen content remained noticeably lower until January. Oxygen stratification, like that of temperature, started in April and was firmly established from the beginning of May. That during the summer of 1981 a well developed vegetation at station 2 m was absent, was shown by the oxygen isopleths: the values were not as high as in July or as low as in August 1980.

A. TEMPERATURE



B. OXYGEN

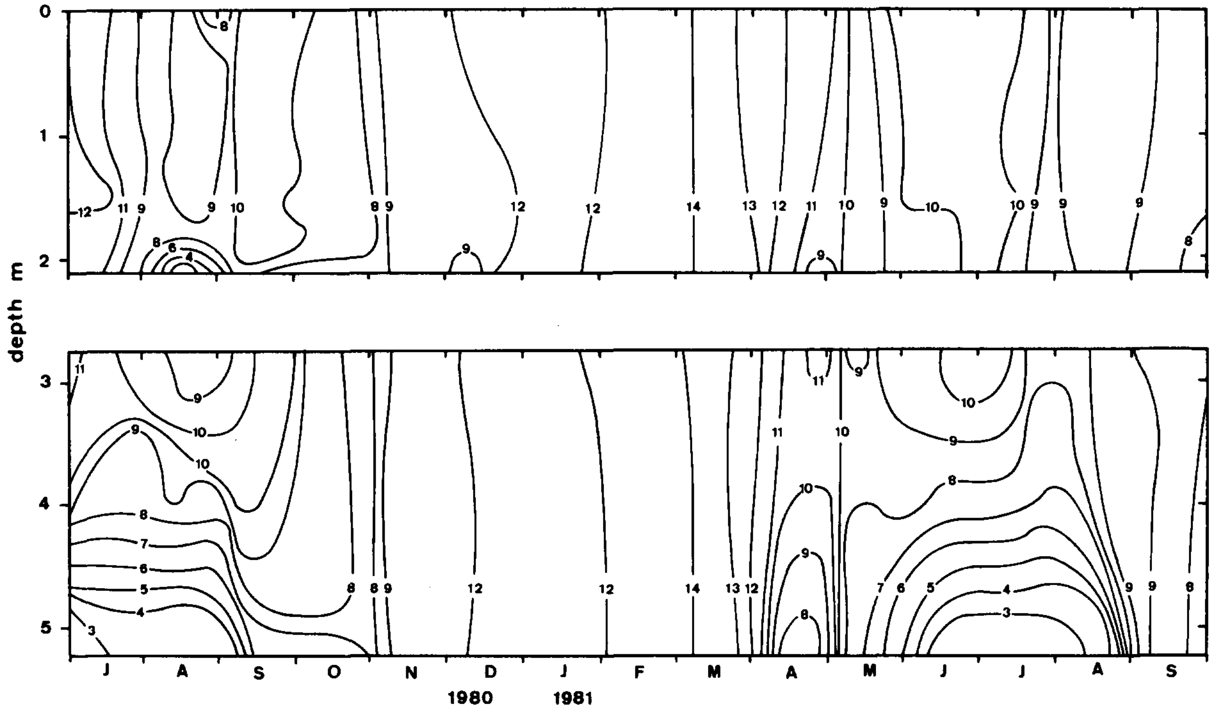


Fig. 19. Isopleths of temperature (A) and oxygen content (B) of littoral water collected along transect. See Fig. 1.

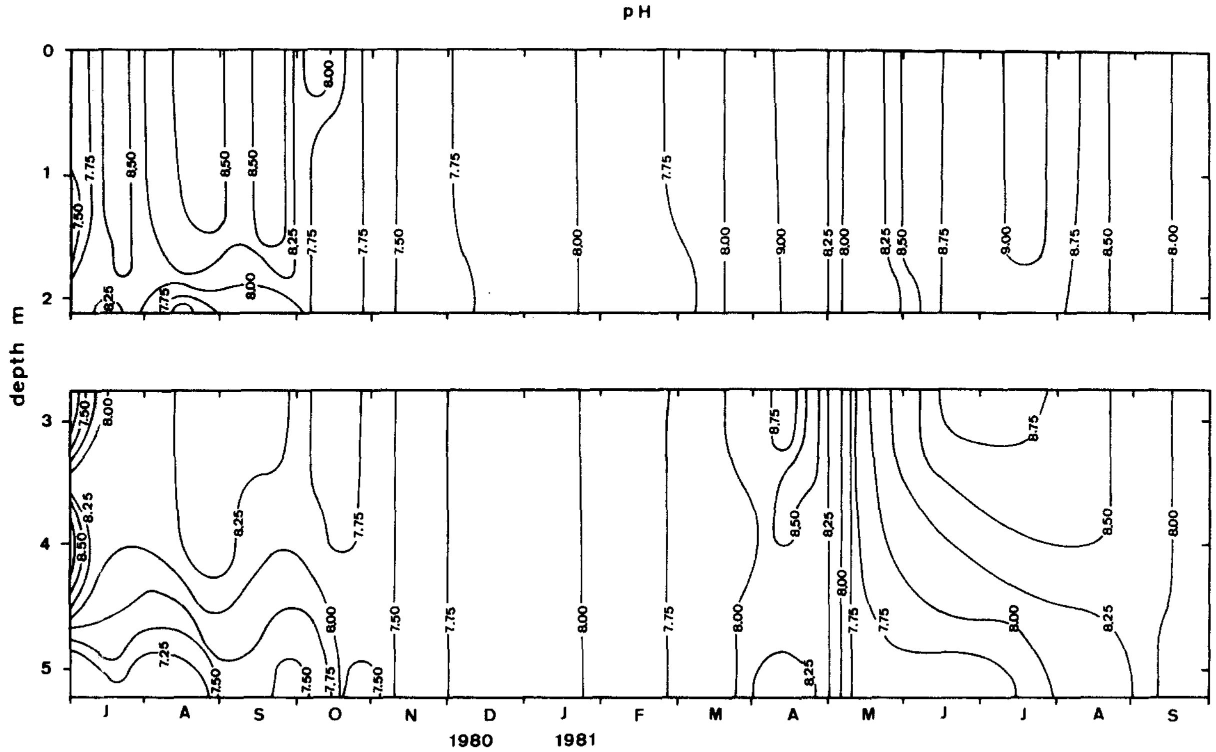


Fig. 20. Isopleths of pH. See also Fig. 19.

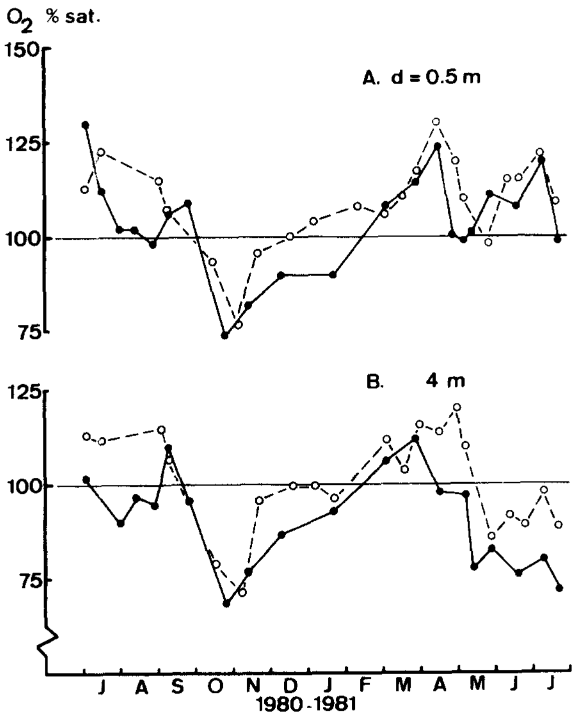


Fig. 21. Comparison of oxygen content of littoral water (dots), with that in the limnetic region (circles), at 0.5 and 4 m. A: 0.5 m depth, i.e. littoral water above vegetation at station 2 m. B: 4 m depth, i.e. littoral water at the bottom at station 4 m.

The changes for pH were similar to those of oxygen (Fig. 20); this is owing to the effects of photosynthesis and respiration on the bicarbonate equilibrium (Wetzel 1975). This also influences markedly the chemical composition of the epiphyton and epipelon (Fig. 7), since $CaCO_3$ precipitates at high pH during photosynthesis and may again dissolve when the pH is low due to the predominance of respiratory activity. Moreover, these processes have side-effects on the lake metabolism since organic substances and nutrients such as phosphorus may co-precipitate (Wetzel & Allen 1972).

Although the seasonal changes in the littoral depend greatly on the processes in the limnetic region, it is clear that biological activities may significantly influence oxygen and pH in the littoral water. The oxygen contents of the littoral and limnetic regions are compared in Fig. 21.

In summer 1980 the epilimnetic water was supersaturated with oxygen. After the autumnal overturn in November the saturation value dropped to 75%. In January equilibrium became re-established. The phytoplankton (Blaauboer 1982; de Kloet

1982) undoubtedly contributed to supersaturation during spring and summer.

The littoral water at 4 m had, except during the overturn, a lower oxygen concentration than the limnetic region at 4 m. This was particularly so in the summer when the epipelic matter was high (Fig. 15), but from November to January considerable differences existed as well.

One may anticipate that above a submerged macrophyte bed, such as at station 2 m in 1980, the oxygen concentration was higher than in the open water. In general, however, the reverse was found (Fig. 21 A). That the plant bed may consume rather than produce oxygen will be dealt with in the section on the depth distribution with *Ceratophyllum* stands.

Growth upon artificial substrates. It has been documented extensively (e.g. Castenholz 1960; Sládečková 1962; Tippett 1970; Round 1973; Wetzel 1975) that artificial substrates may yield periphyton different from that associated with the natural ones. Nevertheless, artificial substrates may be useful tools in the study of the mechanisms underlying the distribution of periphytic organisms (Cattaneo 1978) or food chain aspects (Madsen 1972; McMahon *et al.* 1974), and several workers concluded that carbon fixation rates of algae growing on artificial substrates were similar to those of epiphytic algae (Allen 1971; Hooper & Robinson 1976). The application in the present study was to gain insight into the seasonal development of periphytic algae in relation to the depth.

The area of the substrates was sufficient to allow for weight analyses. The perspex plates (see Methods) were spaced on the basis of the average vertical extinction of the lake water. The plates were hung in a vertical position, to minimize the accumulation of sedimenting material, in the littoral of the SE part of the lake using a float and anchor. Around the anchor the bottom was cleared of macrophytes in order to prevent the shading of the substrates.

After exposure, the plates were covered rather uniformly by algae, but definite colonies also occurred, especially of blue-green and chlorococcal green algae. Filamentous green algae and pennate diatoms predominated. Contrary to those in the epiphyton and epipelon, the diatoms adhered tightly to the substrate. In most cases large quantities of carbonate were deposited, and a considerable amount of detritus had been trapped, but the proportions of the latter were small compared with those in the epiphytic samples. After long exposure the periphyton contained conspicuous numbers of molluscs and insect larvae.

The growth per sample interval upon new plates (Fig. 22) was the highest in June, due mainly to filamentous green algae of the species observed also in the epiphyton. Subsequently the development was comparatively small; it increased again during August and September, and was insignificant thereafter.

During May and June most growth occurred at 0.5 m, and decreased with depth; in July little variation with depth was found, while later it was more at 1 and 2 m than at 0.5 m depth. Thus, the light inhibition of photosynthesis (see also de Kloet 1982) was expressed in the formation of biomass, but not in the case of the filamentous greens in May and June. Every time, the growth at 4 m depth was the lowest.

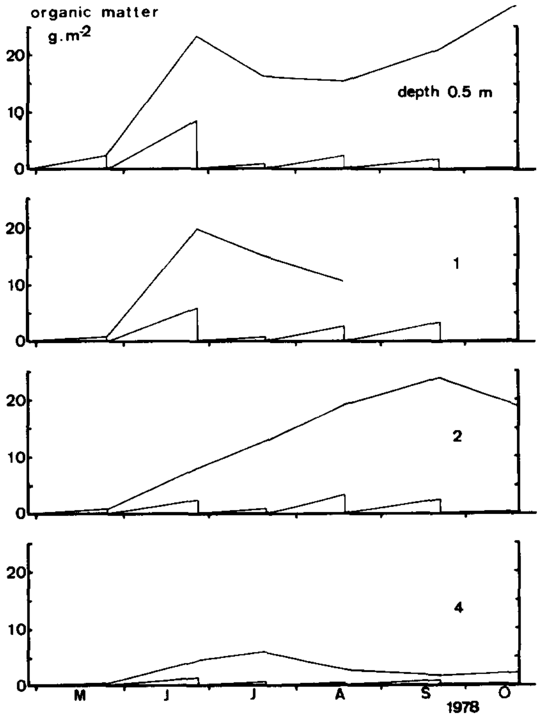


Fig. 22. Developments of periphyton on perspex plates. The lower lines represent growth on new plates per interval, the upper lines the developments on plates exposed from April.

The foregoing results suggest that during the greater part of the summer light was the key factor in the periphytic algal development. In May and June light limitation occurred already at 1 m depth or less, and this was always so at 4 m. In July, however, phosphorus was most likely the growth-limiting factor (Steenbergen & Verdouw 1982). Such a mid summer depression in periphytic growth has often been observed (Cattaneo & Kalff 1980). During the periods before and after summer the growth also decreased with depth. Buth then the lower temperatures may also have played an important role in affecting rates of colonization and of light saturated photosynthesis.

By extrapolation, the compensation depth for the growth of the periphytic algae, say diatoms, was more than 6 m during the greater part of the investigation period.

By serial sampling of the plates the wax and wane of the developed communities was followed. It may be remarked that the changes are not simply functions of algal photosynthesis and respiration, but might also reflect the history of colonization, degree of mutual shading, detachment from the substrate, mortality and mineralization, and grazing.

The relevance of the history of colonization (see Madsen 1972; Hutchinson 1975; Cattaneo *et al.* 1975; Siver 1977, and Perkins & Kaplan 1978) was evident from the following results. In June the periphyton upon the already-colonized substrates increased more than that upon the new ones. This can be explained by a time lag in the development of the latter, but was certainly also due to the filamentous green algae enlarging the substrate area for colonization by diatoms and for the trapping of detritus. In the September-October interval, there occurred little growth on the new substrate at 0.5 m depth, but apparently the conditions still allowed for substantial increase in an already existent community at the same depth.

Probably the detachment of filamentous greens after senescence was the main cause of the loss during July and August at 0.5 and 1 m depth: at 2 m there was still growth, and the development of the filamentous green algae had not been as abundant.

The community at 4 m declined during August and September, while at 2 m and on the new plates the growth was still considerable. It is likely that light was too poor to allow for compensation of the losses due to grazing. It is also possible that due to mutual shading the algae received insufficient light for balancing the requirements of energy for maintenance (Gons & Mur 1980).

Although consumption was not quantified, it can certainly have affected the development, in view of the presence of macro-invertebrates. Consumers of unknown trophic level caused the fall of two plates from 1 m down to the bottom.

The chemical characteristics of the periphyton collected from the plates during May to October are presented in Table 5. The contents carbonate and ash were calculated assuming the percentage carbon of the organic matter to be 50.

In the periphyton of the first category (Table 5A), the data on the depths from 0.5 to 2 m were similar, but differed markedly from those of 4 m, particularly in the lower percentage of carbonate in the latter case. This reflects the fact that light reached saturating values down to 2 m, but was growth-limiting at 4 m. The lower carbonate percentage at 0.5 m than at 1 and 2 m depth reflects light inhibition at 0.5 m.

The percentages of ash and nitrogen were higher at 4 m than at the depths above. This may be explained by differences in species composition. Relatively more diatoms occurred at 4 m, and filamentous greens have a lower percentage of ash and nitrogen (Strathmann 1967; McMahon *et al.* 1974) than diatoms.

The periphyton of the second category (Table 5B) differed considerably from the first one. Here, the filamentous green algae, which predominated after the first interval, played the foremost role. They remained an important component of the

Table 5. Chemical characteristics of periphyton collected from artificial substrates. See text for explanation.

Depth (m)	% organic matter	% $CaCO_3$	% ash	% C	% H	% N
A. Periphyton after one interval of exposure						
0.5	28.9	36	35	18.8	2.2	1.1
1	25.2	45	30	18.0	1.9	0.9
2	28.7	44	28	19.6	2.1	1.4
4	34.8	16	49	19.3	2.9	2.4
B. Periphyton after 2–5 intervals of exposure						
0.5	20.2	60	19	17.4	1.5	0.5
1*	22.3	47	31	16.8	1.3	0.5
2	21.4	54	24	17.2	1.4	0.6
4	20.1	60	20	17.3	1.6	1.1

* Excluding the data of September; see Fig. 22 and text.

substrates all over the investigation period, although less pronounced at 4 m. This was confirmed by the lower ash and nitrogen contents here than in the case of the first category, which contained proportionately more diatoms.

The lower percentage of organic matter was owing to a very high proportion of $CaCO_3$ - even at 4 m depth - indicating that carbonate precipitation was associated not only with photosynthesis per unit biomass, but also depended greatly on that per unit substrate area; with the new plates the specific photosynthetic rates may well have been higher, but this did not result in the same percentage of $CaCO_3$ as the second category, since the biomass was much lower.

The depth distribution of periphytic development on submerged macrophytes and on the artificial substrates used may differ due to several factors, important among which are:

1. *The material nature of the substrate.* While the artificial perspex substrate had fixed dimensions and was biologically inert, the macrophytes have a continuously varying area for colonization and may have influenced the epiphytic development, for example, by precipitation of carbonate and acting as a shelter for macro-invertebrates grazing the epiphyton (Mason & Bryant 1975; Dvořák & Best 1982).

2. *The morphology.* The macrophyte formed a geometrically more diverse substrate for microfloral growth, and collected more sedimenting matter than the perspex plates.

3. *The light regime.* The plates were orientated and spaced in such a way that only the vertical extinction of the lake water determined the percentage irradiation received by the community. In the case of macrophytes light attenuation due to mutual shading plays an important role as well, since the euphotic zone may become reduced dramatically.

It appeared also that the 'perspex' periphyton was both qualitatively and quantitatively different from the epipelon collected at the corresponding depths during 1980 and 1981. This was due to the dominant role of sedimentation and resuspension in changes in the epipelon.

Depth distribution with dense populations of Ceratophyllum. Epiphyton is not evenly distributed over the lengths of submerged marcrophytes because of the gradients both with respect to age, i.e. the time span after first colonization, and the physico-chemical environment, particularly the irradiance. Along these gradients within plant stands, the photosynthetic and respiratory activities may differ greatly; Buscemi (1958) showed that light modulated oxygen stratification occurred in vegetation of *Elodea;* the observations on dense stands of *Ceratophyllum* in Lake Vechten (Figs. 23 and 24), though not as marked, were similar.

During the summer of 1979 and 1980 the depth distribution of light, oxygen, temperature and pH were measured 1-2 h before noon at a fixed location in the SE part of the lake. From the end of July to mid September similar observations were made (Fig. 23).

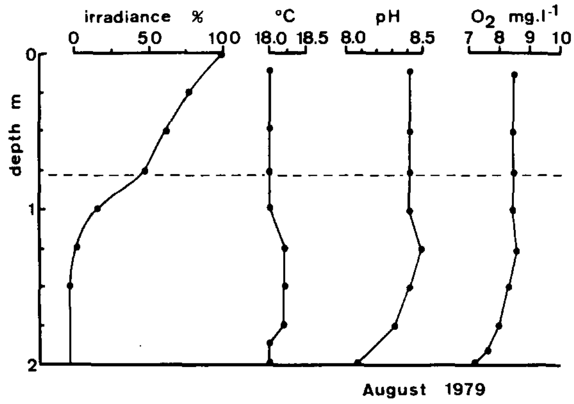


Fig. 23. Depth distribution of light, temperature, pH and oxygen in a dense stand of *Ceratophyllum.*

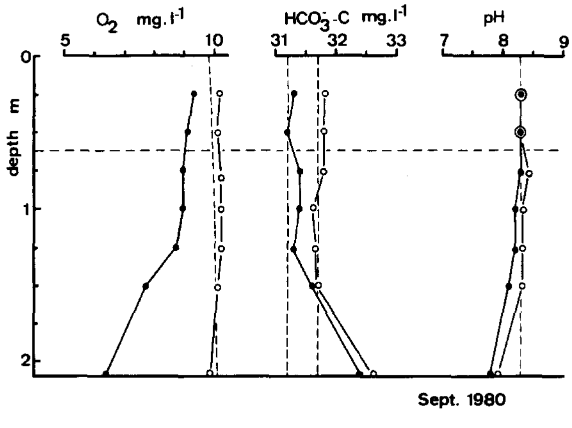


Fig. 24. Diurnal changes in the concentration of oxygen and bicarbonate and of pH in a dense stand of *Ceratophyllum.* Values at midnight given by dots, those at noon by circles. The dashed lines give the values at corresponding depths in the limnetic region.

Between the macrophytes the light decreased sharply: the lower half of the stand was virtually in the dark. The course of oxygen and pH changes was parallel, both exhibiting small peaks well below the plant apices, and decreasing towards the bottom, where both the oxygen concentration and pH were considerably lower than near the surface.

Diel variations in oxygen, pH and HCO_3^- are presented in Fig. 24, and compared with those in the open water. The latter exhibited no diel changes, but between the plants both the oxygen concentration and pH were lower at night than in the day, and at night well below the limnetic values. At noon, though the gradients were very weak because of strong wind, they were similar to those in Fig. 23. Reciprocal gradients were shown by the HCO_3^- concentrations.

These changes were related to the vertical distribution of light (Fig. 23). Within the lower half of the plant stand and upon the bottom only respiration occurred, and even with full sunlight this resulted in markedly lower oxygen concentrations than in the overlying water. The daytime changes within the upper half of the stand, caused by photosynthesis, were never pronounced. The main reasons for this are: 1) diffusion, which will smooth such changes, and 2) community respiration being high, a significant amount of oxygen produced will be consumed.

This was examined in relation to the depth distribution of mass and metabolism of macrophyte and epiphyton. In the same stand where the measurements on oxygen etc. were made (Fig. 23), three similar plant shoots (± 115 cm) were cut at the bottom. These were divided in the laboratory into three portions: the top 15 cm (T), and two equal lengths (± 50 cm) of middle (M) and lower (L) parts (Figs. 25 and 27). These portions were exposed *in situ* to irradiances of, respectively, 50 to 15, 15 to 0, and 0% (Fig. 27).

The concentration of macrophytic and epiphytic matter in the M-portion was the highest (Fig. 25A), and the chemical composition of epiphyton depended greatly on depth. Relative to the organic matter, the highest percentage ash was in the L-portion. The epiphyton of the M-portion had the highest carbonate content, but this was much lower below.

That the deeper part was aphotic was also evident with microscopical observation; very few live organisms were detected, and whereas the material from the upper parts contained large aggregates of carbonate and organic matter, in the lower small greyish fragments were mainly encountered.

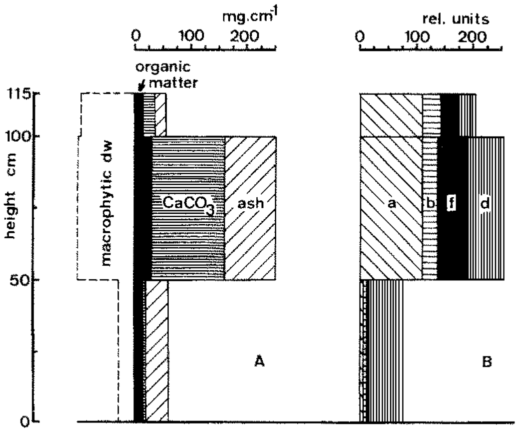


Fig. 25. Depth dependence of the distribution and constitution of epiphyton in a dense stand of *Ceratophyllum*. A: Chemical constituents. Values refer to three shoots. B: Pigments. Abbreviations: a, b, d = chlorophyll *a*, *b*, chlorophyllous breakdown products; f = fucoxanthin.

The results of the pigment analyses were consistent with these findings (Fig. 25B). In the dark deeper parts the epiphyton contained almost exclusively chlorophyll derivatives, but in the upper parts considerably more intact pigments. The pigment per unit organic matter was the highest in the T-portion, with relatively more chlorophyll *b* and less fucoxanthin than in the middle. The microscopical observations confirmed this, because the epiphyton in the M-portion contained comparatively more diatoms and less filamentous green algae (see also Fig. 17).

Using the same samples as for the aforementioned observations, respiration rates in the dark of plant parts and epiphyton of all fractions were measured, and oxygen exchange vs. irradiance curves were established for the 15 cm plant top sections and the epiphyton of the M-portion (see Methods).

The respiration rate per unit organic matter of the macrophyte decreased from 1.7 in the top, and 1.0 in the middle, to 0.5 mg $O_2.g^{-1}.h^{-1}$. The epiphytic rates were about 5 times higher than those of the plant. The upper two fractions did not differ in their specific respiration, which was in both cases 8.0 as against 3.0 mg.$g^{-1}.h^{-1}$ in the L-portion.

The gross photosynthetic capacity of epiphyton was also markedly higher than that of *Ceratophyl-*

lum (Fig. 26). The value for the macrophyte was 6 mg $O_2.g^{-1}.h^{-1}$, which, converted to carbon fixation, was within the range reported by Best (1979), see also Westlake *et al.* (1980). Per mg chl *a*, the epiphytic value was 3.3 mg $O_2.h^{-1}$, a rate close to that reported for benthic diatoms in culture and field samples also incubated on filters (Admiraal 1977), and to that for *Nitzschia palea* from light-limited continuous cultures (Gons & Werkhoven, unpublished). Compared with the respiratory rate, however, the epiphytic photosynthesis was low (cf. Admiraal 1977). Apparently, the included heterotrophic organisms contributed significantly to the oxygen consumption (see e.g. Parsons *et al.* 1977; Harris 1978; and Westlake *et al.* 1980).

The respiration and photosynthesis were computed in relation to depth (Fig. 27). The depth distribution of macrophytic and epiphytic organic matter was smoothed, and the response to *in situ* light (Fig. 23) calculated for two 7.5 cm depth intervals, for the top 15 cm, and 10 cm intervals for the parts below. The specific oxygen exchange in the light of the middle 50 cm and top 15 cm of *Ceratophyllum* was assumed to be the same, and the epiphyton from these parts to have identical curves (Fig. 26). The sum of the net oxygen exchange in light and the respiration in dark of the relevant depth intervals was taken as gross photosynthesis.

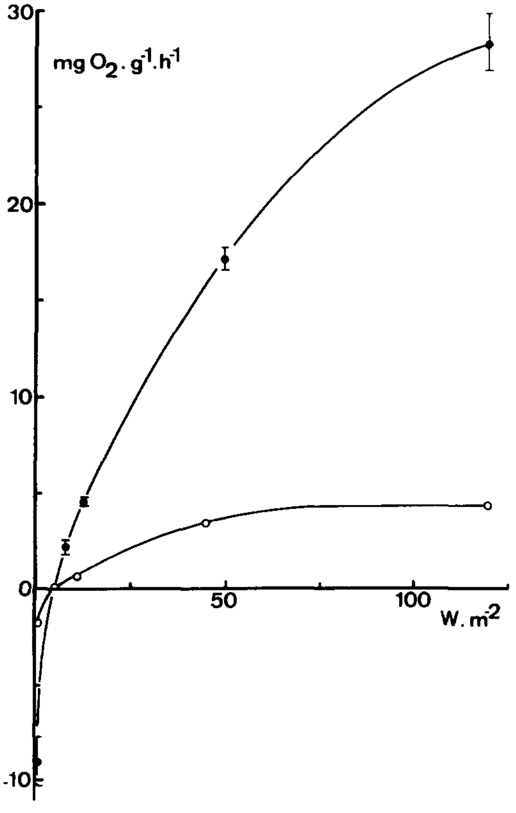


Fig. 26. Photosynthesis per unit organic matter vs. light curves of epiphyton from middle fraction (dots) (see text), and of *Ceratophyllum* apices (circles).

Both in the dark and in moderate to full sunlight epiphyton was the dominant functional component. Photosynthesis was restricted not only to a thin layer on the top of the plant bed but also extended to deeper parts, where the epiphytic matter became more important than the macrophytes.

The oxygen profile (Fig. 23) indicated that the community respiration might be high compared with its photosynthesis. The integrated values of the net productivity of the community (Fig. 27) were so low compared with the respiratory activity that in a 24 hour period the macrophyte stand was oxygen consuming, despite the high photosynthetic capacity. Note that this was even more so since the measurements did not include the macrophytic, epiphytic and epipelic respiration on the bottom in the vegetation. At that time (August) neither the macrophyte nor the total algal community showed signs of decay, but indeed still increased; it was therefore concluded that the heterotrophic utilization required imports of matter produced elsewhere. This aspect was given special attention in the subsequent work.

In the *Ceratophyllum* stand, the light attenuation markedly influenced the epiphytic characteristics, but not so much for the epipelon from 3 to 5 m depth (Figs. 17 and 18). The latter may be explained by the comparatively small change in irradiance: on 9 September 1980 this was no more than that over a 25 cm depth interval with the *Ceratophyllum* stand (Fig. 1).

Seasonal changes in epiphytic and epipelic photosynthesis and respiration. The maximum specific rates of gross oxygen production (p_g^{max}) for epiphyton, collected from the whole length of plant shoots, and epipelon are given in Fig. 28A.

The values were similarly low from October to April; the photosynthetic capacity was markedly higher only during a brief period in summer. In autumn and winter the chlorophyll content of epiphyton and epipelon was similar, but in the summer

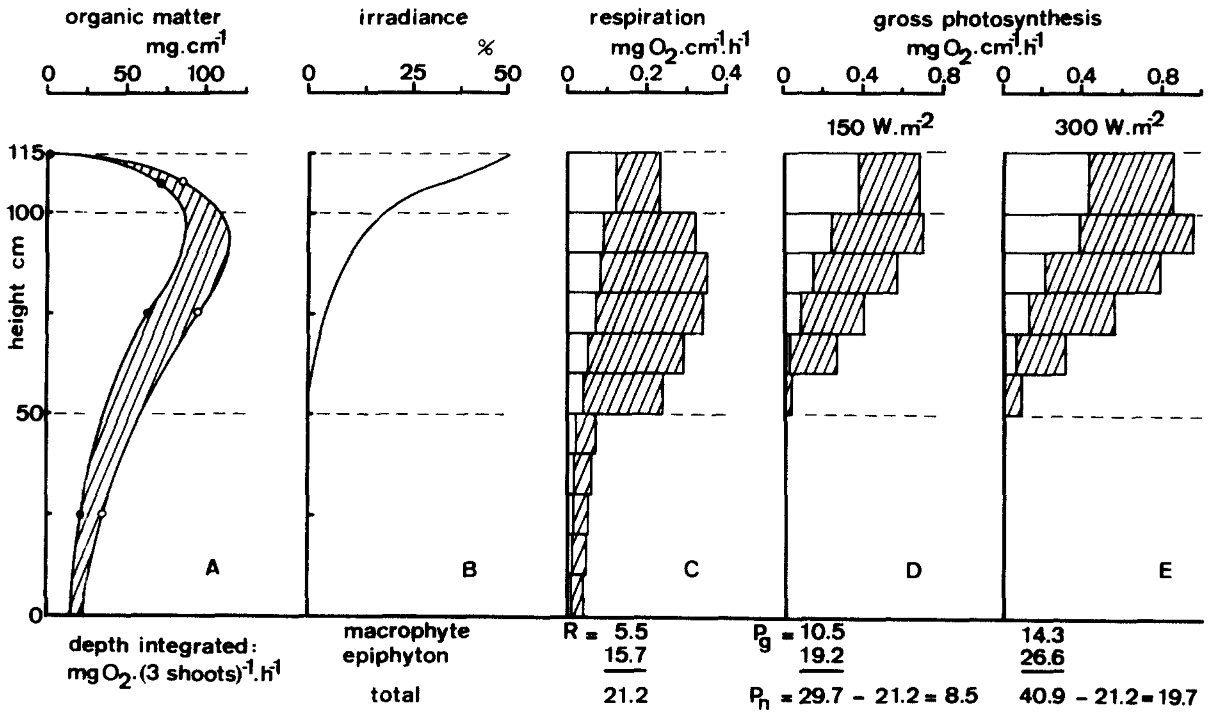


Fig. 27. Depth distribution of organic matter, irradiance, respiration and gross photosynthesis in conditions of moderate and full sunlight. Shaded parts represent the epiphytic contribution to mass and metabolic activity of the vegetation. All values refer to epiphyton and macrophyte of 3 shoots.

months it was quite different (Fig. 11); the latter was true also for the number of algae per unit organic matter (Fig. 17). That the epipelic oxygen production rate in summer was similar to that of the epiphyton was therefore due to a higher photosynthetic capacity of the epipelic algae. This may have reflected the differences in species composition, notably with respect to the contributions of 'planktonic algae' and filamentous greens, but may also be explained by a '*Chlorella*-type' adaptation to irradiance (Jørgensen 1969). Per unit chl *a*, the highest epiphytic value occurred in May 1981, namely 5.4 mg O_2.mg^{-1} for the epiphyton from the plant tips during a bloom of filamentous green algae. In July 1981 a maximum of 21 mg O_2.mg chl a^{-1} was found for the epipelon from 4 m depth.

Although exchange of organic matter with the seston may also result to change in photosynthetic capacity, light and temperature were evidently of primary importance. The rise of water temperature (Fig. 17) during March to mid April 1981 from 3.5 to 14.5 °C, may alone have caused a doubling or more in p_g^{max} (e.g. Steemann Nielsen 1975). This was followed by a period of low light and temperatures: by the end of April the water temperature had decreased to 10 °C. However, in early May it was calm and sunny weather and a clear water phase started. These factors induced a rise of 30–40 cm in the upper parts of the macrophytes, which lay hibernating on the bottom, and dense growth of filamentous green algae upon the raised parts. During the rest of May the irradiation and transparency decreased again, and further development of the macrophytes was arrested until June.

The changes in light and temperature were reflected in the variations in the photosynthetic capacity of epiphyton and epipelon, and also on a chlorophyll basis; but the high values in mid summer and the decrease thereafter were also related to the contribution of detrital matter, which in turn depended on sedimentation and heterotrophic utilization rates (see the final section).

In Fig. 28B the values of the community respiration rates (r) are given. The epiphytic and epipelic values were below 2 mg O_2.g^{-1}.h^{-1} during September-April, but while the epipelic rates remained low

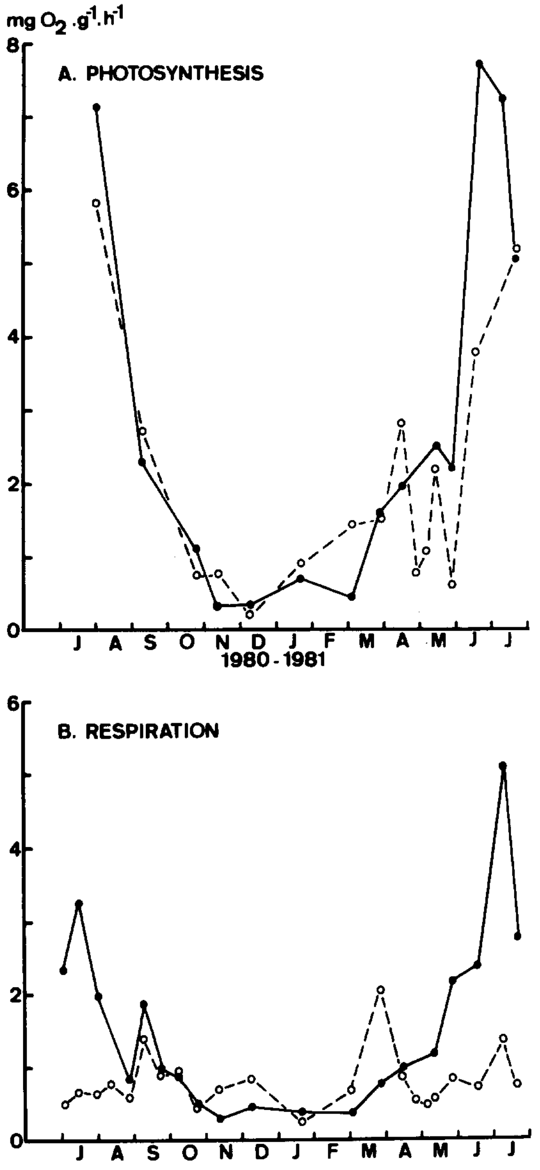


Fig. 28. Seasonal changes in maximum gross photosynthesis (A) and respiration in the dark (B) per unit organic matter of epiphyton (dots) and epipelon (circles).

in summer, those of the epiphyton increased markedly. The respiration of epipelon exhibited no correlation with the photosynthetic capacity, nor any influence of temperature. The seasonal changes in epiphytic respiration rate, however, tended to follow those in p_g^{max}.

The ratios of p_g^{max} and r (Fig. 29) indicated the extent to which the respiration rates can be attributed to either algae or heterotrophic organisms. Most literature data (Steemann Nielsen 1975; Parsons *et al.* 1977; Harris 1978; Westlake *et al.* 1980) indicate the ratio maximum photosynthesis to respiration in dark of a pure algal community to be 5–10. The ratio for epiphyton and epipelon fluctuated around 2. The latter value implies that for the greater part of the year the algae did not contribute more than 40%, but the heterotrophic organisms at least 60% to the oxygen consumption in the dark. Furthermore, since the average daily photosynthetic production rate *in situ* would be much lower than p_g^{max}, the heterotroph consumption would as a rule exceed the autotrophic production.

The relations between *in situ* photosynthesis, depth and p_g^{max}/r are illustrated using the data of 9 September 1980 (Table 6). On this date irradiance conditions were fairly good, the subsurface light reaching a maximum of 165 $W.m^{-2}$ (400–700 nm), and the vertical extinction being 0.56 m^{-1} (see also Fig. 1). The epiphyton was subdivided in the same way as described in the section on the depth distribution. In the stand along the transect (Fig. 1) the macrophytes had on the average 100 shoots per m^2, and this was used as the basis for computation of the integral values; at the central part of the stand the maximum standing crop was more than twice as high.

The epipelon received less light than most of the epiphyton. The epiphyton from the L-portion was photosynthetically inactive, and the response of epipelon from 5 m depth was weak. The highest photosynthetic capacity, both per unit organic matter and chlorophyll, was found in epipelon from 3 and 4 m. Both total and intact chl *a* was lowest in

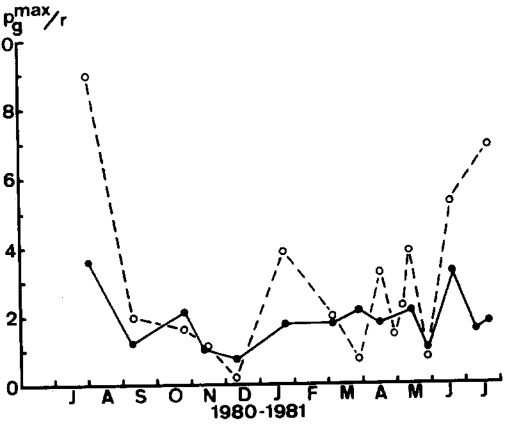


Fig. 29. Seasonal changes in p_g^{max}: r ratio of epiphyton (dots) and epipelon (circles).

Table 6. Epiphytic and epipelic production and respiration on 9 September 1980. See also Fig. 1.

		% surface irradiance	Organic matter ($g.m^{-2}$)	chl *a* ($mg.m^{-2}$)	p_g^{max}/r	P_g^{max}	P_g ($g\ O_2.m^{-2}$.	R day^{-1})	P_n
Epiphyton	T (15 cm)	62–58	4.0	6.7	1.4	0.28	0.12	0.21	−0.09
	M (62.5 cm)	58– 5	37.8	96.4	1.6	2.83	0.80	1.73	−0.93
	L (62.5 cm)	5– 0	15.1	2.6	0.0	0.00	0.00	0.63	−0.63
	Integrated	62– 0	56.9	105.6	1.2	3.11	0.92	2.56	−1.65
Epipelon	3 m	17	23.1	10.4	2.0	0.96	0.40	0.48	−0.09
	4 m	10	24.7	20.4	2.0	1.61	0.35	0.81	−0.47
	5 m	6	48.7	21.5	0.9	1.02	0.03	1.11	−1.08

Note: specific maximum gross photosynthesis and respiration symbolized p_g^{max} and r; daily integrated gross and net production, and respiration have the symbols P_g, P_n and R; P_g^{max} is the potential daily integrated gross production. See text.

the epiphytic L-portion, which also contained less viable diatoms than the remaining epiphyton (Figs. 17 and 18). The epipelon differed from the epiphyton in algal and pigment composition, and had a significantly lower percentage viability of the diatoms.

The daily integrated productions (P_g and P_n) were computed from the diel changes in irradiance and the oxygen exchange vs. irradiance curves over hourly intervals. For all categories P_n was negative. The P_g for epiphyton was greatly exceeded by R. The P_n for epipelon at 3 m was only slightly negative, but due to the decrease in irradiance R was more than twice the P_g at 4 m, and at 5 m depth photosynthesis was negligible.

The seasonal change in p_g^{max}/r (Fig. 29) is now considered in the following perspective. The P_g^{max} values in Table 6 express the gross production should the epiphyton and epipelon receive optimal light during the 24 hours. The epiphytic top fraction realized 43% of this potential, but with the integrated epiphyton this was only 30%. For the epipelon from 3, 4 and 5 m the percentages were, respectively, 41, 21 and 3. Gross photosynthesis of more than 43% of P_g^{max} will only be attained when conditions of light are more favourable than on 9 September 1980, which involves irradiation, daylength and lake water transparency. Such conditions may exist from part of May onwards in summer (Steenbergen & Verdouw 1982), but were rare during 1980 and 1981. Taking 50% of P_g^{max} as the maximum for daily gross photosynthetic production, this balances respiratory losses only when p_g^{max}/r is at least 2.

For the epiphyton (Fig. 29) considerably higher ratios occurred only in mid summer. The epipelon (also at 3 and 5 m depth, Gons, unpublished) more often had values of over 2. Because of low light, however, daily net production of epipelon would be negative, except for favourable conditions of irradiation and vertical extinction during the summer.

Thus, the heterotrophic processes dominated the oxygen exchange of epiphyton and epipelon during the major part of the year. The general increase in epiphyton and epipelon during January to, respectively, October and August, can be explained by imports, the sources and significance of which for the lake's nutrient cycles are discussed below.

Autotrophy, heterotrophy and redistribution processes. Two energy flows drive the processes in the lower littoral of Lake Vechten. In the first place solar energy is stored in the biomass of the submerged macrophytes, epiphytic and epipelic algae. Secondly, energy contained in organic matter, produced both autochthonously and allochthonously, is continuously redistributed and utilized in the various lake parts. Evidence was obtained that submerged vegetation in particular is effective in trapping this form of energy as well. Thus, the lower littoral may be regarded as an energy subsidized lake part (Odum 1971) and be compared with environments such as tidal mud flats and coral reefs.

Changes in epiphytic and epipelic organic carbon can be described as:

$$\Delta C = P_g + I - R - E$$

where: ΔC = net change in organic carbon,
P_g = gross photosynthetic carbon fixation,
I = import,
R = respiratory carbon loss,
and E = export.

The proportions of P_g and I depend on depth, since production by the autotrophs decreases with depth due to the light attenuation, while sedimentation rates tend to increase. This will be complicated, however, with the development of dense macrophyte stands, which changes the light climate and may influence sedimentation rates, and provide an environment for physico-chemical mechanisms for accumulation of organic matter.

From October through winter and early spring, the light conditions in the lower littoral were poor for algal growth. That at these depths light was indeed a key factor was evident from epiphytic and epipelic growth of filamentous green algae near the shore in winter (Gons, unpublished) and the growth upon artificial substrates (Fig. 22). The epiphyton and epipelon were similar in their chlorophyll *a* content and chemical composition, especially in winter (Figs. 7 and 11), and algae known to frequent in the phytoplankton were abundant (Fig. 9A).

Depending on meteorological conditions and lake water transparancy, epiphytic and epipelic algal growth was stimulated in spring and early summer. This first involved filamentous green algae (Fig. 8). During accelerated macrophytic growth these benefitted from improved light conditions because of the substrate reaching close to the water surface, while the accumulation rates of sedimenting matter per unit substrate area were low. As a consequence the 'loose' fraction of the epiphyton was relatively small, while carbonate (Fig. 7A), organic matter (Fig. 6), chl *a* (Figs. 10 and 11) and photosynthetic capacity per unit organic matter (Fig. 28) reached their maximum. In this period, similarity between the species composition of epiphyton and phytoplankton was the least (Fig. 9B).

Thereafter, the epiphytic heterotrophic component became increasingly important, since within the vegetation light was severely attenuated due to mutual shading, and due to the accumulation of deposited matter. Nutrients also possibly limited the growth, particularly of the filamentous greens. Later on, the amounts of loose material increased so that the vegetation might be regarded as sediment enlarged in area and volume. The sediment character was expressed by the abundance of freely motile biraphid diatoms, both numerically (Fig. 8 and 17) and on the basis of pigments (Fig. 14).

When the submerged macrophytes had reached their maximum standing crop, the epiphyton exhibited both great photosynthetic potential and high oxygen consumption rate (Fig. 27, Table 7). That the epiphytic production may be important on a lake basis – even surpassing that of submerged macrophytes – has been concluded by several investigations using different approaches (e.g. Wetzel *et al.* 1972; Kajak *et al.* 1972; Spodniewska *et al.* 1975; Cattaneo & Kalff 1980; Jones 1980). The share of epiphytic production to that of the lake provides information on the trophic state. Cattaneo & Kalff (1980) proposed that increased nutrient loading stimulates the epiphytic algal growth more than that of the macrophytes (see also Fitzgerald 1969). The epiphyton may in turn adversely affect the macrophytic development due to shading (Eminson & Phillips 1978; Phillips *et al.* 1978).

In the case of Lake Vechten, however, it was not

Table 7. Seasonal maxima of organic carbon, chlorophyll, net increase of organic carbon (Δ C), gross photosynthetic carbon fixation (P_g) and respiration (R). The figures in parentheses are the months.

	Organic C ($g.m^{-2}$)	chl *a* ($mg.m^{-2}$)	Δ C	P_g ($gC.m^{-2}.$ day^{1})	R
A. Epiphyton of station 2 m and epipelon of station 4 m during 1980 and 1981					
Epiphyton	80 (10)	206 (10)	4.0 (9/10)	0.6 (8)	1.3 (10)
Epipelon	35 (7)	42 (5)	1.1 (4/ 5)	0.3 (7)	0.5 (7)
B. Periphyton of perspex plates during April-October 1978					
Depth 0.5 m	14 (10)	77 (10)	0.4 (6)	–	–
4 m	3 (7)	23 (10)	0.06 (6)	–	–

the algae but the detrital aggregates that mainly constituted the epiphyton. The data on the oxygen exchange indicated that, except during favourable light conditions such as occurred in the first half of the summer, heterotrophic utilization exceeded the algal production – the import of organic matter explains this. Such an import will consist largely of particulate matter, but may also involve the adsorption or co-precipitation of dissolved compounds (Wetzel & Allen 1972; Wetzel 1975). The imports were massive, thus concealing any specific interaction between substrate and epiphyton: similar chemical and algal species compositions were found with the epiphyton of *Ceratophyllum, Elodea* and *Myriophyllum,* the differences found being rather quantitative and due to the location of the stands.

While newly deposited matter was only loosely associated, the carbonate and mucoid substances secreted by epiphytic bacteria and algae (see Fig. 4 and Allanson 1973) cemented particles to more firmly associated larger aggregates on the macrophyte. This allowed for the development of unique communities of consumers and decomposers having high respiratory activity. The abundance of pennate diatoms may be due to several factors, among which the ability to migrate is one means to escape from being covered by sediment. They might also benefit from the release of nutrients in the course of the utilization of the epiphytic matter by the heterotrophic organisms, or be using certain organic compounds as additional energy source, of which the physiological ability is well known (Hellebust & Lewin 1977; Admiraal & Peletier 1979).

Specific oxygen consumption rates in the dark of epiphyton reached 3 mg O_2.(g org. dry wt.)$^{-1}$.h^{-1} or more in summer (Fig. 26), about two thirds of which was due to heterotrophic organisms. This gives a decomposition rate of approximately 3.5% per day. The value for the epiphyton from the upper plant parts was up to 1.5 times as high, the matter of this fraction being more recent and easily degradable. These rates are substantially higher than those reported for tree-leaf organic matter, but within the range of those for 'mixed dead phytoplankton and detritus in lake water' (Saunders *et al.* 1980).

It is not known to what extent the epiphytic matter was utilized by either animals or bacteria and moulds. It is generally believed that epiphytic matter forms a readily accessible source of food for consumers (Hutchinson 1975). The protein content especially is considered to be a decisive factor (Russell-Hunter 1970). The C:N ratio may therefore serve as an index of nutritional value (McMahon *et al.* 1974), a ratio of 17 being critical. The average epiphytic and epipelic organic C:N ratios in the present study were 9.0 and 10.2, being close to those reported for periphyton on glass slides in lentic systems by McMahon *et al.* (1974), but lower than those calculated by these authors from the data of Stockner & Armstrong (1971). The potential role of macro-invertebrates in the littoral of Lake Vechten is discussed by Dvořák & Best (1982). The abundance of ciliates and rotifers (Gons, unpublished) implies that this micro-fauna may have contributed significantly to the oxygen exchange (Fig. 28B).

The summertime % organic matter and R-value (Table 2), chlorophyll content (Fig. 11) and algae number (Fig. 17) of epipelon were lower than those of epiphyton. Although the photosynthetic capacity reached similar values to those of the epiphyton, the epipelon had considerably lower specific respiration in the dark (Fig. 26B). The latter may be explained by the epiphyton containing more detritus in early stages of decomposition, especially during early summer when the vegetation was still young. From August onwards the respiration rates of epiphyton and epipelon became similar.

On an areal basis, the littoral exhibited great quantitative differences during summer and autumn (Table 7). The epiphyton reached considerably higher concentrations of organic carbon and chl *a*, as well as higher photosynthesis and respiration than the epipelon. This was also true for the value of Δ C, which greatly exceeded that of P_g. That the net increase of organic carbon was for the greater part due to import, appeared also from a comparison with the periphyton on the artificial substrate (Table 7B), which, being vertically placed, trapped far less sedimenting matter. This also resulted, of course, to the lower maxima of organic carbon on the perspex, although chl *a* was more like that of the natural substrates. The seasonal maxima of integral chlorophyll, photosynthesis and respiration of the epipelon are comparable to the values compiled by Moss (1968) and Westlake *et al.* (1980). Information on integral values of epiphyton associated with submerged macrophytes is too scanty for comparison. The chlorophyll maximum of the 'perspex' periphyton has a mid range value among those reported for the periphyton upon rocks and artificial substrates (e.g. Stockner & Armstrong 1971; Allen 1971; Hooper-Reid & Robinson 1978).

Further, the timing of maxima of epiphyton and epipelon differed markedly; this appeared to be due to the greater capacity of littoral with dense vegetation to collect and retain sedimenting matter.

The role of redistribution of detrital matter in the metabolism of lakes was emphasized by Wetzel *et al.* (1972). Gulati *et al.* (1982) studied the seasonal changes in sestonic organic carbon in Lake Vechten. Sedimentation rates were measured in order to link the processes in the productive and anaerobic strata (Cappenberg & Verdouw 1982), but little is known about sedimentation and resuspension in the littoral zone. There is evidence, however, that the following general phenomena (see Wetzel 1975) apply in the case of the littoral of Lake Vechten: 1) depth dependent sedimentation rates, which explains the increase of epipelon with depth (Fig. 15), and 2) vertical and horizontal differential distribution, as indicated by the differences in the chemical composition of epipelon, respectively, with depth (Table 2) and on the southern and northern lake side (Table 4).

Verdouw & Dekkers (1982) measured sedimentation in the limnetic region of Lake Vechten during 1977–1979. The rates observed in March-April were consistently high and those in September-October were even higher. The spring values of about 6 g dry wt. $m^{-2}.day^{-1}$ agreed well with the increase in dry weight of epipelon during the spring of 1981 (Fig. 15). Since resuspension, or at least downward shifts along the bottom, may occur more or less throughout the year, the seasonal trends in sedimentation and in epipelic density were comparable until in July-August when the latter had its maximum.

For reasons not yet understood, from these months the epipelon already decreased almost continuously until winter (Figs. 15 and 30). Perhaps this was associated with the increased turbulence along the bottom due to the start of cooling after the temperature maximum in July (Fig. 19A). The decrease rates generally could not be accounted for by the data on the oxygen exchange. For instance, the decrease in organic matter from mid August to September was about twice as high as predicted from the oxygen consumption rates in the dark.

With the submerged vegetation, in contrast, the accumulation of organic matter continued (Fig. 30) and was fastest in the time Verdouw & Dekkers found the highest sedimentation rates.

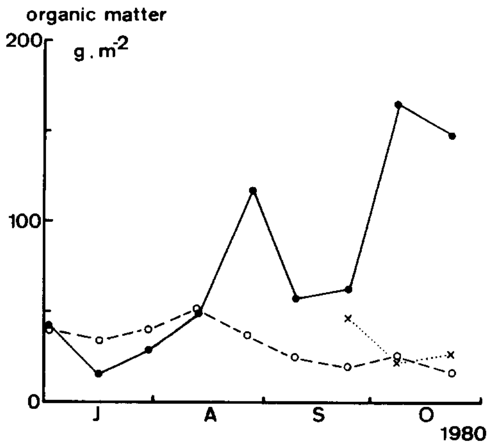


Fig. 30. Influence of dense vegetation on the accumulation of organic matter in the littoral region (epiphyton, dots; epipelon in vegetation, crosses; epipelon at 4 m depth, circles).

On the basis of eq. (3), the carbon flow of the epiphyton was generalized for the May-October 1980 growing season (Table 8). The net import of organic carbon, i.e. I–E, was on the average about 4 times as high as the gross photosynthetic fixation of carbon. A similar proportion was also reported by Pieczyńska (1975) for emergent vegetations, but including the macrophytic production.

This result sheds new light on the functioning of the lower littoral of lakes in general and of the part with submerged vegetation in particular. In the case of Lake Vechten, where the region from the shore to the 5 m depth contour occupies nearly 40% of the total lake area, significant proportions of the seston are diverted from sedimenting to the anaerobic strata, and consequently decomposed in aerobic conditions at comparatively favourable temperatures. No doubt this has far-reaching consequences, both in the regeneration of nutrients and energy flow in the higher trophic levels. Since especially during autumn large amounts of organic matter reach the lower littoral, the decline of the sub-

Table 8. Generalized carbon flow in epiphyton of station 2 m for May-October 1980.

ΔC	P_g	R	I-E
	($mg\ C.m^{-2}.day^{-1}$)		
400–550	150–300	600–700	700–1 100

merged vegetation during the last few years may have great consequences for the seemingly unrelated organisms and processes in the lake.

Summary

The periphyton associated with the submerged macrophytes *Ceratophyllum demersum, Myriophyllum spicatum* and *Elodea* sp., and that on the sandy bottom in the lower littoral of Lake Vechten (The Netherlands) was quantitatively collected from the substrates. The periphyton from the plants is denoted as epiphyton and that from the bottom as epipelon, and includes live micro-organisms, detritus and inorganic matter.

On a dry weight basis the epiphyton was maximal in autumn and often exceeded its substrate. The organic matter, which was mainly detrital, comprised generally about 20% of the dry weight; $CaCO_3$ contributed up to 50% in summer.

During exponential growth of the macrophytes, filamentous green algae, notably species of *Oedogonium. Spirogyra* and *Mougeotia,* predominated. From the end of June freely motile diatoms, belonging mainly to the genera *Nitzschia* and *Navicula,* were the most abundant. Except for June and July, the planktonic species were abundant and, often, predominated in winter and spring.

The chlorophyll *a* in the organic matter was low, about 5 $mg.g^{-1}$ being the upper limit in summer. Phaeophytin and other chlorophyll derivatives contributed about 30% to the total chl *a*. Green algae and diatoms were quantified by linear regression of the pigment ratio chl *b:* chl *a* vs. fucoxanthin: chl *a*. In the summer months the diatom pigments contributed 50% or more to the light absorption by all the photosynthetic pigments.

The epiphyton from the three macrophyte species did not exhibit striking differences.

Epipelon was measured along a fixed transect in the SE part of the lake. Temporal changes were great: at 5 m depth the dry weight varied from about 30 $g.m^{-2}$ in winter to almost 1 900 $g.m^{-2}$ in summer 1981.

In general the epipelon increased with depth. There are indications that epipelon is transported and redeposited along the steep slopes of the lake bottom. Epipelon collected from opposite lake sides differed in chemical composition. The percentages of organic matter and $CaCO_3$ in the epipelon were considerably lower than in the case of epiphyton; also, the energy content of epipelic organic matter was lower.

Epipelic algae comprised mainly pennate diatoms and blue-green algae of the same species as in the epiphyton. Compared with the epiphyton, the epipelon had low numbers of filamentous greens, but more blue-green algae and representatives of the planktonic species. Weight specific densities of algae in epipelon in summer were only a fifth of those in epiphyton. The chl *a* content in the epipelic and epiphytic organic matter was similar in winter, but, contrary to that in the epiphyton, the epipelic chlorophyll remained low in summer.

The epiphyton on *Ceratophyllum* apices received maximally 75% of the surface irradiance. However, for the greater part of epiphyton the light was low, and in dense vegetation part of the epiphyton was virtually in the dark. For the epipelon light was low as well, ranging from 1 to 8% of the surface irradiance at 5 m depth. In summer, the gradients in oxygen concentration and pH were sharp, particularly in the parts with submerged vegetation. In general these gradients indicated the predominance in the lower littoral of heterotrophic processes.

Artificial substrates were exposed at four depths ranging from 0.5 to 4 m. That light was a key factor was demonstrated by both the inhibition of growth near the surface and limitation in the deeper part. In July, however, little variation with depth was found. Filamentous green algae were more abundant at the lesser depths, while diatoms, mostly species other than on the natural substrates, were more numerous at greater depth. The periphyton from the artificial substrates differed both quantitatively and qualitatively from the epiphyton and epipelon on the natural substrates.

The light gradient in dense stands of *Ceratophyllum* caused marked changes in the composition of the epiphyton. In the lower parts of the plant bed, the organic matter and $CaCO_3$ contents of epiphyton relative to ash were low, and the pigments were almost all chlorophyllous breakdown products. The epiphyton of the upper parts exhibited a fairly high photosynthetic capacity, but the respiration was also intense, so that oxygen consumption exceeded its production in the vegetation over the 24 hours. This can be attributed to import of organic matter.

The maximum rate of gross photosynthesis per unit organic matter (p_g^{max}) of epiphyton ranged from 0.3 in winter to 8 mg $O_2.g^{-1}.h^{-1}$ in summer. For epipelon the maximum was 5 mg $O_2.g^{-1}.h^{-1}$. The maximum of specific respiration rate in the dark (r) was 5 for the epiphyton, and 2 mg $O_2.g^{-1}.h^{-1}$ for the epipelon. Except for a relatively brief period in summer, the specific photosynthesis and respiration rates of epiphyton and epipelon were comparable. The p_g^{max}: r ratios indicate that only in very favourable conditions of light does diel photosynthesis exceed diel respiration.

In conclusion, the redistribution processes mainly determine the changes in organic carbon of epiphyton and epipelon. Although integrated photosynthesis may reach high values in the lower littoral of Lake Vechten, the heterotrophic utilization of matter produced elsewhere is more important. The parts covered by vegetation are especially effective in collecting and retaining sedimenting matter, which is thus diverted from anaerobic decomposition in the deeper strata.

Acknowledgements

Without the assistance of Ronny van Keulen – under water and above – in the laboratory and at the drawing board, the work program of 1980 and 1981 would have been much 'diluted' in time and space. To my colleagues in Nieuwersluis thanks are due for their supply of background information and eye-openers. P. H. Best is thanked for introducing me to the littoral and for lots of samples. H. Roon provided unerring transport and assistance in the field. H. J. Korthals and G. Wiegers are thanked for pigment chromatography; M. D. M. Trommel, Th. H. Frank and A. G. Frank-Landman for determination and counting algae; E. M. J. Dekkers for all the CNH-analyses; J. H. A. Dassen and H. Visser for data on the oxygen in the limnetic region (Fig. 21); N. G. Hafkamp and his crew for the construction of the epipelon sampler and assemblages for the artificial substrates; E. M. Mariën for photography and J. H. M. van Kleinwee for typing. Acknowledgements are due to P. Roos (Department of Aquatic Ecology, University of Amsterdam) for the scanning electron photomicrographs. R. D. Gulati and S. Parma are thanked for many improvements on the manuscript. And thank you, Jeanet.

References

Admiraal, W., 1977. Salinity tolerance of benthic estuarine diatoms as tested with a rapid polarographic measurement of photosynthesis. Mar. Biol. 39: 11–18.

Admiraal, W. & Peletier, H., 1979. Influence of organic compounds and light limitation on the growth of estuarine benthic diatoms. Br. phycol. J. 14: 197–206.

Allanson, B. R., 1973. The fine structure of the periphyton of Chara sp. and Potamogeton natans from Wytham Pond, Oxford, and its significance to the macrophyte-periphyton metabolic model of R. G. Wetzel and H. L. Allen. Freshwat. Biol. 3: 535–541.

Allen, H. L., 1971. Primary productivity, chemo-organotrophy and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. Ecol. Monogr. 41: 97–127.

Best, P. H., 1979. Ecophysiological studies on growth and development of the aquatic macrophyte Ceratophyllum demersum L. Thesis, State University of Utrecht. 104 pp.

Best, P. H., 1982. The aquatic macrophytes of Lake Vechten. Species composition, spatial distribution and production. Hydrobiologia 95: 65–77.

Blaauboer, M. C. I., 1982. The phytoplankton species composition and the seasonal periodicity in Lake Vechten from 1956 to 1979. Hydrobiologia 95: 25–36.

Buscemi, P. A., 1958. Littoral oxygen depletion produced by a cover of Elodea canadensis. Oikos 9: 239–245.

Cappenberg, Th. E. & Verdouw, H., 1982. Sedimentation and breakdown kinetics of organic matter in the anaerobic zone of Lake Vechten. Hydrobiologia 95: 165–179.

Castenholz, R. W., 1960. Seasonal changes in the attached algae of freshwater and saline lakes in the lower Grand Coulee, Washington. Limnol. Oceanogr. 5: 1–28.

Cattaneo, A., 1978. The microdistribution of epiphytes on the leaves of natural and artificial macrophytes. Br. phycol. J. 13: 183–188.

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

Cattaneo, A. & Kalff, J., 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. Limnol. Oceanogr. 25: 280–289.

Cholnoky, B. J., 1968. Die Ökologie der Diatomeen in Binnengewässern. Cramer, Lehre, 699 pp.

Dvořák, J. & Best, P. H., 1982. Macro-invertebrate communities associated with water vegetation in Lake Vechten. Hydrobiologia 95: 115–126.

Eminson, D. & Phillips, G., 1978. A laboratory experiment to examine the effects of nutrient enrichment on macrophyte and epiphyte growth. Verh. int. Verein. Limnol. 20: 82–87.

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

Gons, H. J. & Mur, L. R., 1980. Energy requirements for growth and maintenance of Scenedesmus protuberans Fritsch in light-limited continuous cultures. Arch. Microbiol. 125: 9–17.

Gulati, R. D., Siewertsen, K. & Postema, G., 1982. The zooplankton: its community structure, food and feeding, and role in the ecosystem of Lake Vechten. Hydrobiologia 95: 127–163.

Hager, A. & Stransky, H., 1970a. Das Carotinoidmuster und die Verbreitung des lichtinduzierten Xantophyll-cyclus in verschiedenen Algenklassen. III. Grünalgen. Arch. Mikrobiol. 72: 68–83.

Hager, A. & Stransky, H., 1970b. Das Carotinoidmuster und die Verbreitung des lichtinduzierten Xanthophyll-cyclus in verschiedenen Algenklassen. V. Einzelne Vertreter der Cryptophyceae, Euglenophyceae, Bacillariophyceae, Chrysophyceae und Phaeophyceae. Arch. Mikrobiol. 73: 77–89.

Hallegraeff, G. M., 1976. Pigment diversity, biomass and species diversity of phytoplankton of three Dutch lakes. Thesis, University of Amsterdam. 177 pp.

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

Hellebust, J. A. & Lewin, J., 1977. Heterotrophic nutrition. In: Werner, D. (Ed.) The Biology of Diatoms. Blackwell, Oxford. 288 pp.

Hoek, C. van den, 1978. Algen. Einführung in die Phykologie. Thieme, Stuttgart. 481 pp.

Hooper, N. M. & Robinson, G. G. C., 1976. Primary production of epiphytic algae in a marsh pond. Can. J. Bot. 54: 2810–2815.

Hooper-Reid, N. M. & Robinson, G. G. C., 1978. Seasonal dynamics of epiphytic algal growth in a marsh pond: productivity, standing crop, and community composition. Can. J. Bot. 56: 2434–2440.

Hutchinson, G. E., 1975. A Treatise on Limnology. III. Limnological Botany. Wiley, New York. 660 pp.

Iwamura, T., Nagai, H. & Ichimura, S., 1970. Improved methods for determining contents of chlorophyll, protein, ribonucleic acids and deoxyribonucleic acid in planktonic populations. Int. Rev. ges. Hydrobiol. 55: 131–147.

Jeffrey, S. W., 1961. Paper chromatographic separation of chlorophylls and carotenoids from marine algae. Biochem. J. 80: 336–342.

Jeffrey, S. W., 1968. Quantitative thin-layer chromatography of chlorophylls and carotenoids from marine algae. Biochim. Biophys. Acta 162: 271–285.

Jensen, A. & Sakshaug, E., 1973. Studies on the phytoplankton ecology of the Trondheimsfjord. II. Chloroplast pigments in relation to abundance and physiological state of the phytoplankton. J. exp. mar. Biol. Ecol. 11: 137–155.

Jones, R. C., 1980. Primary production, biomass, nutrient limitation, and taxonomic composition of algal communities epiphytic on the submersed macrophyte Myriophyllum spicatum L. in a hardwater, eutrophic lake. Thesis, University of Wisconsin-Madison. 200 pp.

Jørgensen, E. G., 1969. The adaptation of plankton algae. IV. Light adaptation in different algal species. Physiol. Plant. 22: 1307–1315.

Kajak, Z., Hillbricht-Ilkowska, A. & Pieczyńska, E., 1972. The production in several Polish lakes. In: Kajak, Z. & Hillbricht-Ilkowska, A. (Eds.) Productivity Problems of Freshwaters. PWN Warszawa, 918 pp.

Kloet, W. A. de, 1982. The primary production of phytoplankton in Lake Vechten. Hydrobiologia 95: 37–57.

Madsen, B. L., 1972. Detritus on stones in small streams. Mem. Ist. ital. Idrobiol. 29: 385–403.

Mann, K. H., 1975. Patterns of energy flow. In: Whitton, B. A. (Ed.) River Ecology. Blackwell, Oxford. 725 pp.

Mason, C. F. & Bryant, R. J., 1975. Periphyton production and grazing by chironomids in Alderfen Broad, Norfolk. Freshwat. Biol. 5: 271–277.

McMahon, R. F., Douglas-Hunter, R. & Russell-Hunter, W. D., 1974. Variation in Aufwuchs at six freshwater habitats in terms of carbon: nitrogen ratio. Hydrobiologia 45: 391–404.

Milner, H. W., 1953. The chemical composition of algae. In: Burlew, J. S. (Ed.) Algal Culture from Laboratory to Pilot Plant. Carnegie Inst., Washington, D. C. 357 pp.

Moss, B., 1968. The chlorophyll a content of some benthic algal communities. Arch. Hydrobiol. 65: 51–62.

Odum, E. P., 1971. Fundamentals of Ecology. Saunders, Philadelphia. 574 pp.

Parsons, T. R., Takahashi, M. & Hargrave, B., 1977. Biological Oceanographic Processes. Pergamon, Oxford. 332 pp.

Perkins, M. A. & Kaplan, L. A., 1978. Epilithic periphyton and detritus studies in a subalpine stream. Hydrobiologia 57: 103–109.

Phillips, G. L., Eminson, D. & Moss, B., 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. Aquat. Bot. 4: 103–126.

Pieczyńska, E., 1975. Ecological interactions between land and the littoral zones of lakes (Masurian Lakeland, Poland). In: Hasler, A. D. (Ed.) Coupling of Land and Water Systems. Springer, Berlin. 309 pp.

Round, F. E., 1973. The Biology of the Algae. Edward Arnold, London. 278 pp.

Russell-Hunter, W. D., 1970. Aquatic Productivity. Macmillan, New York. 306 pp.

Saunders, G. W., Cummins, K. C. & Gak, D. Z. et al., 1980. Organic matter and decomposers. In: Le Cren, E. D. & Lowe-McConnell, R. H. (Eds.) The Functioning of Freshwater Ecosystems. Cambridge University Press, Cambridge. 588 pp.

Siver, P. A., 1977. Comparison of attached diatom communities on natural and artificial substrates. J. Phycol. 13: 402–406.

Sládečková, A., 1962. Limnological investigation methods for the periphyton ('Aufwuchs') community. Bot. Rev. 28: 286–350.

Sládeček, V. & Sládečková, A., 1964. Determination of periphyton production by means of the glass slide method. Hydrobiologia 23: 125–128.

Spodniewska, I., Pieczyńska, E. & Kowalczewski, A., 1975. Ecosystem of the Mikolajskie Lake, primary production. Pol. Arch. Hydrobiol. 22: 17–37.

Spoehr, H. A. & Milner, H. W., 1949. The chemical composition of Chlorella: effects of envirionmental conditions. Plant Physiol. 24: 120–149.

Steemann Nielsen, E., 1975. Marine Photosynthesis, with Special Emphasis on the Ecological Aspects. Elsevier, Amsterdam. 141 pp.

Steenbergen, C. L. M. & Verdouw, H., 1982. Lake Vechten: aspects of its morphometry, climate, hydrology and physicochemical characteristics. Hydrobiologia 95: 11–23.

Stockner, J. G. & Armstrong, F. A. J., 1971. Periphyton of the experimental lakes area, Northwestern Ontario. J. Fish. Res. Bd Can. 28: 215–229.

Strathmann, R. R., 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. 12: 411–418.

Tippett, R., 1970. Artificial surfaces as a method of studying populations of benthic microalgae in freshwater. Br. phycol. J. 5: 187–199.

Verdouw, H. & Dekkers, E. M. J., 1982. Nitrogen cycle of Lake Vechten (The Netherlands); role of sedimentation. Arch. Hydrobiol. 94: 251–263.

Weber, C., 1973. Research development in the measurement of the response of plankton and periphyton to changes in their environment. In: Glass, G. E. (Ed.) Bioassay Technique and Environmental Chemistry. Ann Arbor Science Publ. 499 pp.

Westlake, D. F., Adams, M. S. & Bindloss, M. E. et al., 1980. Primary production. In: Le Cren, E. D. & Lowe-McConnell, R. H. (Eds.) The Functioning of Freshwater Ecosystems. Cambridge University Press, Cambridge. 588 pp.

Wetzel, R. G., 1975. Limnology. Saunders, Philadelphia. 743 pp.

Wetzel, R. G. & Allen, H. L., 1972. Functions and interactions of dissolved organic matter and the littoral zone in lake metabolism and eutrophication. In: Kajak, Z. & Hillbricht-Ilkowska, A. (Eds.) Productivity Problems of Freshwaters. PWN, Warszawa. 918 pp.

Wetzel, R. G., Rich, P. H., Miller, M. C. & Allen, H. L., 1972. Metabolism of dissolved and particulate detrital carbon in a temperate hard-water lake. Mem. Ist. ital. Idrobiol. 29: 185–243.