LIMNOLOGICAL RESEARCH

in the

MAARSSEVEEN LAKES

1975 - 1980

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General introduction

In 1975 a limnological study of Lake Maarsseveen I was initiated by a group
of aquatic ecologists from the University of Amsterdam. Intended originally as an
eco(-sub)system study of the open-water zone this idea had to be abandoned be-
cause an insufficient number of scientists was convinced of the idea and insuf-
ficient funds were raised. Therefore, the theme was restricted to a study of the
interrelations of the planktonic community. In due time, however, the addition
of several scientists from other institutes extended the project to the study of
the littoral zone as well. Some of the results obtained the last five years are
presented in this report. The principle objective of this report is to be a
pause for reflection on future research. It may also serve as a source of infor-
mation for those interested in the area. Although presented in a preliminary form,
our data and ideas might be of interest to other limnologists. Therefore, the re-
port is written in a language of which we hope it is sufficiently close to English
to serve this purpose of communication.

The future of the research in the Maarsseveen area is uncertain; because of
other duties several participants had to move to other regions, and grants will
expire in a few years. Due to the progress in "democracy" university people have
to spend increasing amounts of time at the conference table. Despite the fact
that many unemployed competent scientists are withering away at home the economic
regression and our social legislation does not allow their participation in this
non-profit research.

However, the original intended and only partially realised idea of research
has to be done! If in the future the science of ecology is to provide a means of
a scientific management of our much maltreated environment, research has to be
done to expose the rules that rule the wax and the wane of populations, their mu-
tual interactions and the relationships to the environmental factors. At the pre-
sent state of limnological knowledge, which is not small but anecdotical, no

really scientific management of surface waters is possible, no computer model is able to cover up our fundamental ignorance, and no single species laboratory experiment reveals how time and history operates on the species in the field.

The ecological problem is one of many dimensions and it has to be attacked from many sides. Being an integration of problems it can only really be solved by an integrated research group. Although it is a first step it is not sufficient that scientists with various interest work on the same body of water. It is of no use to measure primary production on Monday and zooplankton grazing on Thursday. What is needed is a really integrated research plan with standardized techniques and sample programs. Although it is not so difficult to make such a program, there is the psychological problem of working together.

The choice of the Maarsseveen area as a research location was based on scientific, educational and practical considerations. From a scientific point of view Lake Maarsseveen I was chosen because of its unpolluted nature. Unpolluted water is rare in the Netherlands. Also most limnological research is subsidized to study polluted waters. It is worthwhile, however, to have a frame of reference. If the ultimate goal of pollution studies is to generate methods of management which restrict the effect of pollution as far as possible or which correct eutrophication, knowledge of the behaviour of the unspoiled ecosystem is necessary. As a university laboratory we have the freedom to do these base-line studies. In order to be able to concentrate on fundamental ecological problems it was thought to be of importance to choose a lake of simple properties. Secondary hydrographical or hydrobiological complications such as the irregular water movements of a "boezem" (= a system of reservoirs of superfluous polder-water) or a heavy input of allochthonous carbon by leaf fall has to be avoided. The rectangular basin of Lake Maarsseveen I with only one outflow and shrubs or small trees some distance from the shore approaches this ideal situation. It is the choice of a problem-directed as opposed to an object-directed research group.

From a scientific as well as an educational point of view the presence of a polluted water body, Lake Maarsseveen II, quite near to the unpolluted one is of importance. The ability to demonstrate to students what happens to a system when it is loaded with nutrients is of great value. Lake II has more or less similar hydrographical features to Lake I which makes comparisons possible.

The lakes are managed by the "Recreatie Centrum Maarsseveense Plassen". Thanks to the cooperation of this organisation, electricity, tapwater, toilets etc. were at our disposal and made it possible to build a small field station within its guarded boundaries. The field laboratory offers simple laboratory, cooking and sleeping facilities. On the water of both lakes working platforms are anchored at places of maximal depth. The area is in the centre of the Netherlands (see Fig. 1),

with a short traveling time from the universities of Amsterdam and Utrecht. These practical considerations were also the basis of our choice. There are of course also disadvantages. Being a recreation area it can be crowded on good weather summer holidays. These days are, however, rare. On the other hand, the status of recreation area guarantees the unpolluted condition of Lake I. This is a situation hardly to be expected in the overcrowded Netherlands but of particular importance for long term studies.

Acknowledgments

Several students and scientists participated for a short time in the projects. They are mentioned in the particular accounts given by the diverse authors. I would here like to thank in the first place the officials of the "Recreatie Centrum Maarsseveense Plassen", especially its former director, Mr. 0. Jager, and its present director Mr. A. Zoet. Mr. and Mrs. de Graaf are cordially thanked for ready help in many small though necessary things. Mrs. T. Meijs is thanked sincerely for her indefatigable work at the typewriter and the accurate lay-out of the report. The cover of this report was designed by B. Flik.

Introduction to the Lakes Maarsseveen

In former times the area was part of extensive swamps where peat was dug. This digging was done in narrow strips and the land in between the dug out canals (called "petgaten") was used to dry the peat. In this way a pattern of longitudinal strips of alternately water and land (called "zodden") came into existence. In the course of time the narrow pieces of land (the so-called "legakkers") were removed as well or they broke into small islands, and gradually the "zodden" changed in some places into shallow lakes. Some of these have successively been drained into polders and are now used for such purposes as pastures. Recently, in 1960 and 1967 respectively, two "zodden" areas were dredged to gain sand necessary for building roads. In this manner two lakes of over 20 meter depth were formed: Lake Maarsseveen I and Lake Maarsseveen II (see Fig. 2 and 3). Hydrodynamical these lakes are connected by a small though original "zodden". The hydrodynamics of the area is very complicated, and only a general outline can be given. See Fig. 4. North-west of the area, at a distance of about 90 meter from the "zodden" and separated by a dike, the very low-lying polder, called Bethune, is situated. The difference in height between the "zodden" area and the polder is 3 meter. This difference causes an underground movement of water from the last "petgat" (= longitudinal canal) through the dike into the polder

(triangles in Fig. 4). This loss of water is supplemented by a flow from Lake I and especially from Lake II. Probably, the amount of water flowing from Lake I is small. Its origin is rainwater falling on pleistocene dunes in the east and seeping through the bottom. Most water flows from Lake II through ditches to the last "petgat" at the North-western side of the "zodden" (arrows in Fig. 4). Lake Maarsseveen II is fed by water from the river "Vecht".

This complicated flow of water and the fact the water from the "Vecht" and Lake II is heavily polluted whereas the water from Lake I is not, makes the "zodden" extremely interesting. Within this area of narrow canals and strips of boggy land a eutrophication gradient exists. In Fig. 5 an outline of the situation is given. The water in the North-western canal is eutrophic to hypertrophic (zone 1, heavily shaded). Blooms of *Microcystis aeruginosa* are frequent. The phosphate concentration is about 2.5 mg.l^{-1}. The oxygen concentration may be zero near the bottom (1-1.5 meter) and oversaturated near the surface.
The next zone, zone 2 is characterized by a varying water quality. Within the cycle of a year the gradient as expressed, for instance, by the conductivity of the water (see inset Fig. 5) shifts from one end to the other and back again. In the part close to zone 1 *Nuphar lutea* and *Nymphaea alba* are present. More to the East *Ceratophyllum demersum* and *Myriophyllum spicatum* are found.

East from sample station 9 there is probably no penetration of polluted water until station 6 is reached where a zone 3 is found characterized by large tufts of Characea, for instance *Nitellopsis obtusa*. The phosphate concentration is low (0.01-0.03 mg.l^{-1}). The conductivity drops in this zone. Compared to zone 1 the daily amplitudes in oxygen concentration are small.

Zone 4 gradually merges into Lake I. A few houses at the water front of the last canal influence the water quality. The species *Limnanthemum nymphaeoides* is very common. *Oscillatoria princeps* covers the bottom in spring and early summer. In late summer mats of these algae are found floating at the water surface.

The inset of Fig. 5 represents the conductivity at the different sample stations. The gradient character of the water in the "zodden" is clearly demonstrated by this parameter.

The hydrographical and hydrobiological description given above is largely based on a report by Ad Mol, Michiel Schreijer and Paul Vertigaal (1979). The study was done under the auspices of the Research Institute for Nature Management.

Some physical and chemical characteristics of both lakes are given in tabular form below.

Characteristic	Lake I	Lake II
Surface area	70 ha	20 ha
Length long axis	1700 m	850 m
Length short axis	440 m	325 m
Direction long axis	N.W.	N.W.
Maximal depth	32 m	25 m
Depth thermocline	8-13 m	6-11 m
Stratification period	May-October	April-November
Range Secchi disk visibilities summer winter	4-7 m 4-7 m	1.20-3.50
Range vertical extinction coefficients summer winter	$0.41\text{-}0.61\ m^{-1}$ $0.41\text{-}0.61\ m^{-1}$	$2.00\text{-}3.20\ m^{-1}$ $1.00\text{-}1.20\ m^{-1}$
PO_4-concentration range	$0.01\text{-}0.05\ mg.l^{-1}$	$0.4\text{-}7\ mg.l^{-1}$
NO_3-concentration range	$0.4\text{-}2.70\ mg.l^{-1}$	$1\text{-}16\ mg.l^{-1}$

Overview of the work that has been done

Thusfar most work was concentrated on Lake Maarsseveen I. The lake is of an exceptional quality compared to the awfull situation in most parts of the Netherlands. This is readily illustrated by comparing for instance the Secchi-disk visibility up to 7 meter with a value of sometimes 1.20 meter for the polluted Lake II. There is no extensive littoral belt along the shore but thanks to the clear water a well-developed sublittoral exists. The sublittoral vegetation has been mapped by E.Best who recorded that 25% of the total surface area is occupied by a more or less dense cover of submerged macrophytes.The *Chara* meadows are especially extensive in the shallow North-western corner of the lake. This sublittoral zone extends to a depth of about 10 meter. According to the range of extinction coefficients in the table on page 7 at this depth 0.2-1.6% of the surface irradiation is present. A value of 1% is generally accepted as the limit of the photic zone. Among the macrophytic species present some have become more or less rare in the Netherlands, notably the angiosperms *Alisma gramineum* and *Najas marina*. The same holds for several Characea. Extensive studies have been made of the periphyton on macrophytes by Roos and coworkers who especially studied the submerged parts of emergent species such as reed (*Phragmites australis*). They calculate that this species offers a surface area of 6833 m^2 available as a substratum for many organisms. The diatoms are especially present in enormous numbers distributed over 89 identified species. This highly divers community also has a complicated spacial structure. Not only the macrophytes are overgrown but the long stalks of sessile diatoms are also covered by hundreds of smaller species. For instance on a 4 mm stalk of *Cymbella lanceolata* 250 *Achnanthes* colonies or individuals and 50 *Synedra* were counted. With regard to species richness and architecture these jungles are certainly comparable with the tropical ones. Especially at the end of the summer the individuals rise to astronomical numbers. From this time onwards the macrofauna in the littoral zone starts to develop. The highest number of individuals as well as species are found in autumn and early winter (Higler). The close dependency of these larger invertebrates, of which more than 100 species were identified, on the presence of the vegetation was demonstrated by Higler. The presence of artificial (plastic) plants realised a colonisation at least one month earlier than normally because of the late start of the natural vegetation and its epiphyton.

A sharp change in the number of species of the bottom fauna was found by Higler at the 10 m depth zone. We have already learned this is the limit of the photic zone and the sublittoral vegetation. Whether this is a complete explanation is questionable. At about the 10 meter depth a sharp decrease in temperature is

found. As demonstrated by Kersting this thermocline extends not transformed until it collides with the slope of the sublittoral zone. According to Davids and Wegener Sleeswijk this area is characteristic because of the presence of rather large quantities of the testacean species *Corythion* cf. *dubium* and *Cyphoderia ampulla*.

Some very numerous larger invertebrates in the littoral vegetation are the snail *Potamopyrgus jenkinsii*, the chironomid *Endochironomus albipennis* and the bivalve mollusc *Dreissena polymorpha*. It was mentioned by De Wijs and Van den Broek that the tremendously increase in Lake I of *P. jenkinsii* in early summer 1979 made a quantification impossible. This species occurs in relatively low numbers in Lake Maarsseveen II where the relative *Bithynia leachi* is dominant. The ecology of this last species was described by De Wijs and Van den Broek. These two gastropods pose a very interesting ecological situation. Relative to the population in Lake II that of *B. leachi* is reduced in size in the older generation and a new one appears later in time. Since *B. leachi* and *P. jenkinsii* occur in the same habitat and have a comparable behaviour De Wijs en Van den Broek suppose the two species compete and that in Lake I *B. leachi* is partly suppressed by *P. jenkinsii*. Several suggestions as to the mechanisms that lead to this suppression in Lake I are given.

The parasitofauna of both lakes was investigated by Van den Broek. A preliminary conclusion is drawn that the digenean (Cestoda) fauna in Lake I is more varied than in Lake II. The bird parasites especially dominate. In autumn and winter large flocks of coots and ducks aggregate in the more shallow north-western corner of the lake where extensive meadows of Characea are present. The large population of the bivalve mollusc *Dreissena polymorpha* also provides food for diver ducks.

Faunistical the littoral zone of Lake Maarsseveen I is very interesting. Several chironomid species found in the lake have an alpine, subalpine or northern European distribution (Davids, Kouwets and Schreijer). Generally speaking, this means these species occur in rather cold, oxygen-rich environments, biotops not very typical for the Netherlands. Lake Maarsseveen I seems to be rich in species, an example being that 48 species of water mites were identified (Davids, De Groot and Mol). Several species new to the Dutch fauna were found and some of the parasitic species may be new to science.

As all pelagic regions, the open-water zone (because of the relatively small dimensions we prefer to speak of the open-water zone) of Lake Maarsseveen I is rather poor in species numbers. Compared to the littoral zone this fact is especially demonstrated by the few zooplankton species present. A species list of

the phytoplankton was published by Hallegraeff, G.M. (Pigment diversity, bio-
mass and species diversity of phytoplankton of three Dutch lakes, Thesis Uni-
versity of Amsterdam, 1976). The littoral zone being a jungle, the open-water
zone with high uniformity might be called a savanne or even a desert. These dif-
ferences lead to different research methods and research in the open-water zone
is of a quantitative nature and restricted to a few dominant species.

The physical and chemical features of both lakes were studied by Kersting.
The lakes start to stratify in May and the thermocline is present until Novem-
ber. In Lake I an oxycline develops in July and is still well-expressed in No-
vember. The depth of the metalimnetic minimum in the oxygen concentration is be-
low the depth of the maximum temperature gradient. Below this minimum oxygen con-
centration a slight increase is found with increasing depth. However, in autumn
the hypolimnetic oxygen concentration is low. The full circulation period begins
in December and lasts until April.
Of special interest are the internal waves discovered by Kersting. These inter-
nal seiches are well expressed in the hypolimnion and the amplitude can be as
large as 4 meters.

The low nutrient concentrations point to an oligo-mesotrophic nature of Lake
I. In the contribution of Flik additional characteristics are listed, a.o. pri-
mary production which confirm this. A summary of the phytoplankton succession is
presented by Dorgelo. Less than ten species of algae are of importance in a quan-
titative sense. Research is concentrated on these species. In spring and autumn
especially the microscopic picture is dominated by colonial diatoms. The mecha-
nism of the spring succession of these algae is studied intensively at the pre-
sent moment. Superficially speaking, this spring succession is rather stereotype.
Asterionella formosa is the first to begin growing, followed by *Fragilaria cro-
tonensis* and the last of the most abundant diatoms is *Cyclotella comta*. *Stepha-
nodiscus astrea* overlaps the first two species. Looked upon more closely it be-
comes evident that variations from year to year as to the timing, rate of pop-
ulation development, rate of decline etc. are present. The fast rate of disap-
pearance is sometimes especially surprising. We have good reasons to believe
that at this time biotic factors, such as parasites, are of principal importance.

The traditional ^{14}C-technique of measuring primary productivity, incubating
the algae in flasks suspended in the lake itself for some time, was not applied.
Instead laboratory incubations at a representative set of irradiations were per-
formed (see contribution of Flik). Apart from the possibility to calculate the
daily production, this technique also offers the possibility to look at physio-
logical properties of the algae. This is illustrated by a comparison of the po-
tential production per unit of chlorophyll throughout the year. Flik found long

periods of a constant potential in late summer and periods with strongly fluctu-
ating potentials in spring, for instance.

The research group "open-water column" conducted several diel research peri-
ods in the field. The objective was to describe at the same time and place some
potentially interacting phenomena. The philosophy of this type of research as
well as an account of the results of a day in May and one in August is given by
Ringelberg. Those studies were also conducted to obtain an idea of the accuracy
of the work done in the field. The reproducibility of a measurement done under
the changing conditions of the natural situation poses a problem. An attempt was
made to overcome this by applying two different methods for the same type of
measurement and by making a carbon balance of the diel period. An example of the
first is offered by the two methods of measuring zooplankton grazing. Radioac-
tive labeled phytoplankton was offered to zooplankton and the activity of the
animals measured after some grazing time. Alternatively, the initial concentra-
tion and the final concentration of algae were determined for a relatively long
grazing period. Determining the carbon concentration of the phytoplankton at
sunrise at time 0 and 24 hours later the difference must equal the sum of pri-
mary production, algal respiration, grazing and other processes leading to a
loss of algae.

For Lake Maarsseveen I it was found that about 80% of the primary production
can be ascribed to small-sized algae. Therefore the large algae dominating a mi-
croscopic picture are functionally of less importance. This is confirmed by the
grazing studies of Hulsmann. The small-sized species *Cryptomonas erosa* and *C.
ovata* are the main food source of the zooplankton in the lake. The high produc-
tivity of these algae sustain the zooplankton community. It is often thought
that grazing can lead to a strong reduction of an algal population especially
during the spring bloom which is thought to be terminated by a rapidly growing
population of cladocerans. This idea is based on the sequence of events: a re-
duction of diatoms is directly followed by an increase in zooplankton. The stu-
dies in Lake Maarsseveen I do not confirm these ideas. The sometimes extremely
rapid population decline of the spring diatoms are probably caused by parasitic
epidemics. On the other hand, the food source populations of *Cryptomonas* show a
rather constant population size (see figures Dorgelo).

Precise knowledge of the interactions of phytoplankton and zooplankton in
the field can only be obtained if functions of both are studied simultaneously
at the same location. Interactions are present at the species level. It is
pointed out that primary production is estimated at the community level, how-
ever, grazing is estimated at the species level. If the important relation be-
tween the daily algal production is to be related to the daily zooplankton graz-

ing, the first must also be estimated at the species level since not all algae are eaten at the same rate. A first and crude attempt is presented to divide the estimated community production over the different algal species. The starting point is the diel carbon change of these species as calculated from the changes in population size. Although no claims as to the exactness of the presented values in the species specific daily budgets is made, tendencies within the algal community become apparent. For instance, it is argued that the primary production of *Cryptomonas erosa* on a particular day in August can be sufficient to realise the observed doubling of the population size, notwithstanding a considerable loss due to grazing.

Fig. 1. The location of both lakes Maarsseveen (arrow)
in between the Universities of Amsterdam and
Utrecht.

LAKE MAARSSEVEEN I

1 : 5643   —————— 250 METER

Fig. 2. A map of Lake Maarsseveen I with lines of equal depth.

Fig. 3. A map of Lake Maarsseveen II with lines of equal depth.

LAKE MAARSSEVEEN II

100 METER

N

Fig. 4. A schematic map of watercourses around the Maarsseveen lakes.
Roads, houses etc. are omitted. The waterflow from the river
Vecht to Lake II and from there to the "zodden" is indicated
by the arrows alongside the ditches and canals. The seepage
from the "zodden" to the low-lying polder Bethune is indicated
by triangular arrows. Modified from a report by Mol *et al.*, 1979.

Fig. 5. Map of the "zodden" area. The zones of different eutrophication are indicated by different shading. The numbers indicate sample stations. The inset figure presents the conductivity at the various sample stations. Also the demarcation of the zones is indicated in this inset figure. This figure is based on data in a report by Mol et al., 1979.

OXYGEN AND TEMPERATURE MEASUREMENTS IN LAKE MAARSSEVEEN I

K. Kersting

Research Institute for Nature Management

Introduction

During the years 1976, 1977, 1978 each month continuous measurements during 48 hours were made. With a technique described before (Kersting, 1978) oxygen and temperature were measured at different depths while light was measured in the air. In this report some results will be shown. It is not useful to include the figures for all sample periods in this report. For those who are interested a complete set of data can be obtained from the author.

Description of the annual oxygen and temperature dynamics
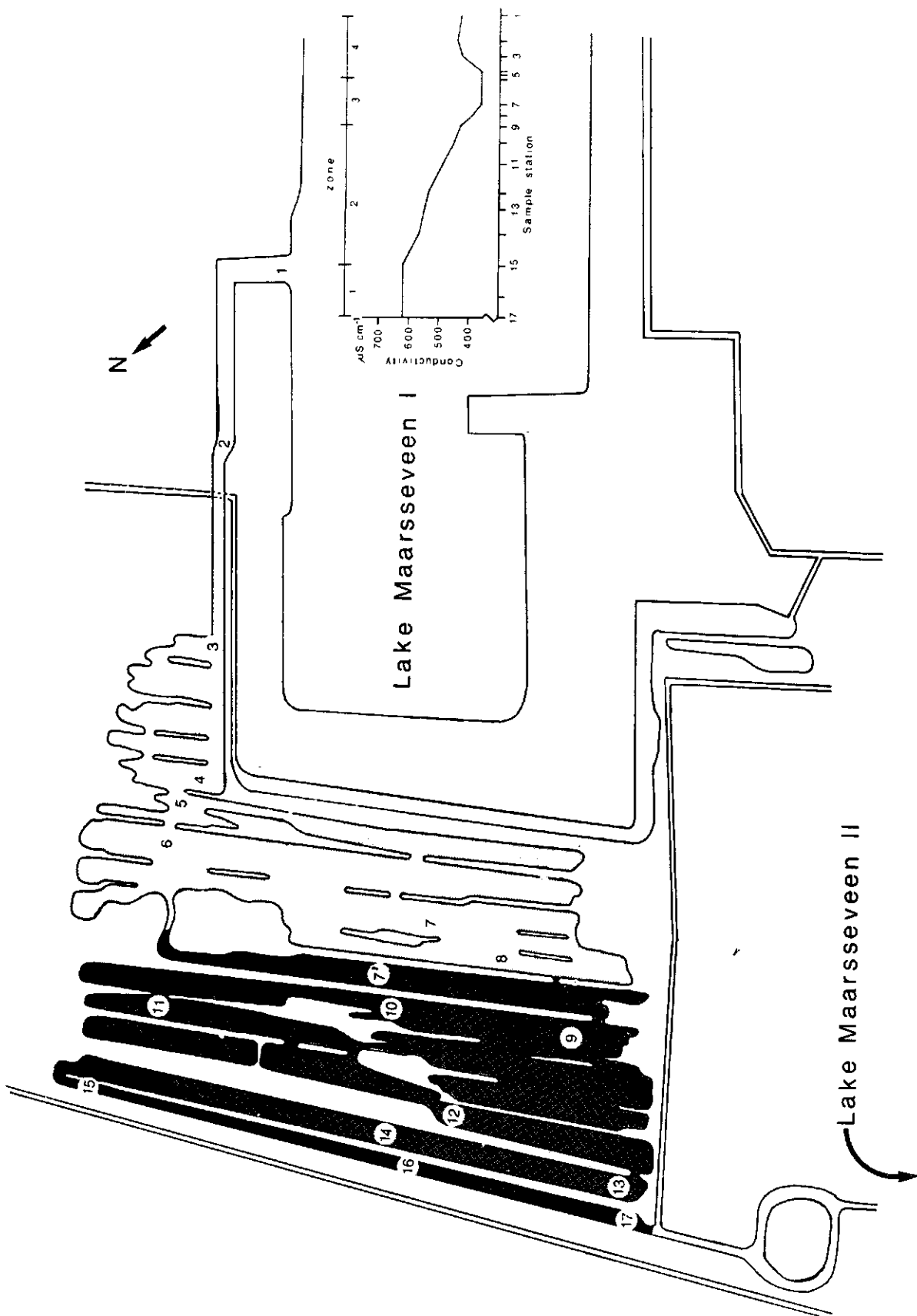
For the description of the annual dynamics the mean values of each 48 hour period is used. In Fig. 1 and 2 the oxygen and temperature profiles are shown. In Fig. 3 and 4 the same data are used to produce the oxygen isopleths and the isotherms. These pictures show that the lake is homogeneous until April. Then the stratification develops and the lake does not become completely mixed again before december. Following the temperature stratification an oxygen stratification slowly develops showing a minimum oxygen concentration between 9 and 11 meters and a hypolimnetic maximum at about 15.5 meters. Compared to the other years, in 1978 the "metalimnetic" minimum was less pronounced. Especially in 1977 the minimum was very deep. In September of that year a layer with a 48 hour mean oxygen concentration of 0.4 ppm at 10 meters depth seperated the oxygen rich epilimnion from the hypolimnion with a maximum oxygen concentration of 2.8 ppm.

The place of the metalimnetic minimum in the oxygen concentration is clearly below the depth of the maximum temperature gradient. An example is given in Fig. 5. In July and August the minimum was between 1.25 and 1.75 meters below the maximum temperature gradient. In September and October the difference was somewhat less (0.75-1.25 meters). In this period the lake is cooling from the surface and the metalimnion is compressed.

During the autumn the deeper hypolimnion becomes very poor in oxygen. In November just before the lake becomes homothermal the oxygen concentration was about 0.1 ppm near the bottom in all three years. The minimum depth of the

1 ppm isopleth was 19 meters in 1976 and 17 meters in the other years. Also the period with an oxygen concentration below 1 ppm near the bottom was shortest in 1976 (47 days in 1976, 84 days in 1977 and 66 days in 1978). The oxygen concentration at the hypolimnetic maximum was highest in 1976, lowest in 1977 and intermediate in 1978.

The differences in oxygen concentration at the hypolimnetic maximum and the metalimnetic minimum correspond with differences in temperature in the three years (see also Stewart, 1976). In 1977 the temperature at the depth of the very low metalimnetic minimum was during the summer between 11.45 and $12^{\circ}C$. In 1976 the temperature varied between 9.89 and $11.47^{\circ}C$ while in 1978 when hardly a metalimnetic minimum developed the temperature was still lower ($9.06-9.97^{\circ}C$). For the hypolimnion a similar temperature effect was present except that the temperature at the depth of the hypolimnetic maximum was highest in 1977, lowest in 1976 and intermediate in 1978. The same sequence is found with the maximum temperature at the bottom: $7.83^{\circ}C$ in 1977, $6.06^{\circ}C$ in 1976 and $6.79^{\circ}C$ in 1978. In Table 1 the comparisons between oxygen and temperature are summarized. It is surprising that in 1976 the hypolimnion stayed coolest resulting in relatively the best oxygen conditions, while the summer that year was extraordinary warm.This apparent contradiction is explained by the fact that in 1976 the lake became stratified very early. The temperature near the bottom in April just after the onset of stratification was $5.46^{\circ}C$. On the other hand in 1977 stratification developed later with a bottom temperature of $7.29^{\circ}C$. In 1978 this temperature was $6.2^{\circ}C$.

In the Figs. 6 and 7 the oxygen and heat content are plotted against time. The lines indicate the amount of oxygen or heat from a particular depth to the bottom or from that depth to the surface. The top lines are the total amounts for the whole watercolumn and are identical in the both ways of calculating. The distance between the lines is a measure of the heat or oxygen contained in the layer between two successive depths. If lines touch this amount is zero and if lines are parallel no oxygen or heat is produced or consumed during the time interval. In Fig. 6A and B the amount of oxygen or heat between the bottom and the particular depth is plotted. This figures are most informative for the bottom layers, say hypolimnion, on the other hand Fig. 7A and B reveal more information about the top layers, say epilimnion. In these figures each line indicates the amount of oxygen or heat in the watercolumn from the surface to the particular depth. The oxygen content of the lake clearly reaches its maximum in winter, the top of the oxygen content coinciding with the lowest heat content. The oxygen content reaches a minimum just prior to the autumn turnover. Comparing Figs. 6

and 7 it is obvious that the annual cycle of the oxygen content is governed by the hypolimnion while the changes in the heat content are mainly caused by the changes in the epilimnion.

Horizontal homogeneity

The intensive oxygen and temperature measurements were carried out from the raft located in the middle of the lake. It was wondered whether these measurements were representative for the whole lake and especially whether the oxygen-depth profile possibly changed drastically going from the open-water zone to the littoral. In order to obtain information about this question on a few occasions measurements of oxygen and temperature depth profiles were made along a transect from the raft to the shore. As examples the measurements in August and September 1977 are given in Fig. 8. Most of the isopleths and isotherms extend horizontally along this transect. These results indicate that the measurements at the raft are representative for the whole lake indeed. The differences, for example the slightly lower depth of the 8 ppm isopleth in August at 35 meters from the shore compared with to the depth at greater distance, are negligeable. It might be that these differences find there cause in the fact that the profiles along the transect were only measured once and not over a 24 or 48 hour period. As will be shown later there may be considerable oscillations of the depths of the isopleths especially in the hypolimnion. Also very weak gradients can suggest a substantial difference. For example in September the 9 ppm isopleth seems to indicate a higher oxygen concentration in the littoral zone. This difference is real but very small. At 0.5 meter depth the oxygen concentration was 9.11 ppm near the shore and 8.96 ppm at the raft at 195 meters from the shore. These small differences are of no importance and it can be concluded as far as these results allow us to do that the measurements in the middle of the lake are representative for the whole lake.

Short term variations

Point measurements of oxygen or temperature give information about that particular moment only. The variation during the day and night especially are important characteristics which can only be revealed by continuous measurements. The magnitude of the variations also indicates the relative value of point measurements. If the variations are small, then point measurements are reliable, if not the value of single measurements is very limited. With the technique of lowering and raising the sensors from the surface to the bottom a complete profile was obtained each hour. The data can be worked out in many ways. One way

of presenting the information is given in Fig. 9. The top panel shows the light
intensities. The profiles are plotted in two ways. The left ones are plots of
all profiles measured during the 48 hour sampling period while the right ones
are the 48 hour means. The width of the band of points in the left hand profiles
is the variation at the particular depths. In order to show the variation through
time and depth the oxygen isopleths and the isotherms are plotted. For each sam-
pling period these sets of 7 plots have been produced. In this report only a few
representative examples will be given.

During the winter the lake is homogeneous. The profiles are straight and nar-
row and the isopleths or isotherms are absent (no integer value at any time or
depth) or more or less vertical and often irregular. In January 1978 a beautiful
example of this was found (Fig. 10). This example also shows very well the in-
crease in oxygen during the day and the decrease during the night.
In April when the stratification period starts there is some variation in both
oxygen and temperature at greater depth while at the surface there is hardly any
variation (Fig. 11). The isopleths become more regular and horizontal. In June,
July and August when the lake is completely stratified there is more variation
around the mean, but still the variation in the oxygen concentration at the sur-
face is small (Fig. 12). From August onwards the lake starts cooling and the
thermocline sinks to greater depths. In the thermocline especially, the varia-
tions in oxygen concentration but sometimes also in temperature become much big-
ger. See example October 1976 (Fig. 13). In December the lake is completely mixed
again and the situation is similar to January. However, the temperatures are
higher and the oxygen concentrations lower.

The results discussed above indicate that the short term variations of the
oxygen concentration are small in Lake Maarsseveen I. This is clearly shown in a
plot against time of the total oxygen content of the water column (Fig. 14A,B,C).
Also the variations in heat content are small during 48 hours (Fig. 14D,E,F). If
the data are plotted on a larger scale relative to the value at the start of the
sampling period the variations become clear (Fig. 15). First of all in January
1978 a beautiful diurnal rhythm in oxygen content is found (Fig. 15A). This situ-
ation is however seldom observed. On most other occasions the curves were more
irregular and surprisingly show a rhythm with a period of 6 to 8 hours (Fig. 15B,
C). The diurnal rhythm which might be present is almost completely obscured by the
rhythm with the short period (Fig. 15B). This rhythm is also present in the plots
of the heat content (Fig. 15E,F). The 6 to 8 hour rhythm is a consequence of the
presence of internal seiches. Water layers of different densities oscillate rela-
tive to one another. A clear and beautiful example of these deep water waves was
observed in August 1976 (Fig. 16). In this example the amplitude was as large as

4 meters at certain depths. The amplitude in the hypolimnion was much greater than in the meta- and epilimnion. The reason for this difference is the much greater surface area of the 10 meter stratum than that of the 20 meter stratum. The example of August 1976 (Fig. 16) is the most extreme situation that was observed during the three years. On many other occasions the internal seiche could hardly be discerned in the plots of the isopleths or isotherms. However, in most cases a rhythm with a period of 6 to 8 hours could be observed in the plots of the total oxygen or heat content of the water column.

In those cases that the internal seiche has a large amplitude this might have consequences for sampling. The water layer in which one assumes to sample need not be in rest at a particular depth. At those places where the oscillating water layers reach the bottom the fauna experiences a fluctuating oxygen and temperature condition. This might influence the distribution of the species. Diurnal rhythms, if present, are obscured by the 6 to 8 hour rhythm which can have a large amplitude. Therefore it is not possible to calculate the metabolism of the lake from in situ measured oxygen concentrations. It is perhaps possible to develop a mathematical model in which the 6 to 8 hour rhythm in the oxygen content is eliminated through superposition of the curves of the heat and oxygen content. No attempts have thus far been made to try this.

References

KERSTING, K., 1978. Automatic continuous oxygen- and temperature-profile measurements. Verh.Internat.Verein.Limnol., 20: 1216-1220.
STEWART, K.M., 1976. Oxygen deficits, clarity and eutrophication in some Madison lakes. Int.Rev.ges.Hydrobiol., 81: 563-579.

Table 1.

Year	Max. Bottom temperature °C	Metalimnion minimum		Hypolimnion maximum	
		oxygen ppm	temperature °C	oxygen ppm	temperature °C
1976	6.06	1.56	9.9 - 11.5	4.04	6.2 - 6.5
1977	7.83	0.41	11.5 - 12.0	2.83	8.2 - 8.3
1978	6.79	2.23	9.1 - 10.0	3.3	7.0 - 7.3

OXYGEN PROFILES 1976
LAKE MAARSSEVEEN I

20 ppm

DEPTH (meters)

OXYGEN PROFILES 1977
LAKE MAARSSEVEEN I

20 ppm

DEPTH (meters)

OXYGEN PROFILES 1978
LAKE MAARSSEVEEN I

20 ppm

DEPTH (meters)

Fig. 1. Monthly oxygen profiles of Lake Maarsseveen I.

TEMPERATURE PROFILES 1976
LAKE MAARSSEVEEN I

20 °C

TEMPERATURE PROFILES 1977
LAKE MAARSSEVEEN I

20 °C

TEMPERATURE PROFILES 1978
LAKE MAARSSEVEEN I

20 °C

Fig. 2. Monthly temperature profiles of Lake Maarsseveen I.

Fig. 3. Oxygen isopleths of Lake Maarsseveen I in 1976, 1977, 1978

Fig. 4. Isotherms of Lake Maarsseveen I in 1976, 1977, 1978.

Fig. 5. Oxygen concentration and temperature gradient at different
depths. Lake Maarsseveen I, 17-19 August 1977.

Fig. 6. A. Oxygen content of the water column below different depths.
B. Heat content of the water column below different depths.

Fig. 7. A. Oxygen content of the water column between surface and different depths.
B. Heat content of the water column between surface and different depths.

Fig. 8. Oxygen isopleths and isotherms at different depths and distances
from the shore.
A and C. Oxygen isopleths, B and D. Isotherms.
A and B. August 18, 1977
C and D. September 15, 1977.

Lake Maarsseveen I

Sept. 15th-17th 1976

Fig. 9. Computer output of data from Lake Maarsseveen I on September 15-17, 1976. For an explanation see text.

Lake Maarsseveen I

January 18-20, 1978

Fig. 10. Computer output January 18-20, 1978. See Fig. 9.

Lake Maarsseveen I

April 26-28, 1977

Fig. 11. Computer output April 26-28, 1977. See Fig. 9.

Lake Maarsseveen I

August 17-19, 1977

Fig. 12. Computer output August 17-19, 1977. See Fig. 9.

Lake Maarsseveen I

October 13-15, 1976

Fig. 13. Computer output October 13-15, 1976. See Fig. 9.

Fig. 14. Total oxygen and heat content of the water column
during 48 hour sample periods.
A, D: January 18-20, 1978
B, E: August 16-18, 1978
C, F: October 11-13, 1978

Fig. 15. Total oxygen and heat content of the water column during 48 hour sample periods compared with the situation at the start of the sampling period.
A, D: January 18-20, 1978
B, E: April 28-30, 1976
C, F: A-gust 18-20, 1976

Lake Maarsseveen I

August 18-20, 1976

Fig. 16. Computer output August 18-20, 1976. See Fig. 9.

OXYGEN AND TEMPERATURE MEASUREMENTS IN LAKE MAARSSEVEEN II

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Introduction

In conjunction with the measurements in Lake Maarsseveen I also measure-
ments were performed in Lake Maarsseveen II. In this report the general fea-
tures of the temperature and oxygen regime of Lake Maarsseveen II will be des-
cribed and some comparisons with Lake Maarsseveen I will be made.

Annual oxygen and temperature dynamics

In the Figs. 1 through 6 the changes during the three years are plotted in
different ways. The temperature regime of Lake Maarsseveen II did not differ es-
sentially from that of Lake Maarsseveen I. The lake is stratified from the end
of April until December. The depth of the thermocline is one to two meters less
than in Lake Maarsseveen I. This is a consequence of the smaller size and the
more protected situation of Lake Maarsseveen II. In spite of this very similar
temperature regime, the oxygen regime of Lake Maarsseveen II differs greatly from
that of Lake Maarsseveen I. Directly after the establishment of the temperature
stratification a strong oxygen stratification developes leading to an anoxic hy-
polimnion in one to two months. In May or June a metalimnion oxygen minimum can
be present, but only for a short period because during the summer the metalim-
nion becomes anoxic too. In the summer the situation can become so extreme that
even the lower part of the epilimnion becomes anoxic. In August 1976 oxygen was
only present in top 4 meters of the water column.

Another important difference is the variation of the oxygen content of the
epilimnion during the year. At 0.5 meters depth in Lake Maarsseveen I the oxygen
concentration varied between 13.5 and 8.8 ppm during the three years. In Lake
Maarsseveen II the concentration varied between 17.1 and 4.2 ppm. It must be born
in mind that these results are based on the 48 hour mean values. As will be shown
later in Lake Maarsseveen II there was a considerable variation within each sam-
pling period. If these variations are taken into account the oxygen concentration
at 0.5 meters depth in Lake Maarsseveen II varied between 3.9 and 19.5 ppm.

In Lake Maarsseveen I the minimum and maximum oxygen concentration coincide
with some delay with the maximum and minimum surface temperature. Consequently

the differences in percentage saturation is small. In Lake Maarsseveen II there
is no such coupling between oxygen and temperature. The highest oxygen value at
0.5 meters was found in August 1976 when the lake had a mean surface temperature
of 21.3 °C. This means a percentage saturation of 225%. The minimum in oxygen
concentration at the surface was not found during the summer, but in November
1976 when the temperature was 9.2 °C.

Also in the plots of the oxygen and heat content of Lake Maarsseveen II
(Fig. 5, 6) the similarity in respect to temperature and the difference in re-
spect to oxygen compared to Lake Maarsseveen I are reflected. The ratio of the
maximum and minimum oxygen content in Lake Maarsseveen II is much greater than
in Lake Maarsseveen I. In the case of comparable oxygen regimes the opposite sit-
uation would be expected because of the smaller hypolimnion of Lake Maarsseveen
II. These plots also reveal the relative importance of the primary production in
Lake Maarsseveen II. In all years an increase in oxygen content was found between
July and August while the surface water was supersaturated. Again it must be
stressed that these conclusions are based on the 48 hour mean values, and that
there is a considerable variation within the sampling period.

Diurnal oxygen regime

As in the paper on Lake Maarsseveen I only a few examples of the complete da-
ta set of the monthly measurements will be presented (Fig. 7, 8, 9, 10). The gen-
eral interpretation of these figures is the same as the one given for Lake Maars-
seveen I. The main difference is the variation of the oxygen concentration in the
epilimnion within the 48 hour sampling period. This can be seen in the plots of
the individual profiles having a considerable spread of the points. It can also
be seen in the plots of the oxygen isopleths where the isopleths extend vertical-
ly in the epilimnion. Especially in the example of July 1976 (Fig. 9) the plot of
the isopleths indicates production of oxygen in the day and consumption during
the night. The variation of the oxygen concentration in July 1976 is enormous. At
0.5 meters depth it varied between 9 and 16 ppm. At greater depths the situation
becomes even more extreme. At 3 meters the variation within 48 hours was between
1 and 13 ppm and at 3.5 meters between 0 and 9 ppm. This example, which is typi-
cal for the summer situation, indicates the importance of continuous measurements.

It might be wondered in the case of Lake Maarsseveen II with its apparent
high productivity, whether it is possible to determine the primary production
from the in situ measurements. The examples of plots of the total oxygen content
of the water column against time (Fig. 11) indicate that the variation is still
small compared to the total content. The example of August 1978 (Fig. 11b) does

reveal a diurnal rhythm, but some irregular variations are present. A more pronounced picture is obtained in the plots of the changes in relation to the starting situation. In January (Fig. 12a) irregular changes occur with especially during the night a decrease. No explanation for this pattern can be given at the moment. In August (Fig. 12b) a clear diurnal pattern is obtained, however, superimposed there is a higher order rhythm. This second rhythm with a period of about 8 hours reveals the presence of an internal seiche in Lake Maarsseveen II also. The main difference with the situation in Lake Maarsseveen I is the ratio of the amplitudes of the two rhythms. In Lake Maarsseveen II the amplitude of the diurnal rhythm caused by the primary production can be bigger than the amplitude caused by the internal seiche. There are several reasons for this, but it is also dependent on the weather conditions. On days with a low radiation input the internal seiche might overrule the primary production rhythm. However, in contrast to Lake Maarsseveen I the primary production can be so high that the internal seiche only leads to a slight distortion of the diurnal rhythm. Not only the high productivity of Lake Maarsseveen II is responsable for the relative importance of the diurnal rhythm. In the summer the hypolimnion is completely anoxic and consequently not stratified in respect to oxygen. Internal seiches will not lead to rhythms in the oxygen content of the hypolimnion because the content is zero and stays zero.

As a final example the situation of December 1978 (Fig. 12c) is illustrative for the fact that also a very weak gradient (1 ppm/25 meters or 0.3 $^{\circ}$C/25 meters) can lead to considerable changes in the apparent oxygen and heat content of the water column. It must however be born in mind that the observed changes with the 6 to 8 hour rhythm are not real changes in concentration. They only emerge from the fact that sampling at fixed depths can mean sampling in different parcels or layers of water.

Fig. 1. Monthly oxygen profiles of Lake Maarsseveen II.

TEMPERATURE PROFILES 1976
LAKE MAARSSEVEEN II

20 °C

DEPTH (meters)

TEMPERATURE PROFILES 1977
LAKE MAARSSEVEEN II

20 °C

DEPTH (meters)

TEMPERATURE PROFILES 1978
LAKE MAARSSEVEEN II

20 °C

DEPTH (meters)

Fig. 2. Monthly temperature profiles of Lake Maarsseveen II.

Fig. 3. Oxygen isopleths of Lake Maarsseveen II in 1976, 1977, 1978.

Fig. 4. Isotherms of Lake Maarsseveen II in 1976, 1977, 1978.

Fig. 5. Oxygen and heat content of the water column below different depths in Lake Maarsseveen II in 1976, 1977, 1978. A. Oxygen content. B. Heat content

OXYGEN CONTENT (mg O$_2$·cm^{-2})

HEAT CONTENT (kcal·cm^{-2})

1978

1977
A

1976

1978

1977
B

1976

Fig. 6. Oxygen and heat content of the water column between the surface and different depths in Lake Maarsseveen II in 1976, 1977, 1978.

Lake Maarsseveen II

March 3-5, 1976

Fig. 7. Computer output March 3-5, 1976. See Fig. 9, page 32.

Lake Maarsseveen II

April 26-28, 1976

Fig. 8. Computer output April 26-28, 1976. See Fig. 9, page 32.

Lake Maarsseveen II

July 19-21, 1976

Fig. 9. Computer output July 19-21, 1976. See Fig. 9, page 32.

Lake Maarsseveen II

October 10-12, 1977

Fig. 10. Computer output October 10-12, 1977. See Fig. 9, page 32.

Fig. 11. Total oxygen and heat content of the water column during 48
hour periods.
A, D: January 16-18, 1978
B, E: August 14-16, 1978
C, F: December 11-13, 1978.

Fig. 12. Total oxygen and heat content of the water column during 48
hour periods relative to the situation at the start of the
sampling period.
A, D: January 16-18, 1978
B, C: August 14-16, 1978
C, F: December 11-13, 1978

SEASONAL CHANGES IN ABUNDANCE OF SOME PLANKTONIC SPECIES
IN THE OPEN-WATER ZONE OF LAKE MAARSSEVEEN I

J. Dorgelo, E. van Donk, I. de Graaf Bierbrauwer

I. PHYTOPLANKTON

Methods.

The phytoplankton of the open-water zone was collected twice a week at noon
with a 3 litre Van Dorn sampler from a moored, floating platform (Fig. 1, place
1). A water column of 10 metres (from surface to thermocline level) was sampled
with depth intervals of 1 metre. These column samples were pooled and 1 litre
was separated for sedimentation of the algae after preservation with iodine.
The sedimented algae were brought in a 100 ml vessel and subsampled with a 1 ml
Hensen-pipette. As enumeration procedure the standard method of the inverted
microscope was used after settling of the subsamples in 10 ml, flat-bottomed
tubes (diameter 24 mm). The portion of the bottom area of the tube counted and
the magnification applied varied with algal density.
For statistical reasons three integral 10 litres column samples were taken at
every sampling day and each of these three main samples were subsampled thrice
for counting.
The phytoplankton of the littoral zone (place 2, spring 1977) was very careful-
ly sampled (to avoid contamination with cells adhered to bottom and macrophytes)
with a small vessel.

Results.

Figs. 2 - 27 demonstrate the blooms of the most abundant species in the
open-water zone during 1977, 1978 and 1979. In 1977 the littoral zone was sampled
until May 17 (between *Phragmites australis*; depth about 30 cm; Fig. 1).
In 1979 the lake was covered with ice from January 9 until March 9, preventing
us from sampling from January 23 until February 6 (ice cover too thick to break
and too thin to walk on).
The late winter/spring blooms and succession of diatoms showed a marked varia-
tion as far as *Asterionella formosa* and *Fragilaria crotonensis* are concerned:
in 1977 and 1978 *F. crotonensis* succeeded *A. formosa*, in 1978 *A. formosa* out-
numbered *F. crotonensis*, whereas in 1979 *F. crotonensis* was absent (viz. less
than 10 cells/ml).

In 1979 *Cyclotella bodanica* was recognised; it might be supposed that the second bloom of *Cyclotella* in 1978 was caused by *C. bodanica* too.

Cryptomonas div.spp. > (15x25 μ) were absent in 1977; in 1979 they appeared later than *Cryptomonas* div.spp. ≤ (10x15 μ).

Phacotus lenticularis was absent in 1977 and 1978. *Chlamydomonas* sp. was absent in 1977 and 1979.

In the littoral zone the same succession of late winter/spring diatoms occurred as in the open-water zone (1977), though the numbers were more fluctuating. The decrease of the number of *Asterionella formosa* in the littoral zone around February 22 was concurrent with strong off-shore winds.

Acknowledgments

Tabular review of phytoplankton dynamics in 1977, 1978 and 1979. Dating of bloom

1977 (February 1 - October 1)

Fig.	Species	> 10 cells/ml during		maximum abundance
2	*Asterionella formosa*	....	- March 25	Febr. 25
		July 15	- Sept. 6	July 29
		Sept 16	-	?
3	*Stephanodiscus astraea*	....	- April 15	March 8
4	*S. astraea* var. *minutula*	....	- March 25	Febr. 18
5	*Fragilaria crotonensis*	Febr 25	- May 17	May 3
		July 15	- Sept. 6	July 29
6	*Cyclotella comta* *C. bodanica*	April 29	- July 22	July 12
7	*Cryptomonas* div.spp. $\leq$ (10x15 μ)	....	-	June 21
8	*Cryptomonas* div.spp. $>$ (15x25 μ)			
9	*Dinobryon divergens* *Phacotus lenticularis* *Chlamydomonas* spec.	May 24	- August 23	July 5

1978 (January 31 - December 22)

Fig.	Species	> 10 cells/ml during		maximum abundance
10	*Asterionella formosa*	....	- May 26	April 14
		July 18	- Sept. 8	Aug. 8
		Sept. 28	- Oct. 24	Oct. 10-13
		Dec. 1	-	?
11	*Stephanodiscus astraea*	....	- March 17	Febr. 14
		March 24	- April 25	April 11
12	*S. astraea* var. *minutula*	....	- April 25	Febr. 21
13	*Fragilaria crotonensis*	Febr. 24	- March 14	March 10
		March 21	- May 26	May 18
14	*Cyclotella comta* *C. bodanica* ?	May 16	- July 7	June 2
		July 25	- August 15	Aug. 8
15	*Cryptomonas* div.spp. $\leq$ (10x15 μ)	....	-	June 30
16	*Cryptomonas* div.spp. $>$ (15x25 μ)	....	- Dec. 12	Oct. 6
17	*Dinobryon divergens*	April 28	- May 18	May 9
		July 4	- August 4	July 14
		Aug. 22	- Sept. 8	Aug. 25
18	*Phacotus lenticularis* *Chlamydomonas* spec.	May 29	- Sept. 22	June 27

periods and maximum abundances according to biweekly sampling.

number (approx.) at max. abundance (cells/ml)	comment
700	–
230	rapid wax
?	–
75	fluctuating numbers
260	fluctuating numbers
320	rapid wane
550	rapid wax
260	rapid wane
	less than 10 cells/ml
700	strongly fluctuating numbers
	less than 10 cells/ml
800	3 peaks
7000	dramatic wane
80	fluctuating numbers
330	rapid wax and wane
?	–
110	–
30	–
400	–
35	great variance
25	–
70	–
40	see second *Cyclotella* bloom 1979
750	strongly fluctuating numbers
95	strongly fluctuating numbers
700	rapid wax and wane
1600	rapid wax and wane
90	rapid wax and wane
440	rapid wax

Continued.

1979 (January 2 - December 28)

Fig.	Species	> 10 cells/ml during	maximum abundance
19	*Asterionella formosa*	(Dec. 78) - April 6	March 2
		April 17 - June 8	May 25
		July 31 - Sept. 11	Aug. 24
20	*Stephanodiscus astraea*	(Nov/Dec 78)-	
		Febr. 6 - April 20	March 2
21	*S. astraea* var. *minutula*	.... - April 17	March 16
22	*Fragilaria crotonensis*	Oct. 26 - Nov. 20	Nov. 2-9
23	*Cyclotella comta*	May 15 - June 22	June 8
24	*C. bodanica*	July 20 - August 31	Aug. 9
25	*Cryptomonas* div.spp. $\leq$ (10x15 μ)	.... -	Oct. 30
26	*Cryptomonas* div.spp. $>$ (15x25 μ)	May 18 -	Oct. 30
27	*Dinobryon divergens*	May 15 - June 8	May 22
		July 31 - Aug. 24	Aug. 9
28	*Phacotus lenticularis*	June 12 - July 31	July 3, 24
		Aug. 17 - Aug. 31	Aug. 17
	Chlamydomonas spec.		

number (approx.) at max. abundance (cells/ml)	comment
2400	rapid wane
560	rapid wax and wane
370	rapid wax and wane
30	-
90	-
25	< 10 cells/ml in spring/summer
650	rapid wax and wane
35	-
1050	strongly fluctuating numbers
90	strongly fluctuating numbers
260	rapid wax and wane
1400	rapid wax and wane
160	rapid wane
85	rapid wax and wane

Fig. 1. Morphometry of Lake Maarsseveen I.
a. Schematic map; 1. floating platform fixed at the bottom (depth 30 m); 2. vegetation of *Phragmites australis* (depth 30 cm).
b. Depth along the line L-L', including the two sampling stations. Length of the lake: about 2.5 km.

Fig. 2. Numbers of live cells per ml (± S.E.) of *Asterionella formosa* in the

Fig. 3. *Stephanodiscus astraea*. See Fig. 2.

open-water zone (and during spring in the littoral zone).

Fig. 4. *Stephanodiscus astraea* var. *minutula*. See Fig. 2.

Fig. 5. *Fragilaria crotonensis.* See Fig. 2.

Fig. 6. *Cyclotella comta*. See Fig. 2.

Fig. 7. *Cryptomonas* div.spp. ≤ (10 x 15 μm). See Fig. 2.

Fig. 8. *Dinobryon divergens*. See Fig. 2.

Fig. 9. Number of live cells per ml (± S.E.) of *Asterionella formosa* in the open-

water zone.

Fig. 10. *Stephanodiscus astraea*. See Fig. 9.

Fig. 11. *Stephanodiscus astraea* var. *minutula*. See Fig. 9.

Fig. 12. *Fragilaria crotonensis*. See Fig. 9.

Fig. 13. *Cyclotella comta*. See Fig. 9.

Fig. 14. *Cryptomonas* div.spp. $\leq$ (10 x 15 μm). See Fig. 9.

Fig. 15. *Cryptomonas* div.spp. > (15 x 25 μm). See Fig. 9.

Dinobryon divergens 1978

Cells/ml

Fig. 16. *Dinobryon divergens*. See Fig. 9.

Fig. 17. *Chlamydomonas* sp. See Fig. 9.

-80-

Fig. 18. *Asterionella formosa.* See Fig. 9.

| | 4 | 8 | 12 | 15 | 19 | 22 | 26 | 29 | 3 | 6 | 10 | 13 | 18 | 20 | 24 | 27 | 31 | 3 | 7 | 9 | 14 | 17 | 21 | 24 | 28 | 31 | 4 | 7 | 11 | 14 | 18 | 21 | 25 | 28 | 2 | 5 | 9 | 12 | 16 | 19 | 24 | 26 | 30 | |
| | | JUNE | | | | | | | | | JULY | | | | | | | | AUGUST | | | | | | | | | | SEPTEMBER | | | | | | | OCTOBER | | | | | | | |

Fig. 19. *Stephanodiscus astraea.* See Fig. 9.

Fig. 20. *Stephanodiscus astraea* var. *minutula*. See Fig. 9.

Fig. 21. *Fragilaria crotonensis*. See Fig. 9.

Fig. 22. *Cyclotella comta.* See Fig. 9.

Fig. 23. *Cyclotella bodanica*. See Fig. 9.

Fig. 24. *Cryptomonas* div.spp. ≤ (10 x 15 μm). See Fig. 9.

Fig. 25. *Cryptomonas* div.spp. >(15 x 25 μm). See Fig. 9.

26 29 | 3 6 | 10 13 | 18 20 24 27 | 31 3 | 7 9 | 14 17 | 21 24 | 28 31 | 4 7 | 11 14 | 18 21 | 25 28 | 2 5 | 9 12 | 16 19 | 24 26 30 2 | 6 9 | 13 16 | 20 23 | 27 30 3 | 7 | 11 14 | 18 21 | 25 28

| JULY | AUGUST | SEPTEMBER | OCTOBER | NOVEMBER | DECEMBER |

26 29 | 3 6 | 10 13 | 18 20 24 27 | 31 3 | 7 9 | 14 17 | 21 24 | 28 31 | 4 7 | 11 14 | 18 21 | 25 28 | 2 5 | 9 12 | 16 19 | 24 26 30 2 | 6 9 | 13 16 | 20 23 | 27 30 3 | 7 | 11 14 | 18 21 | 25 28

| JULY | AUGUST | SEPTEMBER | OCTOBER | NOVEMBER | DECEMBER |

Fig. 26. *Dinobryon divergens*. See Fig. 9.

Fig. 27. *Phacotus lenticularis*. See Fig. 9.

II. ZOOPLANKTON (M. Butter, J. Dorgelo, A. Keijser)

Methods

The zooplankton of the open-water zone was collected weekly in a column of 10 meters (from surface to thermocline level) with a 60 μm net, in combination with a pump (1977) or by vertical hauls (1978; 1979). The hauls were taken from a small boat in order to avoid sampling in the vicinity of the cone of shadow beneath the platform where zooplankton may concentrate at the transition from light to dark. When the pump was used depth intervals of 0.5 meter were chosen and the zooplankton was bulked. In all cases five samples were taken. These (bulked) samples were subsampled three times (1977). For statistical reasons it was judged better to transform raw data to logarithms and to give 95% confidence intervals for the average of the logarithms. Variance analysis showed that the variation due to subsampling techniques is far more important than the variation due to the different methods. Therefore, it was more convenient to bulk the five net hauls and to subsample from these bulked samples (1978; 1979).

Results

In 1977 (February - September) a first inventory of biomass fluctuations of Lake Maarsseveen was made, as expressed in cladoceran, copepod and rotifer species (Figs. 28-40) and as far identifiable due to lack of time. *Daphnia longispina* (Fig. 28) and *Bosmina* (*coregoni* + *longirostris*) (Fig. 29) started to build up a population density exceeding 1 ind./L in March. Maximum densities were 30 (May 3) and 15 inds./L (May 17), respectively. *Daphnia* maintained a fluctuating density around 10-15 inds./L. *Bosmina* showed a decrease below 1 ind./L at the end of June, which continued until August 2.

The copepods (*Cyclops* + *Eudiaptomus*; Fig. 30) also appeared in March. From May 24 onwards *Cyclops* (Fig. 31) and *Eudiaptomus* (Fig. 32) were separately counted. The rotifers had summer maxima: *Conochilus unicornis* (max. abundance about 60 inds./L) in May (Fig. 33), *Kellicottia longispina* (20) in August (Fig. 34), *Keratella cochlearis* (80) in August (Fig. 35), *Asplanchna* (50) in August (Fig. 36), *Habrotrocha* (100) in July/August (Fig. 37), *Polyarthra* (200) in July/August (Fig. 38), *Synchaeta* (5) in July/August (Fig. 39), and *Trichocerca* (20) in August (Fig. 40).

In 1978 and 1979 only cladocerans were counted (*Daphnia longispina*, *Bosmina coregoni* and *Bosmina longirostris*). Figs. 41 and 42 give the results as far as the samples have been enumerated. The fluctuations in the three populations follow the same pattern in both years. The population density of *Daphnia longispina* is

greater than that of the *Bosmina* species. In 1978 *Bosmina longirostris* outnumbered *B. coregoni* from July until November; in 1979 its numbers remained permanently below those of *B. coregoni*, in particular during the second half of the year. The summer drop in density of 1977 (Fig. 29) also occurred in 1979.

Acknowledgments

Thanks are due to C. Ooms, J. Rikveld and C. Teunissen for assistance.

Daphnia longispina

Number/l

100

10

FEBRUARY 8 15 22 1 MARCH 8 15 22 29 APRIL 5 12 19 26 3 MAY 10 17 24 31 JUNE 7 14 21 28 5 JULY 12 19 26 2 AUGUST 9 16 23 30 6 SEPTEMBER 13 20 27

Fig. 28. *Daphnia longispina* (juveniles + adults). Numbers of individuals per liter (± S.E.) in 1977.

Fig. 29. *Bosmina coregoni* + *B. longirostris* (juveniles + adults). Numbers of individuals per liter (± S.E.) in 1977.

Fig. 30. Copepoda. Numbers of individuals per liter (± S.E.) in 1977
(February-May). O—O nauplii; ●—● copepodites + adults.

Fig. 31. *Cyclops*. Numbers of individuals per liter (± S.E.) in 1977 (May-September). O—O nauplii; ●--● copepodites; ●—● adults.

Fig. 32. *Eudiaptomus*. Numbers of individuals per liter (± S.E.) in 1977 (May-September). O—O nauplii; ●--● copepodites; ●—● adults.

Fig. 33. *Conochilus unicornis*. Numbers of individuals per liter (± S.E.) in 1977.

Fig. 34. *Kellicottia longispina*. Numbers of individuals per liter
(± S.E.) in 1977.

Fig. 35. *Keratella cochlearis*. Numbers of individuals per liter
(± S.E.) in 1977.

Fig. 36. *Asplanchna*. Numbers of individuals per liter (± S.E.) in 1977.

Fig. 37. *Habrotrocha*. Numbers of individuals per liter
(± S.E.) in 1977.

Fig. 38. *Polyarthra*. Numbers of individuals per liter (± S.E.) in 1977.

Fig. 39. *Synchaeta*. Numbers of individuals per liter
(± S.E.) in 1977.

Fig. 40. *Trichocerca*. Numbers of individuals per liter (± S.E.) in 1977.

Fig. 41. *Daphnia longispina*, *Bosmina coregoni* and *B. longirostris* (1978). Means of log numbers per m³ with 95% confidence intervals.

Fig. 42. *Daphnia longispina, Bosmina coregoni* and *B. longirostris* (1979). Means of log numbers per m³ with 95% confidence intervals.

PRIMARY PRODUCTION MEASUREMENTS IN LAKE MAARSSEVEEN I

B.J.G. Flik and A. Keyser

Introduction

In 1975 Lake Maarsseveen was chosen as a project for ecosystem research by our department. In the framework of this research it was necessary to get an impression of the production by phytoplankton in the open-water zone. Measurements of the primary production in situ using the oxygen method in light and dark bottles (Gaarder & Gran, 1927) were not possible, because the biomass of the phytoplankton is too low to get measurable differences in oxygen concentrations. So we decided for the carbon-forteen-method (Steemann-Nielsen, 1953) to measure the primary production. However, Lake Maarsseveen being a recreation area, we disliked the use of radioactive material. Therefore the laboratory technique of incubating samples from the lake was introduced. The potential productivity of field samples is measured at different light intensities. It was difficult, however, to obtain a light source sufficiently strong to realize the highest intensity found in the field. To overcome this problem a mathematical model, developed by Fee (1973) was used. High light intensity responses are extrapolated from P versus I curves determined at low light intensities. The very good cooperation with Mr. P. Ruardij in developing these techniques is sincerely acknowledged. Mr. P. Ruardij made also a computer program (modified after Fee). Likewise we want to thank Mrs. I.J. Mous, who did the production measurements in 1976.

Methods

1. Sampling and labeling

Samples of phytoplankton were taken from the raft in the middle of Lake Maarsseveen. The following depths were chosen: 0.5, 1.5, 2.5, 5.5, 10.5 and 15.5 meter. Samples were taken between 8 and 9 a.m., using a Van Dorn water sampler. The samples were sifted through 150 µ plankton gauze to remove the larger zooplankton. Stored in plastic containers they were transported to Amsterdam within one hour. In the laboratory for each depth eight light bottles and one dark were filled with 100 ml sample. To label the algae 1 ml of a solution of $NaH^{14}CO_3$ with an activity of about 3 microCurie was added. The precise determination of the added amount of activity was done by measuring directly with a scintillation counter an aliquot from a bottle, handled in the same way as the others. After

labeling, the bottles (54 altogether) were incubated for 3 hours at different lightintensities. After this period the total content of the bottles was filtered over 0.45 µ Sartorius membrane filters. The filters were rinsed with 0.001 N HCl and placed in scintillation-vials. Using 10 ml of Insta-Gel (Packard) the activity of the samples was counted by a scintillation counter (Isocap-Nuclear Chicago). The output on paper-tape is directly available as input for a computer.

2. The incubator (Fig. 1.)

The incubator (modified after Fee, 1973) was constructed by the workshop of our institute. It consists of eight compartments (E). In each of these compartments there is a disk (B) fixed on a central axis (A). With locking clips six bottles can be attached to the disk (Fig. 2). These bottles have a square cross section and are fixed in such a way that one side is perpendicular to the direction of the light source (F). During the incubation-time the bottles are turning around the central axis, so that for each compartment the bottles get the same light intensity. Another advantage is that sinking of the algae is prevented. The 8 compartments are separated by 2 perspex walls. In between neutral density filters can be placed to realize different ranges of light intensities.
Since the compartments are filled with water, it is possible to make a range of different temperatures as well. In this research we used only one temperature i.c. the prevailing temperature in the upper layer of the lake at the time of sampling. During summer stratification (see Kersting, this report) the samples from the 10.5 and 15.5 meter depth are incubated at too high a temperature and the production is overestimated. However, the low light intensities at these depths make a contribution to the total column production very small. Therefore, this error is neglected.

3. The lightsource

During the measurement of 1976 and 1977 we used a lightsource consisting of 11 fluorescent tubes (Truelite, Durotest daylight 20 TH 12 TXC). These lamps realized a spectrum comparable to the spectrum of sunlight (Fig. 3). The tubes were placed in a zigzag way at the front of the incubator (Fig. 1), in order to realize optimal illumination at the perspex front. Due to absorption by the cooling water and the perspex walls of the compartments a decrease of the light intensity occurred in such a way that the light regime was found as presented in Table 1. The light intensities were measured with a photosensor (Li-cor Quantum Radiometer type Li 185) mounted in a bottle, which was turning in the same way as the others around the central axis during the measurement. The intensities

given in Table 1 are mean values averaged over one complete cycle. In 1978 a new lightsource (Osram Metallogen Lamp HMI 2500 W) was mounted with a spectrum also comparable with that of natural light (Fig. 4). Much higher lightintensities could be realized however. For instance in compartment 8 a lightintensity of 500 $J.m^{-2}.sec^{-1}$ was possible.

4. Calculations

The photosynthetic saturation curves are used to calculate the potential productivity of the algae at a particular depth. Irradiation at the lake surface was measured continuously (Kipp Albedometer). Extinction coefficients determined with a Li-cor Quantum sensor were available (Table 3). Per ten minute interval the calculated irradiation at a particular depth is compared with the potential productivity of the algae at this depth. In this way integrated productions per hour are calculated for each depth sampled. Also the daily production in the water column is calculated. To make this procedure possible the assumptions to be made are listed below.

1. A linear interpolation is possible between the ^{14}C-accumulation in the dark and the assimilation at the lowest light intensity in the incubator.

2. A logarithmic interpolation is used at high intensities but smaller than the saturation value I_H.

3. If I_H is not realized in the incubator (which was mostly the case until the high intensity lightsource was available) a theoretical irradiation at P_{max} was chosen. A value of 55 $J.m^{-2}.sec^{-1}$ was used (Stadelmann et al., 1974). Fee (1973) used a value of $I_H = 110$ $J.m^{-2}.sec^{-1}$. Response curves based on these values are presented in Fig. 5.

4. According to Fee (1973) a quadratic decrease of the productivity must be assumed for light intensities surpassing I_H.
These considerations result in the expression:

$$P = P_{max} \left(1 - \frac{I - I_H}{348 - I_H}\right)^2$$

$$I_H < I < 348 \ J.m^{-2}.sec^{-1}$$

$$I > 348 \ J.m^{-2}.sec^{-1} : P = 0$$

With regard to the methods additional information is given below (see also Table 2).

a. The concentration of organic carbon was measured with a Beckman T.O.C. (Total Organic Carbon analyser) in ppm (parts per million).

b. We called "specific activity" the total ^{14}C-activity in microCuries added to 100 ml lake-water before incubation.

c. The irradiation data presented in Table 2 are integrator counts. 1 count = 600 $J.m^{-2}.sec^{-1}$. Conversion is done by the computer.

Chlorophyll concentrations were determined in the following manner:

After filtering a sample from a particular depth, the algae we extracted in acetone (1976) or alcohol (1977). The extinctions were measured with a spectrofotometer at 665 and 750 nm. The calculations of chlorophyll-a concentrations ($\mu g.l^{-1}$) were made using the simplified formula of Talling and Driver (1963)

$$\mu g \; chl.a. \; l^{-1} = 11.9 \times (E_{665} - E_{750}) \times \frac{V}{L} \times \frac{1}{M}$$

11.9 = a constant

V = amount of extraction solvent in ml

L = length of the lightpath in the cuvet (1 cm)

M = volume of the filtered sample in l.

Results and discussion

In Fig. 6 and 7 the estimated primary production on several days of the years 1976 and 1977 is presented. Comparing these productions with the chlorophyll data of the same days (Fig. 8 and 9) it is clear no estimations of the production on a particular day can be made based on chlorophyll-concentration. Dependence on the daily irradiation is clear. The total daily irradiation strongly fluctuates as can be seen in Fig. 6 and 7. With these monthly production measurements it is impossible to get the yearly primary production in an absolute sense. We only have the possibility to give the range of the daily productions throughout the year. From the mean of these daily productions a quantity can be derived to compare with data from the literature, concerning the trophic status of the lake. In Table 4 we have made a comparison with the classification as given by Wetzel (1975). Based on primary productivity and the parameters chlorophyll-a, phytoplankton concentration and carbon content of the algae, we can say that Lake Maarsseveen I has a trophic status in between the oligomesotrophic and

the mesotrophic one.

When integrated in a total research program, it is usefull to make an estimation of the production over the entire day. For instance, information on the daily production is essential to the study of the impact of zooplankton grazing on algae (Ringelberg, this report). We have to make a restriction concerning the absolute value of the estimation of the primary production over the day, determined with an incubator with low light intensities and the extrapolation method of Fee (1973).

Comparison of our results with simultaneous production measurements in Lake Vechten done according to the traditional in situ method by W. de Kloet (Limnological Institute, Nieuwersluis) give the impression that in the upper layers our estimations are too high. It is possible that the method of extrapolation to P_{max} is not correct and that too high P-values are read from the P vs I curve around P_{max}. When (and that is often the case) the light intensities in the upper layers fall in the range of light intensities around P_{max}, the calculation of the real primary production will be too high. As an example a response curve of a sample from Lake Maarsseveen I is given in Fig. 5. The dotted parts are the extrapolations to a P_{max} at I_H = 55 $J.m^{-2}.sec^{-1}$ (according to Stadelmann et $al.$, 1974) respectively at I_H = 110 $J.m^{-2}.sec^{-1}$ (according to Fee, 1973). In the same figure an example is given of a response curve for samples of Lake Vechten, determined with the high intensity incubator. The calculation of the primary production with the aid of this P vs I curve agrees with in situ measurements of W. de Kloet (unpublished data).

The chlorophyll distribution over the water column and throughout the year is presented in the Figs. 8 and 9. Until May a uniform vertical distribution can be observed. This is a result of the vertical mixing of the water layers until that month. The development of the thermocline gives rise to a high and irregular chlorophyll distribution in the epilimnion. In the hypolimnion a low though uniformly distributed content is present. In October and November the distributions point to the lowering respectively the disappearance of the thermocline (see Kersting, this report).

In Fig. 10 the incubator production of compartment 8 (I = 34.5 $J.m^{-2}.sec^{-1}$) per mg chlorophyll is given. The light intensity was at all measurements the same and differences in chlorophyll content are eliminated. Still there are differences in the production/chlorophyll ratios. Especially during summer and early autumn there are higher ratios in the hypolimnion. In Fig. 11 the mean of the production/chlorophyll ratio over the first 5.5 meter is given. This is done because of the idea that this layer is well mixed. In this figure one can see that the ratio fluctuates strongly during early spring and spring (1977) and that the

ratio is almost constant during summer and autumn (1977). During summer and autumn it is clear that the chlorophyll content is a principal steering factor for the carbon fixation. In spring there are probably other factors beside the chlorophyll content, that regulate the carbon fixation. These factors are unknown, but looking at the wax and wane of two species of diatoms in spring (see Dorgelo, this report) one of the factors can be the physiological status of the algae. Since one of the two major factors that influences the amounts of CO_2 in water is photosynthesis (the other is respiration) we give the results of the inorganic carbon concentrations as well (Fig. 12 and 13). In both figures it can be observed that during the temperature stratification in summer the utilization of CO_2 by photosynthesis in the epilimnion results in a decrease in the amount of inorganic carbon. In the hypolimnion an increase of the inorganic carbon by decomposition is visible.

References

FEE, E.J., 1973. A numerical model for determining integral primary production and its application to Lake Michigan. J.Fish.Res.Board Can., 30: 1447-1468.

FEE, E.J., 1973. Modelling primary production in water bodies, a numerical approach that allows vertical inhomogenities. J.Fish.Res.Board Can., 30: 1469-1473.

GAANDER, T. & G.G. GRAN, 1927. Investigations of the production of plankton in the Oslo Fjord. Rapp. et Proc.Verb.Cons.Int.Explor.Mer., 42: 1-48.

MOUS, I.J., 1976. Primaire produktie in de Grote Maarsseveense Plas van maart tot en met juni 1976. Doctoraal verslag.

RUARDIJ, P., 1975. De primaire produktie in de Grote Plas te Maarsseveen. Doctoraal verslag.

STADELMANN, P., J.E. MOORE & E. PICKETT, 1974. Primary production in relation to temperature structure, biomass concentration and light condition at an inshore and offshore station in Lake Ontario. J.Fish.Res.Board Can., 31: 1215-1232.

STEEMANN-NIELSEN, E., 1952. The use of radio-active carbon (C^{14}) for measuring organic production in the sea. J.Cons.int.Explor.Mer., 18: 117-140.

TALLING, J.F. & D. DRIVER, 1963. Some problems in the estimation of chlorophyll-a in phytoplankton. In: M.S. Doty (ed.): Proc.Conf.Primary Production Measurements, Marine and Freshwater, Univ. Hawaii, U.S. Atomic Energy Comm.Publ. TID-7633, p. 142-146.

WETZEL, R.G., 1975. Limnology, Saunders Company, 743 pp.

Table 1.

Place in incubator	$Joule.m^{-2}.sec^{-1}$	$\mu\ Einstein.m^{-2}.sec^{-1}$
comp. 1	0.4	8.8
comp. 2	1.95	12.7
comp. 3	2.8	19.3
comp. 4	5.2	29.3
comp. 5	7.7	47
comp. 6	12.4	85
comp. 7	18.25	143
comp. 8	34.8	193

Table 2. An example of the additional input for the computer, necessary for the estimation of the total daily primary production in a column of one square meter.

DATE ———————————————	1					
	150976					
INORGANIC CARBON (ppm) ————	33.33	33.33	33.33	33.33	45	44.17
SPECIFIC ACTIVITY (µCi) ——————	3.28					
INCUBATION TIME——————————	3					
	2					
	150976					
VERTICAL EXTINCTION COEFFICIENT ——	0.57					
	9999					
	3					
	150976					
	6					
	0	0	0	2	7	14
	21	28	35	43	48	56
	80	114	131	135	144	157
IRRADIATION PER 10 MINUTES ——	170	184	198	206	216	236
	252	268	283	272	301	320
	326	224	374	314	321	343
	363	408	413	426	372	273
	361	385	177	177	209	156
	77	59	61	103	116	102
	84	55	32	24	18	17
	16	9	13	25	40	25
	24	17	19	15	15	15
	8	4	3	2	1	0
	9999					
	5					
CHLOROPHYLL CONTENT ($\mu g.1^{-1}$)———	150976					
	2.87	2.85	2.92	3.06	1.29	0.93
	9999					
	9					

Table 3. Lake Maarsseveen I: Extinction coefficients and Secchi disk readings in 1979.

DATE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	SECCHI DEPTH
Feb 2	0.71		0.61									0.48									5
Feb 16	0.69											0.69									5
Mar 2	0.85											0.47									4.3
Mar 16	0.7											0.47									5
Mar 30												0.49									4.95
Apr 13		0.77										0.44									5.5
Apr 27	0.68											0.4									5.9
May 13	0.72											0.38									6.75
May 26												0.44									6.8
Jun 7			0.53	0.91								0.43									7.7
Jun 22	0.45											0.44									7.5
Jul 6			0.79									0.29									
Jul 20		0.63										0.44									3.9
Aug 17	0.64											0.51									4.7
Sep 14		0.69										0.41									6
Oct 13		0.59										0.42									4.85
Nov 9	0.6											0.41									

Table 4. Comparison of Lake Maarsseveen with general ranges of primary productivity of phytoplankton and related characteristics of lakes of different trophic categories (after Wetzel, 1975).

	Oligo-trophic	Oligo-mesotrophic	meso-trophic	Lake Maarsseveen
Mean primary productivity ($mg\ C.m^{-2}.day^{-1}$)	50-300		250-1000	250 (25-500)
Phytoplankton density ($cm^3.m^{-3}$)		1-3		1-8
Phytoplankton biomass ($mg\ C.m^{-3}$)	20-100		100-300	100-250
Chlorophyll a ($mg.m^{-3}$)	0.3-3		2-15	0.5-4

Fig. 1. The incubator. A. Central axis. B. Perspex disc. C. Perspex
wall. D. Compartment for neutral density filters. E. Incuba-
tion compartment. F. Light source.

Fig. 2. Perspex disc where upon 6 bottles can be fixed with a special
locking-clip for rotation in the incubator.

Fig. 3. Spectrum of the lightsource with low intensity (A) compared
with the spectrum of daylight (B).

Fig. 4. Spectrum of the lightsource with high intensity (a) compared
with the spectrum of daylight (b).

Fig. 5. Response curves of algae from a depth of 2.5 m. ✱ Maarsseveen 770427 (low intensity light source); ◯ Vechten 790425 (high intensity light source); ▲ P_{max} at I_H = 55 Joule.m^{-2}.sec^{-1} (after Stadelmann); ● P_{max} at I_H = 105 Joule.m^{-2}.sec^{-1} (after Fee).

Fig. 6. Primary production measurements.

Fig. 7. Primary production measurements.

Fig. 8. Depth-time distribution of chlorophyll a.

LAKE MAARSSEVEEN 1 1977

CHLOROPHYLL CONTENT

= 1 MG.M⁻³

DEPTH (M)

0.5—
1.5—
2.5—

5.5—

10.5—

15.5—

20.5—

FEB   MAR   APR   MAY   JUN   JUL   AUG   SEP   OCT   NOV

Fig. 9. Depth-time distribution of chlorophyll-a.

LAKE MAARSSEVEEN I   1977

INCUBATOR PRODUCTION PER UNIT OF

CHLOROPHYLL   (I ₌ 34.5 JOULE.M⁻².SEC⁻¹)

= MG CARBON/MG CHLOR.A

0.5—
1.5—
2.5—

5.5—

10.5—

15.5—

FEB   MAR   APR   MAY   JUN   JUL   AUG   SEP   OCT   NOV

Fig. 10. The carbon fixation per unit of chlorophyll-a of samples taken at
different depth and different times of the year. The productions
at a fixed irradiation of 34.5 J.m⁻².sec⁻¹ (incubator compartment
8) are given.

Fig. 11. Carbon fixation per unit chlorophyll a at a light intensity of 34.5 $J.m^{-2}.sec^{-1}$. The mean of the measurements of the first 5.5 meter are presented.

lake maarsseveen I - inorganic carbon (ppm) - 1976

Fig. 12. Depth-time diagram of isopleths of inorganic carbon.

lake maarsseveen I - inorganic carbon (ppm) - 1977

Fig. 13. Depth-time diagram of isopleths of inorganic carbon.

GRAZING IN LAKE MAARSSEVEEN

A.D. Hulsmann en P. van Rijswijk

The objective of the present study was to investigate whether the grazing by zooplankton is a major factor regulating the wax and wane of phytoplankton. Besides light, temperature and the availability of nutrients grazing might influence the composition of the phytoplankton quantitatively and qualitatively.

The relation phytoplankton-zooplankton was studied in the open-water zone of Lake Maarsseveen. The study was restricted to five dominant phytoplankton species: *Cryptomonas* c.f. *erosa* (Ehrenberg) [1]), *Cryptomonas* c.f. *ovata* (Ehrenberg) [1]), *Cyclotella comta* (Ehr. Kützing)/*Stephanodiscus astrea* (Ehr. Grun.), *Asterionella formosa* (Hassall), and *Fragilaria crotonensis* (Kitton).
The most important zooplankton species are: *Daphnia longispina* (Müller), *Bosmina coregoni* (Baird), *Eudiaptomus gracilis* (Sars) and some *Cyclops* species. Also rotifers are sometimes present in considerable numbers. The first three species are considered real herbivores. The feeding habits of most *Cyclops* species are not yet fully understood.

Methods

The results of seven series of observations performed from May 1978 to May 1979 are reported in this paper (Table 1).
A serie consists of a daytime and a nighttime measurement. The length of each period is determined by the time of sunset and sunrise and thus depends on the seasonal variation in daylength.
A standard procedure is used in all experiments.
One hour before sunset or sunrise water from the lake was collected. Using a Van Dorn sampler three liters were taken at depths of 1, 2, ... 10 m. This water was mixed and filtered through 150 μm gauze to remove the larger zooplankton species. Zooplankton was collected by taking several vertical hauls through the 10-0 m water column, using a 150 μm zooplanktonnet.

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[1]) It is not quite clear which *Cryptomonas* species occur in Lake Maarsseveen, but they look very much like *C. ovata* and *C. erosa*. The smaller one is not an earlier phase of *C. ovata*. In a pure culture of *C. ovata* never a cell that looks like *C. erosa* is found.

Until the start of the observation the zooplankton was stored in a dark and cold place. Nine 10 liter glass jars were filled with the filtered lake water. To three of them zooplankton was added in a concentration several times the natural one (Zoo I). To three jars twice this concentration was added (Zoo II). The exact concentration of zooplankton was determined at the end of the observation by counting the total numbers in the jars.

The ambient concentration of each zooplankton species in the lake was estimated by counting individuals in one vertical haul from 10-0 m with a 150 μm planktonnet.

To ensure a natural light and temperature regime the jars were transferred to the lake. The jars were placed in an iron framework fixed at a depth of five meters in the lake. To prevent settling of the algae the jars were rotated every three hours. At the start of each observation period three phytoplankton samples of 1 liter were taken from the mixed lake water (initial value). These samples were fixated with a Lugol's solution (JKJ). At the end of the experimental period three samples of 1 liter were withdrawn from each jar and fixated with Lugol's solution.

Cell numbers were counted using an inverted microscope. The zooplankton of each grazing chamber was fixated with formalin and counted.

Data from fifteen observations are given in Tables 2 (a/e) in terms of numbers of phytoplankton cells per liter, averaging the triplicate counts of each jar and averaging triplicate jars. Standard errors range from 9% to 16%.

Since 1979 the centric diatoms (*C. comta* and *S. astrea*) were counted as one group instead of counting *C. comta* seperately. When these two diatoms occur simultaneously it is impossible to make a distinction in routine countings of large numbers.

The zooplankton species were divided into two groups. In the first place species thought to be predominantly responsible for the grazing effect in the jars. In Table 4a these species, *D. longispina*, *B. coregoni* and *E. gracilis* are given as individuals per liter. They are also represented as percentages of this group. The ambient concentration in the lake is given in Table 4c.

The other group consists of species either too small or present in too low a concentration to have a measurable grazing effect. For instance, nauplius larvae and rotifers. Non-herbivorous species such as *Cyclops* also belong to this group. Their numbers per liter are given in Table 4b.

The distribution independent Mann-Whitney-U test was used to test whether or not

the differences in phytoplankton numbers are statistically significant (5% prob-
ability). Of interest are the differences between: initial value (1), final val-
ue in the controls (2), final value in the grazing jars Zoo I (3), and Zoo II
(4). The result of this statistical analysis is given in Table 3.

Effects of the population density

In order to realise differences in initial and final values large enough a treat
as a grazing effect, the natural zooplankton concentration had to be increased.
Concentrating the zooplankton may be detrimental to the feeding behaviour of the
animals. Two effects are possible; too many herbivorous zooplankters causes a
deficiency in food. This results in a decrease in grazing-rate. Another possi-
bility is what might be called a true crowding effect, for instance, a mutual
physical disturbance. The animals are inable to behave and to feed normally. Al-
so this results in a decrease in grazing-rate.

On the other hand, concentrating the zooplankton is not quite as artificial as
it appears to be. The zooplankters tend to occur in dense patches in the lake.
Measuring their numbers by taking a vertical net haul does not give information
about the actual densities. The densities in which the zooplankton occurs in
patches is many times the density, as calculated by dividing the numbers caught
by the sampled volume. Two different densities were used, the density in the
Zoo II jars being twice that of the Zoo I jars. The grazing rate per capita (per
herbivorous zooplankter) was calculated. If a density effect in the grazing jars
is present the grazing rate at the highest concentration is expected to be sig-
nificantly lower. Over one year of experiments we have noticed that there is no
or a negligible effect, when the population density (herbivorous and non-herbi-
vorous zooplankters) is lower than 700 animals per liter, and lower than 400
herbivorous animals per liter. In most cases a density effect in the Zoo II jars
was present. Therefore no conclusions were drawn from these observations. In one
Zoo I jar (780927) only,the critical concentration was surpassed.

Results

Cryptomonas erosa

In all experiments a marked decrease in C. erosa cells in the presence of
the zooplankton was found. Most diminuations, related to the initial values, are
statistically significant. The same holds for comparisons with the final values
in the control jars.

In nine out of fourteen cases there is a significant difference between the fi-
nal number of both zooplankton concentrations. This indicates that at least at

the low zooplankton concentration *Cryptomonas* was not depleted.

About half the final values of the control jars were lower than the initial values, two of them significantly. In this respect there seems to be no difference between day- and nightperiods.

Cryptomonas ovata

Most final values of the grazing chambers are significantly lower than the initial values. Also the difference between the final values of the blanks and the zooplankton jars is significant in most cases. In eight out of fourteen cases there is a significant difference between the final value of both zooplankton jars.

Control jars gave variable results showing a decrease or an increase in *C. ovata* cells, though only one out of fourteen in a significant way.

Asterionella formosa

The results suggest that no influence of the grazing zooplankton on the population of *A. formosa* is present. The cell counts do not show a particular decrease of this diatom in the grazing chambers.

Centric diatoms

Comparison of the final values of the grazing chambers with the initial cell numbers does not indicate a large grazing effect. However, in nine out of fourteen cases the final concentrations in the control jars show an increase in cell numbers. Also the final values of the grazing chambers were lower than those of the controls in twelve out of fourteen observations. Notwithstanding the fact that few differences are significant these results suggest a grazing effect on these diatoms.

Fragilaria crotonensis

This alga was not always present in detectable quantities in Lake Maarsseveen. If present no significant decrease in numbers as a result of grazing was apparent. On the contrary, in several cases an increase in cell numbers was found in the presence of zooplankton. In the low concentration zooplankton chamber seven out of nine final values were higher than the initial *Fragilaria* concentration. In the high concentration zooplankton jar seven out of ten cases show an increase in cell numbers. This suggests a beneficial activity of the zooplankton.

In the present study there is no evidence that cells of *A. formosa* and of *F. crotonensis* are ingested by zooplankton. However, an artificially increased

initial concentration of these diatoms in the grazing chambers might have pre-
vented the detection of a grazing effect. The large colonies of these algae
might have been concentrated when collecting the zooplankton. Together with the
animals these colonies might have been introduced into the grazing chambers.

Zooplankton

There was no large change in the zooplankton composition throughout the pe-
riod of observations. Apart from spring 1978 when they were exceptionally abun-
dant, *Bosmina coregoni* does not exceed 10% of the community of grazers. *Daphnia
longispina* tends to be the most abundant zooplankter (50-60%) together with *Eu-
diaptomus gracilis* (30-40%). In spring 1979 *E. gracilis* exceeded *D. longispina*
in terms of individuals per liter.

Hardly a difference between daytime and nighttime numbers in the catches was
present. Most of the zooplankton in Lake Maarsseveen is restricted to the upper
part of the water column. Taking a vertical haul from 10-0 m possible differ-
ences in vertical distribution are cancelled. In order to determine the concen-
tration at which a density effect would occur the amount of zooplankton added
to the jars was variated throughout the year. The community of grazers in the
Zoo I jars ranged from 7-100 times the concentration in the lake and in the Zoo
II jars from 15-214 times this concentration (Table 1).

The concentration in the lake was found by taking a vertical haul from 10-0 m.
As the vertical distribution over this ten meter is not homogenous and patches
might occur, local densities can be much higher. Hence the concentration in the
jars is less artificial.

Discussion

Cryptomonas erosa (Table 5 and Fig. 1a,b,c)

C. erosa was observed in Lake Maarsseveen throughout the whole year in den-
sities ranging from 1×10^5 - 4×10^5 cells per liter. Consistently being present
in high and relatively constant numbers makes *C. erosa* an important species in
Lake Maarsseveen.

The results as presented in Table 5 indicate that the cells were grazed both
during day- and nighttime. Calculating the grazing impact the effect of cell
division must be taken into account. However, the total increase Δa in the con-
trol jar overestimates the cell division in the grazing jar. Half this value was
supposed to be valid for the grazing chambers. So the actual grazing effect was

calculated as the sum of $\frac{1}{2}$ Δa and Δb being the difference between initial and final cell number of the grazing jar. In Fig. 1a the grazing impact expressed as the decrease in cells per grazer per hour is presented. The shaded bars represent the dark periods. Diurnal differences seem to exist, but no consistent pattern throughout the year was present.

The initial values of each dark- and lightperiod represent the actual concentration in the lake at sunset and sunrise. The difference between those values gives information about the changes in the lake during the first period of each observation. Two important processes determine the cell concentrations, grazing and cell division. A net increase in the lake means cell division dominates grazing. This is represented as a rising line in Fig. 1b. A net decrease means that grazing is dominant over cell division. In four out of six observations cell division dominated the grazing during the dark period.

The control jars often showed a decrease in cell numbers probably as a result of handling the phytoplankton. Another possibility is that the cells got attached to the walls of the jars. In most cases this decrease is less pronounced or absent during the dark period, a higher cell division probably compensated most of the losses (Fig. 1c).

The Figs. 1b and 1c show that similar tendencies were present in the lake and in the control jars. In periods that a high cell division can be concluded from the control jars, the concentration in the lake also showed an increase in cells of *C. erosa* (mostly during the nighttime). In periods the cell number decreased in the control jars also the lake concentration showed a net decrease indicating that grazing dominated cell division.

The following conclusions can be made from the presented data:

1. *C. erosa* was grazed by zooplankton, both during day- and nighttime.
2. Diel differences in grazing seem to be present. However, no systematic difference is apparent.
3. In most cases the activity of cell division was higher during the nighttime.
4. If cell division is high there is a net increase in cell numbers in the lake, cell division exceeding grazing. This occurs mostly during the nighttime. If cell division is low, cell numbers decrease in the lake. Grazing dominates cell division in this case.

Cryptomonas ovata (Table 6, Fig. 2a,b,c)

This large *Cryptomonas* species is present in Lake Maarsseveen throughout the whole year though less abundant than the smaller *Cryptomonas erosa*. Concentrations

range from 0.1×10^4 - 4×10^4 cells per liter. *C. ovata* is eaten both during day- and nighttime, as can be concluded from Table 6. Fig. 2a represents the grazing impact calculated as the sum of $\frac{1}{2}$ Δa and Δb. The estimated grazing effect is expressed as decrease in cell numbers per grazer per hour. The shaded bars represent the dark periods. As with *C. erosa* there were differences in day- and night-time grazing, but no consistent pattern throughout the year was apparent.

Fig. 2b represents the processes in the lake during the first period of each observation. In only two out of seven cases there is an increase in *C. ovata* cells during the nighttime in the lake. This suggests that in most cases grazing is dominant over cell division during the dark period.

As can be seen in Table 6 cell numbers decrease in the control jars during the nighttime in five out of seven cases. This decrease is less pronounced or absent during the daytime. This means that the division of *C. ovata* cells is maximal during the daytime.

From the Figs. 2b and 2c can be read that a close connection exists between the changes in the lake and the processes in the control jars. An increase in the jars coincides with a net increase in *C. ovata* cells in the lake. Therefore, cell division dominated grazing. In periods that cell division is less, grazing plays a more important role.

Four conclusions can be made with respect to *C. ovata*:

1. The alga was eaten by zooplankton, both during day- and nighttime.
2. No proof can be found for a consistent diel rhythm in the grazing rate.
3. Activity in cell division was probably higher during the daytime.
4. If cell division is maximal there is a net increase in cells in the lake (mostly during the daytime). If cell division is low, there is a net decrease in cells in the lake.

Centric diatoms (*Cyclotella comta* and *Stephanodiscus astrea*)
(Table 7 and Fig. 3a,b,c)

Occurring simultaneously it is hardly possible to distinguish *C. comta* from *S. astrea* in routine countings. In February, March and April a bloom of *S. astrea* was followed by an increase in *C. comta* numbers. The species was present untill September. In wintertime the population density was minimal.

Considering the large activity in cell division (Table 7) in the control jars it is difficult to interprete the processes in the grazing chambers. Grazing may be masked by cell division. In four cases cell numbers increased in the grazing jars.

Almost always the decrease in cell numbers in the grazing jars is maximal dur-
ing periods of a low activity in cell division. In Fig. 3a the estimated grazing
rate as decreases in cell numbers per grazer per hour is shown. Three experi-
ments only show a notable grazing rate (observation 1, 2 and 3). These results
do not justify the conclusion that a periodicity in grazing exists. During most
observation periods the grazing rate was more or less the same both the day-
and nighttime. There is no evidence for a diel periodicity in cell numbers in the
lake, the density at sunset alternately being higher and lower compared to the
one at sunrise.

In nine out of fourteen cases there is an increase of centric diatoms in the
blanks, these increases being higher in periods showing an increase of the con-
centration in the lake.

The following conclusions can be made with respect to the centric diatoms.

1. Small decreases only were found in the grazing chambers. However, the consis-
   tent increases of cells in the controls suggest that the centric diatoms were
   eaten by the zooplankton.
2. There is no evidence for a consistent periodicity in grazing rate.
3. There appears to be no diel rhythm in the cell division respectively grazing
   activity as can be concluded from the observations in the lake and from the
   experiments.
4. A period of high activity in cell division coincided with an increase of cen-
   tric diatom numbers in the lake, the cell division being dominant over grazing.
   If the activity in division was low, the grazing dominated the cell division.
   This resulted in a net decrease in the lake.

Asterionella formosa and *Fragilaria crotonensis*

These two diatoms were not always present in Lake Maarsseveen. As a matter
of fact they only occurred in detectable numbers during their relatively short
bloom periods. It is not clear what kind of a role these algae play in the zoo-
plankton feeding process. There rarely was a decrease in cell numbers in the graz-
ing jars. The changes in the blanks are very inconsistent and often did not agree
with the changes in the lake.

General discussion

The results indicate that herbivorous zooplankton in Lake Maarsseveen feeds
on *C. erosa*, *C. ovata* and the centric diatoms. Most observations show a signifi-

cant decrease in cell numbers using the Mann-Whitney-U test.

No significant changes could be found in the *Asterionella formosa* and *Fragilaria crotonensis* populations. With regard to these diatoms it is necessary to make some additional notes.

1. No observations have been performed during a bloom of *A. formosa*, only at the end of a bloom period.

2. The method used may have a marked influence on the calculated grazing on the diatom species *A. formosa* and *F. crotonensis*.

Considering the experimental results and the observations in the lake, it is plausible that there exists a periodicity in cell division as far as the *Cryptomonas* species are concerned. This periodicity is less pronounced or absent in the centric diatoms. The centric diatoms alternately show a maximal activity during the daytime and the nighttime. *C. erosa* has a maximal cell division during the nighttime and *C. ovata* during the daytime. In periods of a maximal cell division grazing plays an inferior role. This results in a net increase in cell numbers. In periods with a less pronounced cell division, grazing is relatively of more importance (though the actual grazing may be the same or even less). This results in a net decrease in cell numbers in the lake.

Grazing rates calculated in terms of a difference between the initial value and the final value in the grazing chambers, often result in an underestimation of the grazing rates. This is especially the case in periods of a maximal cell division. On the other hand calculating grazing rates as the difference between the final value in the grazing chambers and the final value in the control jars results in an overrating. The observations often point to a difference in day- and nighttime grazing. A consistent diel rhythm can not be found. However, our results do not exclude the possibility of a more or less constant grazing rate. In that case, the diel differences must be ascribed to the rhythms in cell division. This last process was hard to quantify. In any case the relative importance of grazing over cell division is subject to diel changes. It is this balance that is of interest in the wax and wane of the phytoplankton.

The grazing by zooplankton seems to be limited to the smaller phytoplankton fraction (cells not retained when filtered through 30 μm gauze). The primary production of these algae is significantly higher than the primary production of the larger fraction (Ringelberg, this report).

The filtering rate (the volume of ambient medium containing the number of cells eaten in a given time) of the herbivorous zooplankton in the lake can be calculated using Gauld's formula:

$$F_1 = \frac{\ln N_1 - \ln N_3 \cdot V}{G \cdot t} \times 1000$$

$$F_2 = \frac{\ln N_2 - \ln N_3 \cdot V}{G \cdot t} \times 1000$$

F $=$ filtering rate in $ml.grazer^{-1}.hour^{-1}$

N_1 $=$ initial value in cells per liter

N_2 $=$ final value in the control jars in cells per liter

N_3 $=$ final value in the grazing chambers in cells per liter

G $=$ number of grazing zooplankters per jar

t $=$ grazing time

V $=$ volume of the jar in liters

Table 8 shows the filtering rates calculated for the three algae that are apparently eaten by the zooplankton. Filtering rates are expressed in ml per grazer per hour. Two filtering rates are calculated a) using the initial values in the jars (F_1) and b) correcting for the processes in the blank (F_2). The filtering rates for *C. erosa* (mean value 0.54 $ml.G^{-1}.hr^{-1}$) and for *C. ovata* (mean value 0.57 $ml.G^{-1}.hr^{-1}$) are quite similar in most observations. The filtering rates for the centric diatoms are significantly lower (mean value 0.17 $ml.G.^{-1}hr^{-1}$). This indicates that the *Cryptomonas* species are being ingested in the same ratio as they occur in the lake. No selection for the one or the other is present. The filtering rate based on the ingestion of the centric diatoms is lower. This could be the result of selection. This selection can occur during the filtering process or a "selection" inside the body can occur. It is possible not all ingested centric diatoms are being digested and some will come out sufficiently unchanged to be counted as such. Often animals were seen with complete centric diatoms at the end of the digestive tract. However, the apparently lower grazing activity on centric diatoms may also result from the method used. If some centric diatoms have sunk to the bottom of the jar within three hours (interval at which the jars are rotated), they are not available as food. A higher sinking rate can be the result of a heavier cell and the fact that the centric diatoms are immobile where the Cryptomonads are mobile.

The herbivorous zooplankton in Lake Maarsseveen appears to feed predominantly on algae that are present throughout almost the whole year. These algae have

the capacity to compensate the losses due to zooplankton grazing by means of a very high reproduction rate.

The filtering rates for *C. erosa* and *C. ovata* are rather constant throughout the year. The filtering rate does not change with the actual concentrations of algae in the lake. This indicates that the percentage eaten is independent of the quantity of food available. Therefore, the zooplankters filter maximally. A maximal filtering rate is assumed to occur when the food concentration falls below a critical value, the incipient limiting level. Above this level the filtering rate declines and the feeding rate becomes constant. The data suggest that the herbivorous zooplankton has to filter maximally in order to obtain enough food for growth and maintenance. It may even be necessary to filter continuously to satisfy their needs. Since the lake is of a rather mesotrophic nature, a maximal filtering rate is to be expected. For this reason it might not be plausible to expect a diel grazing activity in this lake.

Acknowledgments

Table 1. Survey of observations.

date	length of the light period (hr)	length of the dark period (hr)		concentration factor Zoo I	Zoo II
780516	16	8	D	7	18
780517			L	14	30
			D	20	25
780802	15	9	L	35	123
780802			D	65	172
780913	12	12	D	13	28
780914			L	31	48
780927	12	12	D	54	99
780928			L	8	15
781010	11	13	D	61	77
781011			L	37	54
781025	10	14	D		100
781026			L	96	214
790417	14	10	D	26	32
790418			L	52	81

D: observation during the dark period.

L: observation during the light period.

Table 2a. Number of cells per liter of the dominant species at the beginning and at the end of the observation periods.

Cryptomonas erosa

date		initial (1)	control (2)	Zoo I (3)	Zoo II (4)
780516	D	1.88×10^5	1.50×10^5	0.03×10^5	0.08×10^5
780517	L	2.72 "	0.32 "	0.14 "	0.10 "
780517	D	-	1.84 "	1.00 "	0.31 "
780802	L	1.73 "	0.99 "	0.16 "	0.02 "
780802	D	1.11 "	1.05 "	0.15 "	0.09 "
780913	D	2.87 "	3.41 "	1.57 "	0.84 "
780914	L	4.13 "	2.29 "	0.69 "	0.23 "
780927	D	1.94 "	1.94 "	1.42 "	1.38 "
780928	L	2.60 "	2.44 "	1.42 "	0.21 "
781010	D	1.94 "	1.59 "	0.43 "	0.17 "
781011	L	1.45 "	0.77 "	0.20 "	0.14 "
781025	D	2.18 "	2.44 "	-	0.46 "
781026	L	2.40 "	2.55 "	0.72 "	0.34 "
790417	D	2.29 "	1.85 "	1.30 "	0.77 "
790418	L	1.74 "	2.40 "	1.56 "	0.88 "

- not counted

Table 2b.

Cryptomonas ovata

date		initial (1)	control (2)	Zoo I (3)	Zoo II (4)
780516	D	0.79×10^4	0.62×10^4	0.46×10^4	0.44×10^4
780517	L	0.58 "	0.87 "	0.19 "	0.39 "
780517	D	-	0.81 "	0.73 "	0.27 "
780802	L	0.71 "	0.70 "	0.08 "	0.01 "
780802	D	1.10 "	0.76 "	0.03 "	0.07 "
780913	D	1.68 "	1.72 "	0.50 "	0.19 "
780914	L	1.85 "	1.45 "	0.51 "	0.18 "
780927	D	1.74 "	1.67 "	1.24 "	0.99 "
780928	L	1.68 "	1.63 "	1.12 "	0.41 "
781010	D	2.84 "	2.52 "	1.02 "	0.17 "
781011	L	2.00 "	1.76 "	0.21 "	0.12 "
781025	D	2.58 "	2.88 "	-	0.29 "
781026	L	4.30 "	4.51 "	1.17 "	0.12 "
790417	D	0.15 "	0.11 "	0.10 "	0.06 "
790418	L	0.04 "	0.10 "	0.05 "	0.03 "

Table 2c. Number of cells per liter of the dominant species at the beginning and at the end of the observation period.

Centric diatoms

date		initial (1)	control (2)	Zoo I (3)	Zoo II (4)
780516	D	1.16×10^4	0.96×10^4	0.70×10^4	1.18×10^4
780517	L	0.27 "	0.78 "	0.73 "	0.92 "
780517	D	-	1.81 "	1.86 "	0.92 "
780802	L	1.12 "	1.67 "	0.99 "	0.51 "
780802	D	1.30 "	1.17 "	0.72 "	1.09 "
780913	D	0.20 "	0.21 "	0.10 "	0.09 "
780914	L	0.21 "	0.20 "	0.15 "	0.11 "
780927	D	0.25 "	0.40 "	0.28 "	0.24 "
780928	L	0.30 "	0.26 "	0.21 "	0.19 "
781010	D	0.19 "	0.24 "	0.13 "	0.19 "
781011	L	0.16 "	0.28 "	0.22 "	0.21 "
781025	D	0.32 "	0.44 "	-	0.34 "
781026	L	0.42 "	0.44 "	0.42 "	0.35 "
790417	D	0.47 "	0.62 "	0.54 "	0.59 "
790418	L	0.59 "	0.55 "	0.52 "	0.49 "

- not counted

Table 2d.

Asterionella formosa

date		initial (1)	control (2)	Zoo I (3)	Zoo II (4)
780516	D	0.88×10^6	1.10×10^6	1.03×10^6	1.04×10^6
780517	L	1.22 "	1.35 "	1.10 "	0.95 "
780517	L	-	1.24 "	0.90 "	0.70 "
780802	L	0.04 "	0.01 "	0.01 "	0.01 "
780802	D	0.05 "	0.02 "	0.02 "	0.04 "
780913	D	0.007 "	0.005 "	0.003 "	0.002 "
780914	L	0.004 "	0.004 "	0.003 "	0.004 "
780927	D	0.015 "	0.012 "	0.016 "	0.013 "
780928	L	0.013 "	0.012 "	0.014 "	0.012 "
781010	D	0.16 "	0.22 "	0.22 "	0.20 "
781011	L	0.26 "	0.22 "	0.19 "	0.18 "
781025	D	0.000 "	0.001 "	-	0.000 "
781026	L	0.000 "	0.003 "	0.000 "	0.005 "
790417	D	0.011 "	0.012 "	0.026 "	0.015 "
790418	L	0.008 "	0.045 "	0.009 "	0.025 "

Table 2e. Number of cells per liter of the dominant species at the beginning and at the end of the observation period.

Fragilaria crotonensis

date		initial (1)		control (2)		Zoo I (3)		Zoo II (4)	
780516	D	0.78 x 10^5		1.03 x 10^5		0.81 x 10^5		1.28 x 10^5	
780517	L	0.64	"	0.74	"	1.59	"	1.17	"
780517	D	–		0.59	"	0.58	"	0.55	"
780802	L	x		x		x		x	
780802	D	x		x		x		x	
780913	D	x		x		x		x	
780914	L	x		x		x		x	
780927	D	0.18	"	0.09	"	0.14	"	0.13	"
780928	L	0.22	"	0.09	"	0.10	"	0.18	"
781010	D	1.12	"	0.90	"	2.57	"	2.74	"
781011	L	1.68	"	1.10	"	2.84	"	2.72	"
781025	D	1.96	"	1.30	"	–		7.87	"
781026	L	1.85	"	1.55	"	3.08	"	1.48	"
790417	D	0.00	"	0.00	"	0.01	"	0.03	"
790418	L	0.00	"	0.03	"	0.06	"	0.17	"

– not counted

x not present in detectable numbers

Table 3. The differences in phytoplankton numbers between the initial values (1) and the final values in the blanks (2) and in the grazing chambers Zoo I (3) and Zoo II (4) are statistically tested using the Mann-Whitney-U test.

date		*Cryptomonas erosa*						*Cryptomonas ovata*					
		1-2	1-3	1-4	2-3	2-4	3-4	1-2	1-3	1-4	2-3	2-4	3-4
780516	D	0	-	-	-	-	0	0	0	0	0	0	0
780517	L	-	0	-	0	-	0	0	0	0	-	0	0
780517	D	0	-	-	-	-	-	0	0	0	0	0	0
780802	L	0	-	-	-	-	-	0	-	-	-	-	0
780802	D	0	-	-	-	-	0	0	-	-	-	-	0
780913	D	0	-	-	-	-	-	0	-	-	-	-	-
780914	L	-	-	-	-	-	-	-	-	-	-	-	-
780927	D	0	0	0	-	-	0	0	-	-	-	-	0
780928	L	0	-	-	-	-	-	0	-	-	-	-	-
781010	D	0	-	-	-	-	-	0	-	-	-	-	-
781011	L	0	-	-	-	-	0	0	-	-	-	-	-
781025	D						-						-
781026	L	0	-	-	-	-	-	0	-	-	-	-	-
790417	D	0	-	-	0	-	-	0	0	0	0	0	-
790418	L	0	0	0	-	-	-	0	0	0	-	-	-

date		*Asterionella formosa*						Centric diatoms					
		1-2	1-3	1-4	2-3	2-4	3-4	1-2	1-3	1-4	2-3	2-4	3-4
780516	D	0	0	0	0	0	0	0	-	0	0	0	+
780517	L	0	0	0	0	0	0	0	0	0	0	0	0
780517	D	0	0	-	0	-	0	0	0	0	0	0	-
780802	L	-	-	-	0	0	0	+	0	-	-	-	-
780802	D	0	0	0	0	+	0	0	-	0	0	0	+
780913	D	0	0	-	0	-	0	0	-	-	-	-	0
780914	L	0	0	0	0	0	0	0	0	-	0	-	0
780927	D	0	0	0	0	0	0	+	0	0	0	-	0
780928	L	0	0	0	0	0	0	0	0	0	0	0	0
781010	D	0	0	0	0	0	0	0	0	0	-	0	0
781011	L	0	0	0	0	0	0	+	0	0	0	-	0
781025	D					0						0	
781026	L	0	0	0	-	0	+	0	0	0	0	0	0
790417	D	0	0	0	0	0	0	0	0	0	0	0	0
790418	L	0	0	0	0	0	0	0	0	0	0	0	0

Table 3. (Continued)

Fragilaria crotonensis

date		1-2	1-3	1-4	2-3	2-4	3-4
780516	D	0	0	0	0	0	0
780517	L	0	0	0	0	+	0
780517	D	0	0	0	0	0	0
780928	L	0	0	0	0	0	0
781010	D	0	0	+	+	+	0
781011	L	0	0	0	+	+	0
781025	D					+	
781026	L	0	0	0	0	0	0
790417	D	0	0	0	0	0	0
790418	L	0	0	0	0	+	+

Legenda: 0 difference not statistically significant
+ a significant increase
- a significant decrease
D dark period
L light period

Table 4a. 'Herbivorous' zooplankton in the jars (numbers per liter).

		Zoo I			Zoo II		
date		*Bosmina*	*Daphnia*	*Eudiaptomus*	*Bosmina*	*Daphnia*	*Eudiaptomus*
780516	D	12 (17.6)[1]	25 (36.8)[1]	31 (45.6)[1]	57 (31.8)[1]	63 (35.2)[1]	59 (33.0)[1]
780517	L	53 (36.6)	57 (39.3)	35 (24.1)	94 (38.5)	91 (37.3)	59 (24.2)
780517	D	81 (38.8)	98 (46.9)	30 (14.3)	45 (47.7)	110 (36.2)	49 (16.1)
780802	L	16 (9.2)	84 (48.3)	74 (42.5)	57 (9.4)	341 (56.2)	209 (34.4)
780802	D	30 (9.4)	204 (64.2)	84 (26.4)	67 (7.9)	502 (59.4)	276 (32.7)
780913	D	6 (4.4)	70 (51.9)	135 (48.4)	13 (4.6)	59 (43.7)	131 (47.0)
780914	L	20 (6.5)	197 (63.5)	93 (30.0)	18 (3.8)	299 (62.9)	168 (35.3)
780927	D	8 (1.3)	368 (60.3)	234 (38.4)	24 (2.1)	605 (54.3)	486 (43.6)
780928	L	5 (5.3)	62 (66.0)	27 (28.7)	6 (3.5)	101 (59.4)	63 (37.1)
781010	D	6 (1.9)	188 (60.8)	115 (37.3)	8 (2.4)	216 (64.7)	111 (32.9)
781011	L	7 (3.8)	120 (64.5)	59 (31.7)	10 (3.7)	162 (59.5)	100 (36.8)
781025	D	12 (5.4)	79 (35.4)	132 (59.2)	14 (3.0)	199 (42.8)	252 (54.2)
781026	L	14 (6.5)	95 (44.4)	105 (49.1)	39 (8.2)	200 (42.0)	237 (49.8)
790417	D	10 (12.0)	17 (20.5)	56 (67.5)	15 (8.6)	12 (6.9)	147 (84.5)
790418	L	12 (9.3)	42 (32.6)	75 (58.1)	19 (7.9)	62 (25.7)	160 (68.4)

[1]) in parentheses percentages of the total herbivorous community in the jar

Table 4b. Rest group zooplankton in the jars (numbers per liter).

		Zoo I				Zoo II			
date		*Cyclops* spp.	*Cono- chilus*	Nombre Naupliën	*Kelli- cottia*	*Cyclops* spp.	*Cono- chilus*	Naupliën	*Kelli- cottia*
780516	D	31	62	15	19	92	499	34	47
780517	L	41	185	17	34	82	30	21	39
780517	D	56	813	22	21	73	477	23	28
780802	L	131	12	16	34	359	11	44	174
780802	D	174	1	8	25	460	6	51	102
780913	D	160	0	9	18	406	0	21	49
780914	L	138	0	4	9	228	0	8	18
780927	D	582	0	11	6	1183	0	16	13
780928	L	37	0	0	1	75	0	1	2
781010	D	141	0	8	0	131	0	6	0
781011	L	78	0	1	0	129	0	2	0
781025	D	107	0	21	18	202	0	34	38
781026	L	96	0	10	9	210	0	36	36
790417	D	74	119	27	0	122	163	40	0
790418	L	70	137	20	0	134	247	27	0

Table 4c. 'Herbivorous' zooplankton in the lake (numbers per liter).

date	*Bosmina*	*Daphnia*	*Eudiaptomus*
780516	3.00	5.50	1.50
780802	0.18	3.40	1.34
780913	0.32	6.00	3.80
780927	0.30	4.35	6.75
781010	0.12	3.09	1.92
781025	0.12	1.12	0.98
790417	0.42	0.38	4.68

Table 5. *Cryptomonas erosa*. Changes in cell number per liter per hour (control jars) respectively in cell number per grazer per hour (Zoo I and Zoo II jars).

date		initial values	control 2-1	Zoo I 3-1	3-2	Zoo II 4-1	4-2
780516	D	1.88 x 10^5	- 4750	- 340	- 270	- 126	- 99
780517	L	2.72 "	- 15000	- 111	- 8	- 67	- 6
780802	L	1.73 "	- 4930	- 60	- 32	- 19	- 11
780802	D	1.11 "	- 670	- 33	- 31	- 13	- 13
780913	D	2.87 "	+ 4500	- 80	- 113	- 61	- 77
780914	L	4.13 "	- 15330	- 92	- 43	- 67	- 35
780927	D	1.94 "	0	- 7	- 7	- 4	- 4
780928	L	2.60 "	- 1330	- 105	- 90	- 117	- 109
781010	D	1.94 "	- 2690	- 38	- 29	- 41	- 33
781011	L	1.45 "	- 6180	- 61	- 28	- 44	- 21
781025	D	2.18 "	+ 1860			- 26	- 30
781026	L	2.40 "	+ 1500	- 78	- 85	- 43	- 46
790417	D	2.29 "	- 4400	- 119	- 66	- 87	- 62
790418	L	1.74 "	+ 5280	- 10	- 46	- 25	- 45

Table 6. *Cryptomonas ovata*. Changes in cell number per liter per hour (control jars) respectively in cell number per grazer per hour (Zoo I and Zoo II jars).

date		initial values	control 2-1	Zoo I 3-1	3-2	Zoo II 4-1	4-2
780516	D	0.79 x 10^4	- 212	- 6	- 3	- 2	- 1
780517	L	0.58 "	+ 181	- 2	- 3	- 1	- 1
780802	L	0.71 "	- 67	- 2	- 2	- 1	- 1
780802	D	1.10 "	- 378	- 4	- 2	- 1	- 1
780913	D	1.68 "	+ 33	- 7	- 7	- 4	- 5
780914	L	1.85 "	- 333	- 4	- 2	- 3	- 2
780927	D	1.74 "	- 58	- 1	- 1	- 1	- 1
780928	L	1.68 "	- 42	- 5	- 4	- 6	- 6
781010	D	2.84 "	- 246	- 4	- 4	- 6	- 5
781011	L	2.00 "	- 218	- 9	- 7	- 6	- 5
781025	D	2.58 "	+ 214	-	-	- 3	- 4
781026	L	4.30 "	+ 210	-15	-16	- 9	- 9
790417	D	0.15 "	- 40	- 1	- 0.1	- 1	- 0.3
790418	L	0.04 "	+ 7	0	- 0.3	0	- 0.2

Table 7. Centric diatoms. Changes in cell number per liter per hour (control jars) respectively in cell number per grazer per hour (Zoo I and Zoo II jars).

date		initial values	control 2-1	Zoo I 3-1	3-2	Zoo II 4-1	4-2
780516	D	1.16×10^4	− 250	− 8	− 5	+ 0.1	+ 1
780517	L	0.27 "	+ 318	+ 2	− 0.2	+ 2	+ 0.4
780802	L	1.12 "	+ 367	− 0.5	− 3	− 0.7	− 1.3
780802	D	1.30 "	− 144	− 2	− 2	− 0.3	− 0.1
780913	D	0.20 "	+ 8	− 0.6	− 3	− 0.3	− 0.4
780914	L	0.21 "	− 8	− 0.2	− 0.1	− 0.2	− 0.1
780927	D	0.25 "	+ 125	+ 0.04	− 0.2	0	− 0.1
780928	L	0.30 "	− 33	− 0.8	− 0.4	− 0.5	− 0.3
781010	D	0.19 "	+ 38	− 0.1	− 0.3	0	− 0.1
781011	L	0.16 "	+ 109	+ 0.3	− 0.3	+ 0.2	− 0.2
781025	D	0.32 "	+ 86			+ 0.03	− 0.1
781026	L	0.42 "	+ 20	0	− 0.1	− 0.1	− 0.2
790417	D	0.47 "	+ 150	+ 0.8	− 1	+ 0.7	− 0.2
790418	L	0.59 "	− 29	− 0.4	− 0.2	− 0.3	− 0.2

1. initial value
2. final value control jar
3. final value Zoo I jar
4. final value Zoo II jar
D = dark period SS-SR
L = light period SR-SS

Table 8. Filtering rates in Lake Maarsseveen ($ml.grazer^{-1}.hr^{-1}$).

date		*C. erosa*		*C. ovata*		centric diatoms	
		F_1	F_2	F_1	F_2	F_1	F_2
780516	D	7.61	7.19	0.99	0.55	0.93	0.58
780517	L	1.28	0.36	0.48	0.65	-0.43	0.03
780802	L	0.91	0.69	0.84	0.83	0.05	0.20
780802	D	0.69	0.68	1.26	1.13	0.21	0.17
780913	D	0.23	0.30	0.48	0.49	0.27	0.29
780914	L	0.48	0.32	0.35	0.28	0.09	0.08
780927	D	0.04	0.04	0.05	0.04	-0.01	0.05
780928	L	0.53	0.49	0.36	0.33	0.32	0.19
781010	D	0.38	0.33	0.25	0.22	0.09	0.15
781011	L	0.97	0.66	1.10	1.04	-0.16	0.12
781025	D	-	-	-	-	-	-
781026	L	0.56	0.59	0.61	0.63	0.00	0.02
790417	D	0.67	0.42	0.49	0.11	-0.17	0.17
790418	L	0.06	0.24	-0.12	0.38	0.07	0.03

| $\bar{F}$ | | $0.54\ ml.G^{-1}.hr^{-1}$ | | $0.57\ ml.G^{-1}.hr^{-1}$ | | $0.17\ ml.G^{-1}.hr^{-1}$ | |

| mean F excluding: | | observations 780516 and 780927 | | observation 780927 | | observation 780927 | |

Fig. 1A. Grazing impact ($\frac{1}{2}\Delta A$ + ΔB) expressed as the decrease in *Cryptomonas erosa* cells per grazer per hour. Shaded bars represent the dark periods.

CRYPTOMONAS EROSA

changes in cells l^{-1}

in situ

Fig. 1B. Changes in the actual concentration of *C. erosa* cells in Lake Maars-
seveen during the first period of each experiment. Changes in cells.l^{-1}.
d = dark period
l = light period

C. EROSA

changes in cells l^{-1}

CONTROLS

exp. 1   2   3   4   5   6   7

Fig. 1C. Changes in *C. erosa* cells in the control jars. Changes in cells.l^{-1}.
d = dark period
l = light period

Fig. 2A. Grazing impact ($\frac{1}{2}\Delta A + \Delta B$) expressed as the decrease in *Cryptomonas ovata* cells per grazer per hour. Shaded bars represent the dark periods.

Fig. 2B. Changes in the actual concentration of *C. ovata* cells in Lake Maars-
seveen during the first period of each experiment.
Changes in cells.1^{-1}.
d = dark period
l = light period

Fig. 2C. Changes in *C. ovata* cells in the control jars. Changes in cells.1^{-1}.
d = dark period
l = light period

Fig. 3A. Grazing impact ($\frac{1}{2}\Delta A + \Delta B$) expressed as the decrease in centric diatom cells per grazer per hour. Shaded bars represent the dark periods.

CENTRIC DIATOMS

changes in cells l^{-1}

in situ

Fig. 3B. Changes in the actual concentration of centric diatoms in Lake Maarsseveen during the first period of each experiment. Changes in cells.l^{-1}.
d = dark period
l = light period

CENTRIC DIATOMS

changes in cells l^{-1}

CONTROLS

exp.   1   2   3   4   5   6   7

Fig. 3C. Changes in centric diatoms in the control jars. Changes in cells.l^{-1}.
d = dark period
l = light period

TWO DIEL STUDIES OF A WATER COLUMN IN LAKE MAARSSEVEEN

J. Ringelberg

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4. Discussion

5. Literature

1. Introduction

Our present research in the open-water column is based on the following considerations. It is thought necessary to measure parameters of the phytoplankton and zooplankton community simultaneously. For instance, to make possible an optimal comparison of primary production and grazing, estimates of both processes have to be made at the same place and time. A scenario is needed to fix the times and depths of sampling and measuring.

A second starting-point is the preference to employ more than one method in measuring a certain phenomenon. The uniqueness of the research situation in the field is a drawback to ecological progress. Circumstances might differ within days or even hours. Another source of variation in field data results from the rather crude methods employed and the unfavourable working conditions. These factors make an evaluation and interpretation of ecological field data difficult. The simultaneous application of methodological different measurements contributes to an interpretation of data.

In the third place the 24 hours period is thought to be a basic ecological unit of time. It is important to compare the ecosystem's phases of anabolism and catabolism. Also, the cycle of changing radiation intensities steers circadian processes.

During a research season the effort of a university group (with many other duties to do as well) can be focussed a few times only. The most crucial periods in the development of the ecosystem must be chosen. The research was aimed at periods of large changes in the phytoplankton community. Whether large changes could be expected or not, had to be extrapolated from the weekly routine sampling and the picture of wax and wane in previous years. In 1978 only two so-called "crucial research programs" were realised. Several research workers from other laboratories participated: Dr. R.D. Gulati, Limnological Institute Nieuwersluis; Dr. J. Vosjan, Netherlands Institute for Sea Research; Drs. A.D. Brinkman, Technical University Twente; Ir. K.D. Maiwald, Waterloopkundig Laboratorium, Wageningen. They are thanked sincerely. The central group consisted of J. Dorgelo, B. Flik, A. Keijser, R. Lingeman, K. Kersting (Research Institute for Nature Management), A. Hulsmann, P. van Rijswijk and J. Ringelberg, assisted by D. de

Zwart, J. Peters, Y. Ligtermoet, I. Beenders, I. de Graaf Bierbrauwer.

2. Crucial Research Period 1978-1.

Of the three days of research (May, 16-17-18, 1978) the data of only one day
are discussed here. In some instances data from the other days had to be used to
fill in gaps. The 24 hours were divided into a daytime period ranging from sunrise
to sunset and a nighttime one from sunset to sunrise again. The water column was
divided into an upper and a lower ten meter part. Until April the water of the
lake is well mixed but in May the development of a thermocline starts. In summer
this thermocline is found between 8-13 meter (see Kersting,this report). The col-
umn parts were supposed to be mixed. In most cases water taken at one meter inter-
val was mixed to compose a sample representive for the depth range. Data from
the upper ten meter column are presented here only.

2.1 Phytoplankton species abundance.

Population density of six most abundant phytoplankton species is given in
Fig. 1. For a more extensive overview throughout the year see Dorgelo, this report.
Although still the most abundant ones, the species *Asterionella formosa* and *Dino-
bryon divergens* rapidly declined. The other species have constant population sizes.
With the exception of *A. formosa* and *D. divergens* no difference in numbers were
found between the upper and lower column parts. For the species mentioned a some-
what lower concentration was found in the 10-20 meter column.

A more detailed distribution of the particle volume over the upper 10 meter
column is presented in Fig. 2. Samples, taken with a Van Dorn water sampler, were
filtered over 30 μm gauze and fixated with formaline. The total particle volume
was counted with a Coulter Counter. With regard to particle volume inhomogeneity
of the upper water layer is small.

It was thought justified to regard the upper ten meter column well mixed for
phytoplankton.

2.2 The Carbon Content.

The carbon concentration was determined with a Beckmann Carbon Analyser. From
samples filtered over 150 μm gauze two fractions were estimated: Total Carbon
(T.C.) and Dissolved Inorganic Carbon (D.I.C.). Subtracting the latter from the
first gives the amount of Dissolved Organic Carbon (D.O.C.). To determine par-
ticle carbon (P.O.C.) the analyser is not sensitive enough. Therefore,a liter
lake water prefiltered over 150 μm, resp. 30 μm gauze, was filtered over a 0.45

µm glass fiber filter. To resuspend the particles in 10 ml filtered water an ultrasonic fibrator was used. In this way it was thought to get a 100 fold increase in particle concentration. This method was found to be rather inaccurate and abandoned in later research. Nevertheless it is worthwhile to have a look at table 1. By subtraction P.O.C. > 30 - < 150 µm was calculated. Some remarks are:

1. Dissolved Organic Carbon seems to increase during the period of observation. Compare the sunrise concentrations: 10.3 → 14.2 → 16.4 (upper 10 meter) or 9.0 → 13.3 → 13.8 (lower 10 meter).

2. D.O.C. concentration is slightly higher in the upper ten meter.

3. Since *Asterionella* and *Dinobryon* decreased during this crucial period one would expect the P.O.C. fractions to diminish. This is not obvious from the figures.

4. The concentration of the small fraction is the same in both parts of the column. It is not known whether the nature of small particles is the same in both parts. Large particle organic carbon seems to be absent in the 10-20 m column.

5. The proportion between D.O.C. and P.O.C. is very high in the lake at this time. This might be due to an underestimation of P.O.C., however. Some cells might have been damaged by the procedure of concentration. The D.O.C. was determined from untreated samples.

6. The carbon content of the < 30 µm fraction averaged twice the content of the large fraction in the upper column part. Due to large errors the absolute proportion of both fractions in the 10-20 meter column has no meaning.

The carbon content of the phytomass was also calculated from the cell volumes of the different species (measurements P. van Rijswijk). The following relations (from Strathmann 1967) were used:

Asterionella formosa (volume 1076 μ^3)
$\log C = 0.758 \log V - 0.422 = 1.876 \rightarrow C = 75 \times 10^{-9}$ mg C per cell

Cyclotella comta (V = 4083 μ^3)
$\log C = 0.758 \log V - 0.422 = 2.3151 \rightarrow C = 207 \times 10^{-9}$ mg C per cell

Dinobryon divergens (V= 625 μ^3, measurement Hallegraeff 1977 for Maarsseveen species).
$\log C = 0.866 \log V - 0.460 = 1.961 \rightarrow C = 91 \times 10^{-9}$ mg C per cell

Cryptomonas erosa (V = 576 μ^3)
$\log C = 0.866 \log V - 0.460 = 1.930 \rightarrow C = 85 \times 10^{-9}$ mg C per cell

Cryptomonas ovata (V = 6049 μ^3)
$\log C = 0.866 \log V - 0.460 = 2.814 \rightarrow C = 653 \times 10^{-9}$ mg C per cell

Fragilaria crotonensis (V = 297 μ^3)
$\log C = 0.758 \log V - 0.422 = 1.4523 \rightarrow C = 28 \times 10^{-9}$ mg C per cell

The phytomass carbon content as calculated and the P.O.C. concentration determined using the Beckman Carbon Analyser is mentioned in Table 2. Samples taken at sunrise are compared. Though both methods are crude a sufficient correspondence between the pairs is present. It seems the order of magnitude of these data can be trusted.

2.3 Zooplankton species abundance.

On behalf of the grazing studies routine zooplankton countings were made several times. In order to establish the vertical day and night distribution of the most abundant species a detailed sampling program was executed on May 17, 1978 at 11.30 h and at 23.30 h (miss J. Peters). The samples were taken with a closing net (meshwidth 150 μm) over vertical distances of 2 meter to a depth of 10 meter and over vertical distances of 3 meter from 10-19 meter. At each depth range hauls were made twice. All individuals in the samples were counted. In Fig. 3 the vertical distribution of three species is presented. The centres (gravity) of the distributions were used to test differences in vertical distribution ($s_1^2 = s_2^2 \rightarrow$ Student's t-test: H_o ($\mu_1 = \mu_2$); $s_1^2 \neq s_2^2 \rightarrow$ F test, see Sokal and Rohlf 1969). Of the six species studied (see Table 3) five were found to have a centre of distribution higher up in the column at night. For *Bosmina coregoni* this was the other way round. A significant difference was present for *Eudiaptomus gracilis*, only.

With the exception of *B. coregoni* all species were caught in larger numbers during the night. Differences amounted to 1.77 higher night catches for *D. longispina*. The total daytime catch of *Bosmina* was 1.5 times higher than the night catch.

2.4 Primary production.

Primary productivity was determined using a light incubator (measurements B. Flik and A. Keijser). At sunrise and noon mixed samples from the 0-10 m and the 10-20 m column were taken. These samples were filtered either over 150 μm or 30 μm gauze. P vs I curves were determined for both fractions. At the lake irradiation was measured continuously with a Kipp radiometer connected to an integrator. Extinction in the lake was measured daily. From the phytoplankton response curves and the light regime in the lake the daily production was calculated. However, the highest light intensity realised in the incubator was lower than some of the high intensities encountered in the field. Therefore the P vs I curves had to be extrapolated to these high field values. It was felt better to use parts of real curves instead of fixed values as in the method of Fee (1973).

High intensity parts of P vs I curves of sunrise and noon phytoplankton deter-
mined with a high intensity incubator in August were fitted to the present res-
ponse curves. These parts are indicated by broken lines in the Figs. 4a,b and
5a,b. (See for the August curves the Figs. 9 and 10). The composed P vs I curves
were used in the calculations of the daily production. This was the best we could
do. The P vs I curves for sunrise and noon phytoplankton differ considerable. The
sunrise algae showed a high photosynthetic capacity at low light intensities but
a rapid inhibition at higher intensities. Also P_{max} is considerable higher in
this early morning plankton. These differences in light adaptation pose a grave
difficulty in the calculation of daily production. It is common practice to base
these productions on incubations of a few hours at a convenient time of the day.
In this case, using either the early morning curve or the noon curve results in
a daily production of 493 or 192 mg C per column part ($0-10$ m,m^2) (fraction < 150
μm). Studies by B. Flik in which every one or two hours plankton was collected
and P vs I curves determined learned that in the case of a high sunrise response
phytoplankton behaved as noon plankton after about 10 o'clock. At this time adap-
tation seems to be complete. Of course, complications must be present. It is
realised the velocity of adaptation depends on several factors including irradi-
ation intensity, circulation within the water column etc. In this first step ap-
proximation the productivity of sunrise algae was changed gradually into noon
phytoplankton productivity around 10 o'clock (Table 4). This procedure resulted
in a daily production of 285 mg C per column.

No simple solution to the problem of diurnally changing response curves is
apparent. Incubating samples in situ means fixating phytoplankton at particular
depths. This increases or decreases the velocity of the adaptation process de-
pending on whether the plankton is fixated near the surface or at greater depth.
Daily primary production was estimated for the algae smaller than 30 μm and
smaller than 150 μm. On May 16, 1978 the values were 162 resp. 285 mg C per col-
umn part ($0-10$ m,m^2). The difference 123 mg C must be an approximation of the
production of the algae between 30 and 150 μm. The daily production of the small
fraction is higher than that of the large fraction. On a carbon base (see Table
4) the production of the small fraction is somewhat lower.

Phytoplankton respiration.

The incubation period being short (3 hours), it was thought the labeled car-
bon absorbed by the phytoplankton is not used for respiration during this period.
Consequently gross production was measured. At the end of the light incubation
period the noon samples were divided into two equal parts. Of one part the radi-
ation activity was measured with a liquid scintillation counter. The other half

was placed in darkness for 13.3 hours to determine respiration losses. Grave difficulties were encountered due to ^{14}C assimilation in the dark. In stead of a decrease an increase in activity was found occasionally. The noon samples especially demonstrated this phenomenon. An example is given in Table 5. During this research period unexpected increases in ^{14}C incorporated in particles retained on 0.45 μm filters were also found in samples incubated at low light intensities. For this reason some data derived from dark or low light intensity incubations had to be disregarded. For instance, the two last values in the productivity series in Table 5 will not be found in the P vs I curve of Fig. 5a. These "twilight" incorporations of ^{14}C in particles > 0.45 μm have been found occasionally at other times.

The decreases in ^{14}C during the dark period seemed to be proportional to the ^{14}C incorporation in the previous light period. This might be in accordance with the idea of a higher cell formation activity when the previous production is high. A simple proportionality was assumed and the relative respiration rate was calculated from 13 measurements with noon plankton on May 15 and 16, fraction < 150 μm: $\overline{R} = 0.023 \text{ h}^{1}$, s = 0.026, $s_r = 0.007$. At the end of the light incubation period it will take some (unknown) time before this recently incorporated ^{14}C enters the pool of organic carbon available for metabolism. Therefore this rate of respiration must be an underestimation of the real respiration rate.

2.5 Grazing by zooplankton.

The influence of zooplankton was determined by two methods. In the first place zooplankton freshly caught in the lake was offered phytoplankton that had been incubated for several days with ^{14}C-bicarbonate. After a short grazing period the activity of the different species of zooplankton was measured. These determinations were performed by R. Gulati, Limnological Institute, Nieuwersluis. With the second method freshly caught and concentrated zooplankton was placed in 10 liter glass vessels with 150 μm filtered natural phytoplankton. The grazing periods ranged from sunrise to sunset (17 hours) and from sunset to sunrise (7 hours) again. Cell counts of the most abundant phytoplankton species were made. The initial value was compared with the end values in the glass vessels with and without zooplankton. For a detailed description of the methods, see Hulsmann, this report.

Both methods provide a different kind of information. The first one measures the uptake rates of labeled material by different species of zooplankton. Nothing can be said about the phytoplankton species eaten nor whether detrites is eaten also. With the second method nothing can be said about the consumption by the

different zooplankton species. However, the impact on the different species of
phytoplankton is measured. It is worthwhile to compare the results of both meth-
ods. This can be done only by lumping the effort of the different zooplankton
species respectively the impact on the different phytoplankton species. In both
cases information is lost. Problems arise, however. Two different parameters of
the ^{14}C method can be used: 1. the grazing percentage per hour, that is the per-
centage of the phytoplankton that is eaten by the zooplankton community, 2. the
filtration rate of the individual zooplankter expressed as the volume filtered
free of algae by an animal of a particular species per hour. In both cases the
question arises what is meant by phytoplankton. If not all phytoplankton species
are eaten equally well and the composition of the phytoplankton used in the graz-
ing experiment is not exactly the same as the one found in the lake an error is
introduced if these parameters are used in calculating the amount eaten by the
zooplankton. For instance, in the case the phytoplankton used in the grazing ex-
periments contains a higher amount of algae that is eaten the grazing in the
lake is overestimated.

There is no doubt not all species of phytoplankton are eaten to the same ex-
tent. From a large number of experiments throughout the year it has become evi-
dent the species *Cryptomonas erosa* and *C. ovata* are eaten especially. Also, but
to a lesser extent, *Cyclotella comta*, *Dinobryon divergens* and perhaps *Asterio-
nella formosa*. For the present grazing community, mainly consisting of *Daphnia
longispina* and *Bosmina coregoni* (see Table 3) it is fairly certain *Fragilaria
crotonensis* does not play a role. It is, however, very difficult to determine
an accurate grazing percentage or filtering rate using the field method. Since
the grazing period is rather long, the difference between the initial and the
end concentration in the grazing chamber is composed of an increase by cell di-
vision and a decrease by grazing. The socalled "blanc" does not give exact in-
formation on the rate of cell division since this can be different in the ab-
sence of a possible fertilizing effect of zooplankton faeces. It is possible
that this grazing chamber method underestimates the filtering rate. If, for in-
stance, a part of the ingested *Cyclotella comta* is defaecated again this method
underestimates the filtration rate compared to the ^{14}C method.
With these imperfections in mind a comparison of the results of both methods
must be made. As a common unit the carbon content is chosen. Consequently, the
numbers of the different algal species were converted into carbon content ac-
cording to the method described in part 2.1.

In Table 6 the results of the laboratory method are mentioned. These data are

percentages of a phytoplankton community from the field, filtered through a 30 µm mesh and incubated for several days with ^{14}C-bicarbonate in large containers in the laboratory. Zooplankton from the 0-5 and 5-10 m column was brought into the laboratory and used within a short time in a natural concentration. The number of grazers (*D. longispina* + *Bosmina* spec. + *Eudiaptomus gracilis*) in the upper part of the lake is 1.8 fold higher (averaged over the day and night period, see Table 3). Therefore the difference in grazing percentage might be due to a difference in grazer concentration. The percentage of grazing is low between sunrise and noon, higher between noon and sunset and the highest at night. The overall grazing percentage is -0.875 % per hour.

In Table 7 the grazing percentages as estimated by the field method are mentioned. A smaller number of estimates is available and the information is presented in another format. The grazing impact on particular species of phytoplankton is determined. Consistent data are found for the species *Cryptomonas erosa* and *C. ovata*. Unless the extremely high sunset value (-8.84) is not omitted no difference between day and night time grazing is found. For *A. formosa* and *C. comta* variable percentages are found. For the first species very low grazing (?) percentages as well as increases in cell numbers are found. One night (May 17-18, 1978) an increase in cell numbers of *Cyclotella* occurred. This increase was even larger in the presence of zooplankton resulting in a positive "grazing percentage" (+1.22). An increase also occurred in the field (see Fig. 1). For *Cryptomonas erosa* and *C. ovata* more or less the same grazing percentages are found throughout the year (see the contribution of A. Hulsmann, this report). The mean value found in this study (-1.05 % per hour) is in rather good agreement with the grand mean found in the laboratory study (-0.875 % per hour). Since the grazing percentage found in the laboratory study holds for the total algal community present it might be supposed this experimental community largely consisted of cells comparable to *C. erosa* and *C. ovata* in the way of food. This experimental community originated from a natural one filtered through 30 µm. The *Cryptomonas* species pass a filter of this size so do cells of *Cyclotella comta* and part of the *Asterionella formosa* cells. Perhaps this is why the grazing percentage found in the laboratory study is somewhat lower than the one found by the cell count method.

From the results of both kinds of determinations it must be concluded that about 1% of the species *Cryptomonas erosa*, *C. ovata* and probably *Cyclotella comta* are eaten. It is certainly not right to suppose this grazing percentage holds for the total phytoplankton community.

In Table 8 the filtration rates per zooplankton species are mentioned. In 13 out of 15 determinations the filtration rate per individual is higher in animals

originating from the 0-5 meter column. The mean difference is 1.26. The grazing
percentage was also found to be higher in the 0-5 meter column. This was explain-
ed, however, by a higher concentration with regard to the 5-10 m part. This ex-
planation does not hold in this case. A diurnal difference in filtering rates
is not as apparent as the diurnal difference in grazing percentages.

There are several ways possible to approximate daily ration of the zooplank-
ton. In the first place the grazing percentages as found in the laboratory study
might be used (method 1). There are two ways of defining the phytoplankton com-
munity eaten. It might be defined as the fraction < 30 µm (1.1) or as consisting
of the species *Cyclotella comta*, *Cryptomonas erosa* and *C. ovata* (1.2). For May
16, 1978 calculations are mentioned in Table 9.
In the second place the percentages as found in the field method can be used
(method 2). Since grazing experiments were not performed on May 16, data from
May 17 are used combined with concentrations found on May 16. The three food ra-
tions obtained are 256.2, 72.6 and 83.8 mg C per column per day. The grazing
population represents a mean (n = 9) total particle carbon content of 1630 ± 113
mg C per column (0-10 m, m^2) (data Dr. R. Gulati). Therefore the daily ration on
May 16 seems to be approximately 15.7%, 4.5% respectively 5.1%. A value of about
5% seems to be more realistic than 16%. Also for this reason a calculation of
the food ration can better be based on the grazing percentages and the concen-
tration of both *Cryptomonas* species. Whether *Cyclotella* is included does not
matter too much. It can be concluded that the ^{14}C laboratory method and the
field/counting method lead to the same result. However, information about the
algal species eaten is necessary for a realistic calculation of the ration. This
information can not be obtained by the ^{14}C method. On the other hand the field/
counting method is extremely laborious. Furthermore it does not provide informa-
tion about the filtering rate per individual species. This information is neces-
sary to further fill in the zooplankton impact picture. Since the depth distri-
bution of the different species is known (Table 3), it is possible to calculate
the grazing impact at different depth and time of the day. Such a first step de-
tailed calculation is omitted here. In the above calculations a constant algal
carbon content throughout the day is assumed. This content is not constant. To
calculate the food ration a changing carbon content of the algae, due to prima-
ry production and respiration, has to be brought into the calculations. This is
done in a second step overall balance calculation in the next paragraph.

2.6 Carbon balances

A first attempt to integrate the phytoplankton and the zooplankton community might be the calculation of the transfer of matter between both compartments. Serious difficulties arise, however, and a calculation with the present data must be looked upon as a tryout of possibilities and impossibilities. Also, a balance can be considered an instrument to appraise the methods used in the description of the field situation.

A relative simple compartment is the algal fraction smaller than 150 μm but larger than 30 μm. No zooplankton grazing is assumed. Therefore the only fluxes are production and respiration. At sunrise May 16, a carbon content of 900 mg C per column (0-10 m, m^2) was determined. For this fraction primary production was estimated at +124 mg C. Respiration was calculated using the mean value of 0.023 mg carbon per mg carbon per hour (see paragraph 2.4). This relative respiration rate was found as the decrease in ^{14}C fixed over a previous production period. Therefore the respiration was approximated as a loss of primary production. Starting with sunrise every hour the increase by primary production was calculated. The respiratory loss was calculated over the cumulative production minus previous respiratory losses. This calculation possibly leads to an underestimation of the respiration, because the existing pool of carbon is neglected. On the other hand the carbon just fixed is thought to be available for respiration directly. This is not true. A respiration increasing with the amount of primary production is a not unreasonable assumption. The metabolism of carbohydrates in the algal cell consists of maintenance and the making of new material leading to cell division. The first is small compared to the second. This second source of respiration is proportional to a primary production of a previous period.

In Table 10 the balance of this phytoplankton fraction is presented. At sunset a value of 990 mg C is calculated and one of 980 mg C is determined. At sunrise again a value of 967 is calculated. No determination is available at this time.

In the same table the diel carbon change for the small phytoplankton fraction is presented. Grazing was calculated over the whole fraction. In the previous paragraph this was reasoned to be erroneous. Starting at sunrise with a carbon content of 1850 mg, at sunset a value of 1786 is calculated and a value of 1620 found. The last one is most probably too low. At sunrise the calculated value is 1690 which seems to be too low. Since it is known that some species of the small fraction are grazed upon only, fluxes per algal species have to be calculated.

2.7 Some general remarks

The study of the open-water zone is restricted to the epilimnion. At the
time of this research, May 15-17, a first expression of the thermocline was pre-
sent. Therefore, this thermocline can not have functioned as a barrier layer.
Outside the stratification period the column is thought to be completely mixed.
Therefore also in that case the study can be restricted to the upper 0-10 m lay-
er. This particular column part was approximately homogenous for phytoplankton
species, indeed. For the larger zooplankton it does not hold, however. Also a
diel shift could be observed within the upper ten meter. For a study of the re-
lation between phytoplankton and zooplankton it is necessary to make vertical
subdivisions even at this time of the year.

During the research period a rapid decline was present of two dominant spe-
cies, *Asterionella formosa* and *Dinobryon divergens*. The very high incorporations
at low light intensities and in darkness of ^{14}C in particles larger than 0.45 µm
are possibly related to the dying of these species. At other times of the year
no similar incorporations were encountered. The process seems to be largely un-
known. It seems to be checked by high light intensities.
From the large differences in the production response curves when sunrise and
noon phytoplankton is compared, it must be concluded that more frequent determi-
nations of the P vs I curves are necessary to estimate the daily production.

Grazing was determined by two methods. Since both methods give different
though necessary information, both methods must be applied to study the grazing
impact on the phytoplankton. As far as it can be concluded from this first ex-
perience a rather good agreement exists between those results that can be com-
pared.

The making of a carbon budget is mere bookkeeping and serves as all book-
keeping no objective in itself. (However, according to Thienemann: "Ökologie
(ist) (oder) die Gesamthaushalt der Natur"). It serves two purposes. In the first
place it is a control on the methods applied. These methods are crude. The cir-
cumstances to work are unfavourable in the field. This results in variable data
that are hard to verify by repeated measurements. Measuring the same process or
state by different methods and entering these data in a balance helps to get an
idea of what the field measurements are worth. The crude budgets presented in
this study illustrate this point.
The second purpose of a budget is to get insight into the relations (processes)

between the components i.c. the phyto- and zooplankton community. The actual measurement of fluxes in the field is difficult at the present moment. Making a budget model helps if the time dimensions are short. For instance, the daily amount of grazing calculated by multiplication of the grazing percentage and the standing stock (see page 164) is a crude approximation since the diel change in carbon content of the algae is not taken into account. A daily ration calculated in the first way amounted to 83.8 mg C in the column. According to the budget calculation presented in Table 10 and based on the same grazing percentages the daily ration amounted to 108 mg C. The grazing studies in the field have produced the very important result that some species of the algae only provide a substantial part of the zooplanktons food. This loss by grazing must be compensated by primary production. It can be argued that production rates must be higher in the species liable to grazing. However, it is not possible to measure primary production of individual species in the field. To get insight into the relations between phytoplankton and zooplankton populations in the field it is necessary to determine the species specific production.

3. Crucial Research Period 1978-2

On August 2-3, 1978 the upper 10 meter column was studied only. A thermocline was present ranging from 8-13 meter. The column was divided into a 0-5 m and a 5-10 m part. The results of one 24 hour period are discussed, mostly of the 0-5 meter stratum only.

3.1 Phytoplankton species abundance and vertical distribution.

In Fig. 6 the abundance of the different species during some time before and after the research period is presented. Compared to the previous crucial period *Asterionella formosa* is less abundant ($\simeq$ factor 100), but is in a steady state population. The densities of *Cyclotella comta*, *Cryptomonas ovata* and *C. erosa* are comparable to the ones found in May. From the last two species especially can be said that the population density fluctuates around a rather constant level throughout the year. See also the figures presented by J. Dorgelo, this report. On the other hand *Dinobryon divergens* is declining very rapidly, as was the case during the previous period. Well below a depth of 5 meter many dead colonies of this species were found, especially at 10.5 meter. Also detritus of another origin was found at this depth.

Profiles of the vertical distribution are presented in Fig. 7. The steepest
temperature gradient was found between 8 and 13 meter (see also K. Kersting,
this report). This thermocline is a discontinuity layer also for some phyto-
plankton species, for instance, *Fragilaria crotonensis*, *Cyclotella comta*, *Cryp-
tomonas ovata* and *Dinobryon divergens*. For the species *Asterionella formosa* and
Cryptomonas erosa the thermocline is no barrier. Within the epilimnion,species
able to swim, such as *D. divergens*, *Cryptomonas* spp. and *Ceratium hirundinella*
are not equally distributed. Therefore it can not be said the phytoplankton is
homogenously distributed over the epilimnion this time of the year.

3.2 The carbon content

No extensive determinations of the carbon concentrations in the lake were
made this time. The carbon analyser used in research period 1978-1 was found to
have a too high detection level. Also concentrating the phytoplankton was
thought rather inaccurate. However, a new technique was introduced and compared
with the previous one. A small sample is enclosed in a glass ampulla together
with a reduction agent. The concentration of the inorganic carbon developed is
measured with an infrared analyser (measurements were made by Ir. A. Hulsmann
using the apparatus of the Netherlands Institute for Sea Research. Dr. G.C. Ca-
dée is thanked for hospitality and advice). From cell counts the carbon content
per species was calculated using the formulae of Strathmann (1967) (Table 11).
Comparable values are listed in Table 12. Carbon concentrations estimated by
the ampulla method are slightly higher than those determined by the Total Carbon
Analyser. The absolute values derived from both methods are very close. The car-
bon contents calculated from the cell counts are much lower. This discrepancy is
due to the relative large amount of detritus present in the lake at this time of
the year.

3.3 Zooplankton species abundance

Zooplankton was sampled on August 2 and 3, in both cases at noon. Three ver-
tical net hauls were made from 10-0 meter. Each sample was subsampled three
times. For several species the mean numbers per liter are mentioned in Table 13.
A more detailed sample program was performed at noon and midnight (August 2).
The vertical distribution is presented in Fig. 8. The species abundance as esti-
mated according to the two methods can be compared (see Table 14). With the ex-
ception of *Bosmina*, there is no statistical difference between daytime and night-
time catches. If the column estimates of vertical hauls and those calculated by
addition of the separate closing net numbers are compared it is obvious that the

first method results in smaller numbers for *Eudiaptomus gracilis* adults, copepodites and *Cyclops* spec. The estimates of *Daphnia longispina* and *Asplanchna* are the same, however. It is possible that strong swimmers such as the copepods are able to avoid the slowly rising open net. An extremely high number of nauplius larvae were caught with the vertical haul. This might be an error.

3.4 Primary production

Daily production was estimated as described for crucial research period 1978-1. An incubator with a sufficient high irradiance was used this time. Therefore no extrapolations of the P vs I curve were needed to get productivity rates at the high light intensities encountered in the field. Phytoplankton sampled at sunrise and noon was divided into a fraction < 30 μm and < 150 μm. Mixed phytoplankton taken between 0-5, 5-10 and 10-20 meter depth was incubated for a period of about 4 hours. Examples of P vs I curves are presented in the Figs. 9 and 10. Obviously, sunrise and noon phytoplankton have very different response curves. Dark adapted sunrise algae have a high productivity at rather low light intensities but a considerable inhibition as soon as the optimal irradiation has been surpassed. No productivity plateau is present as is the case with light adapted noon phytoplankton. These noon algae have a low productivity response (a low P_{max} value) but also a low inhibition at high light intensities. Throughout the year such a kind if difference between dark and light adapted phytoplankton is not always found.

In Fig. 11 the response curves of phytoplankton sampled at the same time (noon) but at different depth is presented. The P_{max} value decreases with depth. The responses of the 0-5 and the 5-10 meter interval algae are very close. On the other hand phytoplankton originating from 10-20 m has an aberrant photosynthetic response. The productivity potential is low and irregular. This low response potential combined with the low irradiance at this depth makes the amount of the daily production negligible.The difference with both other P vs I curves emphasizes the change at the 8-10 meter zone at the beginning of the thermocline.

To calculate the daily production a combination was made between sunrise and noon productions. Around 10 o'clock sunrise productivities were merged gradually into noon productivities. Since the velocity of the adaptation process is not known this merging of two responses is arbitrarily done. Knowledge must be gathered about this adaptation process and, of course, the vertical displacement velocity of the algal cells. The still existing difference in response of algae from 0-5 m and 5-10 m depth (Fig. 11) is an indication this vertical mixing is too slow to annihilate response differences within the 0-10 m zone after half a

day.

The daily production for two different size class fractions and three depth intervals is presented in Table 15. For the 0-5 m interval the hourly productions throughout the day are given in Table 16. The small fraction contributes for 90% to the daily production.

3.5 Grazing by zooplankton

As for crucial research 1978-1 grazing percentages were determined by the ^{14}C method (Dr. R. Gulati) and the method of cell counts (A. Hulsmann, P. van Rijswijk). The grazing percentages and other relevant data are listed in Table 17 and 18. Freshly caught zooplankton in natural concentrations was brought into the laboratory three times a day: at sunrise, at noon and sunset. In between these periods the zooplankton was stored. Animals were used three times at the times indicated in Table 17. With the cell count method the grazing periods ranged from sunrise to sunset and from sunset to sunrise. The phytoplankton used in the grazing experiment has a high carbon content compared to the phytoplankton present in the lake (see Table 11). Probably the algal concentration has increased during the incubation in the laboratory. This increase does not affect filtering rates since the concentrations are below the insipient limiting level (see contribution of A. Hulsmann). On the other hand a change in phytoplankton composition might have affected the grazing percentages as found with the ^{14}C-method (see crucial research period 1978-1), since *Cyclotella*, for instance, seems to be a less favoured foodsource this time (see Table 18).

The grazing percentages were statistically analysed. First of all the ^{14}C-grazing percentages were normalized to percentages per hour per mg C zooplankton (see Table 17). The underlined data were thought to belong to the same statistical population ($\overline{x_1}$ = 5.204; s_1 = 1.239; n_1 = 10). The hypothesis H_0 was tested whether single data or pairs of data belong to this population of grazing percentages. In case of a pair a F-test was used to look at the similarity of variances of both groups. In no case the variances of the pairs were found to be significantly different from the population variance. A t-test was used to calculate the probability of $\overline{x_1}$ = $\overline{x_2}$. The results are given in Table 17. It is concluded that the grazing percentages of the first experiments in each series differ significantly from the percentages of the succeeding experiment. Strictly speaking this does not hold for the 07 hour pair of data but the testparameter has a value sufficiently close to the one at the 5% level to be suspicious (t_s = 2.052 compare $t_{0.05(10)}$ = 2.228). This result suggests time influences the results, for instance, it is possible to think of an adaptation of the animals

once they are brought into the laboratory.

It is also concluded that the high grazing percentages at 20 resp. 05 hour do not belong to the collection of dates found during the rest of the day. This might be due to an error in the experiments. However, with regard to the suggestions in the literature of a diel rhythmicity in grazing these aberrant percentages might be looked upon as an expression of a higher grazing activity at sunset and sunrise. Assuming a mean zooplankton concentration of 0.147 ± 0.024 mg C.l^{-1} in the experiments, a mean grazing percentage is calculated of 0.765 % per hour for the zooplankton community. The error of this mean is at least 9%, maximal 25% (9% for the determination of the percentage itself and 16% for the extinction of the zooplankton community). This makes the ^{14}C-data quite comparable to the ones found with the counting method (Table 18). According to Hulsmann an error percentage of 9-16% must be expected in this case.

Both methods to estimate the grazing impact on the phytoplankton lead to comparable results. Apart from rendering different information both methods have advantages and disadvantages. The cell count method is tedious and time consuming. Moreover, the error in cell counts is large and the detection level for differences correspondingly low. Long incubation periods were used. This means that the grazing estimate has the character of an ingestion rate. Also the long incubation time permits the phytoplankton to change cell numbers for instance by cell division. This affects the calculated grazing percentages. A correction using the change in cell numbers in the chambers without zooplankton is an approximation only, since the behaviour of the phytoplankton might be different in the presence of zooplankton.

The ^{14}C laboratory method is a relatively rapid one with a high level of detection and a relatively small error of determining cell radioactivity. However, the drawbacks of this method are found in the possibility of a changed phytoplankton community composition and an abnormal behaviour of the zooplankton. Since the various phytoplankton species might have different rates of photosynthesis the radioactivity of the various species can be different. This species dependent labeling is another source of error if the method is used for mixed algae.

3.6 Carbon balances

Previous calculations of the daily budget were made for the whole phytoplankton community. Mean rates were used to calculate the phytoplankton lost due to grazing. The information available for particular species could not be used because information on the production term in the budget formula is available for the whole community only. As long as no direct measurement of the dai-

ly production per species population can be made it is hard to get an idea of
the basic ecological processes leading to the growth and the decline of popula-
tions in the field. To overcome this shortage a model is introduced to estimate
this desired production by calculation. Since information had to be created as-
sumptions had to be made. The model is in a preliminary state of which an out-
line is presented. No claim as to the exact value of the different terms is
made.

The carbon content per species is known at sunrise August 2 (C(i,0)) and
August 3 (C(i,24)), 1978 (Table 11). Differences in these specific concentra-
tions are caused by primary production P(i), respiration R(i), grazing G(i) and
diverse factors leading to a loss of carbon L(i). Therefore

$$C(i,0) + P(i) - R(i) - G(i) - L(i) = C(i,24)$$

holds. P(i), R(i) and L(i) are unknown, but $\Sigma P(i)$ is the total production on the
particular day. Respiration was assumed to be proportional to the production per
species. A high photosynthetic activity might lead to a high cell division ac-
tivity. A proportional increase of metabolism can be expected. Obviously, a more
direct estimation of the respiration per species is needed. Grazing rates are
determined per species. The factor L(i) is mentioned for the sake of complete-
ness but is only used for *Dinobryon divergens* to "explain" the rapid disappear-
ance from the scene.
Per species primary production is calculated with five minutes interval accord-
ing to

$$P(i) = F(i) . \frac{C(i,t)}{\Sigma\ C(i,t)} . P(t)$$

The species specific primary production is assumed to be proportional to the
relative carbon content of the population and a calibration factor F(i). Twelve
recurrent calculations lead to an hourly production, respiration and grazing.
Every hour a new empirical total primary productivity value is introduced. The
grazing percentages were changed at sunset. At the end of 12 x 24 = 288 runs
the calculated carbon content of the population must be equal to the one found
in the field. If this is not the case the calibration factor was changed until
both concentrations were the same. This procedure was repeated for all dominant

species. The result is presented in Table 19. To start at the end, the five domi-
nant species have a total production of 219 mg C per day per column part (0-5 m,
m²). This is 7 mg C short of the value found (226 mg, see Table 4) and entered
in the computations. This might be an error or point to an ommission of a source
of production. If we include the species *A. formosa* and *D. divergens* into the
large size class (30-150 μm) the production of this fraction is 23 mg. This cal-
culated value equals the empirically found value. Therefore, the species neglect-
ed most probably belongs to the small size class (< 30 μm). An amount of 41% of
the daily production is respired by the phytoplankton. This respiration is a
very weak point in the model. In the first place a species specific rate must
become available. Grazing amounts to 21% of the daily production. The grazing
rates used in the calculation are based on comparable results found with two dif-
ferent methods. This amount of grazing cannot be neglected as a factor influ-
encing the population dynamics of the phytoplankton species. *Cryptomonas erosa*
and *C. ovata* are the most important sources of food. These small flagellates
have a high photosynthetic potential as illustrated by *C. erosa*. After alloca-
ting the total primary production over the different species a large amount is
left for *C. erosa*. This means a jump of a population carbon content of 59.92 to
149.21 mg C per column (0-5 m, m²) within a day is possible. Therefore it is not
necessary to assume the large difference in cell numbers found between sunrise
of August 2 and August 3 is due to a counting error.

4. Discussion

In Table 20 certain characteristic data are summarized. For both research
periods the impression of a dying phytoplankton is present. In May this is es-
pecially the case since the population numbers of two abundant species, *Asterio-
nella formosa* and *Dinobryon divergens* are rapidly decreasing. In August the po-
pulation density of these species is lower and *Dinobryon* is dying off again.
The carbon content of the whole community, as calculated from the cell counts,
is 4-5 times lower in August. Detritus has accumulated, however, and the total
particular carbon, as determined chemically, has increased. Notwithstanding
this decrease in the standing stock phytomass the daily primary production in
the water column is remarkably the same. Though dominant in numbers and biomass
about twenty percent of the primary production only originates from these con-
spicuous colonial forms. Eighty percent must be ascribed to small cells, espe-
cially *Cryptomonas erosa* and *C. ovata*. The microscopic picture is dominated by
the net plankton but during these two periods the functional aspects are domi-

nated by the inconspicious species. It is remarkable these flagellates have a
constant population size throughout the year. Since the zooplankton largely
feeds on these species one wonders whether the regulation of the population
size is due to or notwithstanding the grazing of these animals. Compared to May
the food uptake of the zooplankton is twice as high in August. The abundance of
the total grazer population has increased but less. Therefore part of the higher
food uptake must be caused by the increase of the temperature. The same factor
probably increased the productivity since no larger standing crop was found in
August. The larger phytoplankton species are of minor importance as a source of
food in this lake. Therefore zooplankton does not play a direct role in termi-
nating the development of a algal population. The rather abrupt termination of
the spring bloom, also in this lake, cannot be explained by increased grazing
of a growing zooplankton population. The fast decrease of some species, such as
Asterionella and *Dinobryon* must be ascribed to other factors. To understand the
population dynamics of the grazer community in Lake Maarsseveen (and not only
in this lake) it is of importance to measure the daily primary production of
the relevant algal species and at the same time the species specific grazing
rate of the zooplankton. It will be no small matter to overcome the difficul-
ties but worthwhile because it seems we have no idea of the dynamic interactions
in the field.

5. Literature

FEE, E.J., 1973. A numerical model for determining integral primary production
and its application to Lake Michigan. J.Fish.Res.Board Can., 30: 1447-1468.

FEE, E.J., 1973. Modelling primary production in water bodies, a numerical ap-
proach that allows vertical inhomogenities. J.Fish.Res. Board Can., 30:
1469-1473.

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

SOKAL, R.R. & F.J. ROHLF, 1969. Biometry. Freeman and Company, San Francisco.

STRATHMANN, R.R., 1967. Estimating the organic carbon content of phytoplankton
from cell volume or plasma volume. Limnol.Oceanogr., 12: 411-419.

Table 1. The carbon content in the 0-10 m column (mg.l^{-1}).

Time of day	D.O.C.	P.O.C.		D.O.C. / P.O.C.	<30 / >30-<150
		< 30 µm	> 30 - < 150 µm		
Sunset May, 15	7.8 ± 1	0.202 ± 0.004	0.162 ± 0.013	21.4 ± 3.3	1.2 ± 0.1
Sunrise May, 16	10.3 ± 1	0.185 ± 0.006	0.090 ± 0.009	37.5 ± 4.0	2.0 ± 0.3
Sunset May, 16	7.6 ± 1	0.162 ± 0.007	0.098 ± 0.015	29.2 ± 4.7	1.6 ± 0.3
Sunrise May, 17	14.2 ± 1	0.179 ± 0.006	0.075 ?	55.9	2.4
Sunset May, 17	15.2 ± 1	0.314 ± 0.009	0.132 ± 0.030	34.1 ± 3.9	2.4 ± 0.6
Sunrise May, 18	16.4 ± 1	0.084 ± 0.005	0.093 ± 0.028	92.7 ± 11.2	0.9 ± 0.3

The carbon content in the 10-20 m column (mg.l^{-1}).

Time of day	D.O.C.	< 30 µm	> 30 - < 150 µm	D.O.C. / P.O.C.	<30 / >30-<150
Sunset May, 15	6.7 ± 1	0.163 ± 0.005	0.013 ± 0.125	38.1 ± 8.6	12.5 ± 121
Sunrise May, 16	9.0 ± 1	0.147 ± 0.003	0.032 ± 0.005	50.3 ± 6.3	4.6 ± 0.8
Sunset May, 16	9.2 ± 2	0.126 ± 0.003	0.001 ± 0.009	73.0 ± 17.6	126.0 ± 1137
Sunrise May, 17	13.3 ± .5	0.172 ± 0.019	0.002 ± 0.029	76.4 ± 7.3	86.0 ± 1256
Sunset May, 17	14.3 ± .2	0.320 ± 0.014	0.104 ± 0.028	33.7 ± 1.5	3.1 ± 1.0
Sunrise May, 18	13.8 ± .9	0.059 ± 0.004	0.089 ± 0.064	93.2 ± 21.2	0.7 ± 0.6

Table 2. Comparison of phytomass carbon content calculated
and determined (mg C.liter^{-1}).

date	determined	calculated
May, 16	0.275	0.270
May, 17	0.254 ?	0.215
May, 18	0.177	0.167

Table 3. Depth distribution zooplankton on May, 17, 1978 at 11.30 h and 23.30 h. Individuals per liter. Z_m = center of distribution. Data J. Peters.

Depth meter	*Daphnia longispina*				*Bosmina coregoni*			
	11.30 h		23.30 h		11.30 h		23.30 h	
	mean	S.E.	mean	S.E.	mean	S.E.	mean	S.E.
0-2	7.02	3.76	12.77	0.29	4.81	2.63	2.23	0.13
2-4	3.04	0.71	12.77	0.35	4.79	0.35	3.18	0.25
4-6	8.5	0.09	6.99	1.83	9.39	1.46	3.65	0.33
6-8	2.4	0.35	3.6	0.99	2.28	0.09	3.42	0.66
8-10	1.56	0.32	1.82	0.35	2.29	0.54	2.91	0.41
10-13	0.35	0.11	0.76	0.02	0.51	0.12	0.76	0.04
13-16	0.29	0.11	0.38	0.02	0.42	0.06	0.28	0.01
16-19	0.19	0.01	0.27	0.01	0.25	0.03	0.29	0.19
Z_m	4.44	0.43	3.58	0.55	5.04	0.20	6.17	0.01

Depth meter	*Cyclops* spec.				*Nauplius* larven			
	11.30 h		23.30 h		11.30 h		23.30 h	
	mean	S.E.	mean	S.E.	mean	S.E.	mean	S.E.
0-2	3.63	2.39	5.61	0.19	0.19	0.02	0.51	0.13
2-4	3.74	1.03	3.85	6.28	0.45	0.08	0.53	0.02
4-6	4.22	0.14	3.39	0.91	0.86	0.08	0.78	0.15
6-8	1.00	0.02	1.62	0.83	0.72	0.21	1.05	0.25
8-10	1.50	0.09	1.19	0.54	0.76	0.01	1.13	0.38
10-13	0.30	0.13	0.53	0.05	0.40	0.2	0.36	0.01
13-16	0.38	0.08	0.22	0.05	0.35	0.01	0.15	0.01
16-19	0.28	0.06	0.25	0.11	0.23	0.15	0.21	0.06
Z_m	5.00	0.22	4.47	0.28	8.55	0.71	6.46	1.21

Table 3. (Continued).

| Depth meter | Eudiaptomus gracilis | | | |
| | 11.30 h | | 23.30 h | |
	mean	S.E.	mean	S.E.
0-2	0.8	0.38	2.26	6.28
2-4	1.3	0.02	2.87	0.25
4-6	2.2	0.18	2.36	0.15
6-8	1.23	0.26	0.93	0.23
8-10	1.87	0.47	1.29	0.6
10-13	0.60	0.45	0.71	0.10
13-16	0.52	0.12	0.39	0.10
16-19	0.22	0.05	0.25	0.11
Z_m	7.76	0.23	5.81	0.01

| Depth meter | Eudiaptomus adult | | | | Eudiaptomus copepodites | | | |
| | 11.30 h | | 23.30 h | | 11.30 h | | 23.30 h | |
	mean	S.E.	mean	S.E.	mean	S.E.	mean	S.E.
0-2	0.57	0.30	1.53	0	0.22	0.08	0.73	0.16
2-4	0.74	0.01	1.59	0.32	0.56	0.02	1.27	0.06
4-6	1.15	0.05	1.48	0.05	1.06	0.23	0.89	0.10
6-8	0.62	0.13	0.55	0.17	0.61	0.14	0.38	0.06
8-10	0.92	0.37	0.82	0.36	0.95	0.10	0.48	0.24
10-13	0.28	6.28	0.35	0.1	0.32	0.29	0.36	0.01
13-16	0.3	0.03	0.22	0.04	0.22	0.09	0.17	0.06
16-19	0.15	0.04	0.14	0.01	0.07	0.01	0.12	0.1

Table 4. Primary Productivity (mg $C.m^{-2}.h^{-1}$) of three phytoplankton fractions. May 16, 1978, 0-10 m column.

Time of day	Productivity		
	< 30 µm	< 150 µm	>30-<150 µm
5- 6	0.10	3.44	3.34
6- 7	6.59	18.54	11.95
7- 8	22.43	32.61	10.18
8- 9	26.19	37.07	10.88
9-10	27.47	39.00	11.53
10-11	13.11	26.70	13.59
11-12	8.68	19.83	11.15
12-13	8.65	19.75	11.10
13-14	8.61	19.20	10.59
14-15	8.12	18.20	10.08
15-16	7.44	18.10	10.66
16-17	8.47	7.99	0
17-18	6.30	5.33	0
18-19	4.37	8.59	4.22
19-20	4.85	8.16	3.31
20-21	0.93	2.89	1.96
Total	162.31	285.40	124.54
See also Table 1	mg $C.(mg\ C)^{-1}.h^{-1}$		
	0.88		1.38
	1.00		1.27

Table 5. Comparison of activity (dpm) of particles < 30 μm incubated for
three hours at different light intensities (first column) and
activity of half of these samples (x 2) after a period of 13.3
hour in total darkness (Noon sample May 16, 1978, 0-10 m).

light incubation dpm		dark incubation dpm
decreasing light intensity →	1404	1127
	1028	1785
	846	1031
	738	2180
	636	1191
	588	1434
	544	2170
	888	3310
dark	948	2604

Table 6. Grazing percentages per hour as estimated by the ^{14}C laboratory method (Dr. R. Gulati).

Time of day	0-5 meter	5-10 meter	sums
Sunrise	- 0.93 - 0.33 - 0.77	- 0.47 - 0.20 - 0.60	- 3.30
Noon	- 2.00 - 0.53 - 0.77	- 1.10 - 0.50 - 0.80	- 5.70
Sunset	- 1.80 - 0.83 - 2.40	- 0.60 - 0.40 - 0.73	- 6.96
Sums	-10.35	- 5.40	MEAN - 0.875

Table 7. Grazing percentages per hour as estimated by the field method counting cells (Ir. A. Hulsmann).

Time of day	*C. erosa*	*C. ovata*	Mean	*A. formosa*	*C. comta*
Sunrise	- 1.79	- 1.41	- 1.60	- 0.08	- 0.77
Sunset	- 8.84 ?	- 0.93	- 0.93	+ 0.32	- 0.95
	- 0.64	- 0.49	- 0.56	- 0.23	+ 1.22
Mean	- 1.22	- 0.93	- 1.05		

Table 8. Filtration rates $(ml.animal^{-1}.h^{-1})$ of some zooplankton species as found by the laboratory ^{14}C-method (Dr. R. Gulati). Mean values and standard deviations are given.

Zooplankton species	Sunrise		Noon		Sunset	
	0-5 m	5-10 m	0-5 m	5-10 m	0-5 m	5-10 m
E. gracilis big	0.278 ± 0.108	0.139	0.315 ± 0.031	0.280 ± 0.054	0.354 ± 0.105	0.228 ± 0.022
E. gracilis small	0.075	0.102	0.149 ± 0.024	0.120	0.140	0.116
D. longispina big	0.266 ± 0.030	0.150 ± 0.092	0.323 ± 0.084	0.240 ± 0.057	0.262 ± 0.132	0.207 ± 0.077
D. longispina small	0.079 ± 0.015	0.082 ± 0.029	0.107 ± 0.015	0.096 ± 0.018	0.114 ± 0.055	0.102 ± 0.018
Bosmina spec.	0.187 ± 0.018	0.141 ± 0.041	0.196 ± 0.032	0.183 ± 0.32	0.199 ± 0.062	0.176 ± 0.036
Sums	1.499		1.919		1.896	

Table 9. A first step approximation of the daily food ration of the grazer
zooplankton calculated according to different methods.

Time of day	depth range	[c] < 30 μm	grazing %	period and column value	method 1.1
Sunrise	0- 5 m	185	0.93	73.1	mg C per 0-10 m, m² column per light period (17 h)
	5-10 m	185	0.47	37.0	
Noon	0- 5 m	185	0.57	38.5	
	5-10 m	185	0.50	39.5	188.1
Sunset	0- 5 m	162	0.80	45.4	per dark period (7 h)
	5-10 m	162	0.40	22.7	68.1

Time of day	depth range	[c] some algae	grazing %	period and column value	method 1.2
Sunrise	0- 5 m	28.8	0.93	22.8	mg C per 0-10 m, m² column per light period (17 h)
	5-10 m	28.8	0.47	11.5	
Noon	0- 5 m	28.8	0.57	14.0	
	5-10 m	28.8	0.50	12.2	60.5
Sunset	0- 5 m	28.8	0.80	8.1	per dark period (7 h)
	5-10 m	28.8	0.40	4.0	12.1

Time of day	column	grazing percentage x carbon content (mg C.m⁻³)			method 2
		C. erosa	*C. ovata*	*C. comta*	mg C per 0-10 m, m² column per light period (17 h) 72.2
Sunrise	0-10 m	1.79 x 10.4	1.41 x 15.7	0.77 x 2.7	
Sunset	0-10 m	0.64 x 10.4	0.49 x 15.7	0.77?x 2.7	per dark period (7 h) 11.6

Table 10. Diel carbon change of phytoplankton (mg C per column (m^2; 0-10 m) per period). Date May 16, 1978. Lake Maarsseveen I.

Time of Day	In Lake Determined	Primary Production	Algal Respiration	Zooplankton Grazing	Budget Value
Sunrise 04 h	1850	Phytomass < 30 μm			
per light period		+ 162	- 37	- 176	
Sunset 21 h	1620	← Compare →			1786
per dark period		0	- 23	- 73	
Sunrise 04 h	1790	Compare			1690

Time of Day	In Lake Determined	Primary Production	Algal Respiration	Zooplankton Grazing	Budget Value
Sunrise 04 h	900	30 μm < Phytomass < 150 μm			
per light period		+ 124	- 34	0	
Sunset 21 h	980	← Compare →			990
per dark period		0	- 23	0	
Sunrise 04 h	N.D.				967

Table 11. Number of species on different dates and calculated carbon content. The noon values originate from samples taken at short depth intervals. Numbers and content per column as indicated.

Species	2-8-1978 0-10 m;m² sunrise number x 10⁷	C-content	3-8-1978 0-10 m;m² sunrise number x 10⁷	C-content	3-8-1978 0-5 m;m² noon number x 10⁷	C-content
Asterionella formosa	57±22	42.75	66±20	49.50	15.34	11.51
Fragilaria crotonensis					0.8	0.22
Cyclotella comta	23± 3	47.61	18± 1	37.26	9.35	19.35
Cryptomonas erosa	141±39	119.85	348±31	296.80	82.95	70.51
Cryptomonas ovata	25± 1	163.25	21± 1	137.13	11.04	72.09
Dinobryon divergens	41±10	37.31	47±10	42.77	20.29	18.46
Chlamydomonas spec.	49±16		101± 9			
Closterium spec.			25± 3	284.75	0.55	6.26
Ceratium hirundinella					1.26	
Total carbon per column part		411		563		192

Species	3-8-1978 5-10 m;m² noon number x 10⁷	C-content	4-8-1978 0-10 m;m² noon number x 10⁷	C-content	1-8-1978 0-10 m;m² noon number x 10⁷	C-content
Asterionella formosa	19.68	14.76	44± 7	33.00	49± 4	36.75
Fragilaria crotonensis	1.06	0.30				
Cyclotella comta	5.78	11.96	24± 2	49.68	23± 2	47.61
Cryptomonas erosa	60.28	51.24	286±84	243.10	219±27	186.15
Cryptomonas ovata	12.30	80.32	24± 7	156.72	28± 3	182.84
Dinobryon divergens	17.24	15.69	16± 7	14.56	73± 8	66.43
Chlamydomonas spec.			126±40		56±16	
Closterium spec.	0.68	7.75	5± 1	56.95	3± 1	
Ceratium hirundinella	0.37					
Total carbon per column part		174		554		519.78

Table 12. Comparison of data derived from different methods to determine carbon content. All data in mg.l^{-1} ± standard deviation. (a) Samples directly from the lake (Ir. A. Hulsmann); (b) Initial values in grazing chambers (Ir. A. Hulsmann); (c) cell count data from Table 11.

P.O.C. fraction		ampulla method	T.O.C. Analyser	calculated from cell counts
Sun-rise	< 150 μm	0.27 ± 0.2 (n=3) (b)	0.20 ± 0.03 (n=21) (b)	0.04 (c) 0.06 (c)
	< 30 μm		0.20 ± 0.05 (n=19) (b)	
Noon	< 150 μm	0.30 (n=1) (a)	0.22 ± 0.02 (n= 8) (a)	0.04 (c)
	< 30 μm		0.25 ± 0.12 (n= 6) (a)	
Sun-set	< 150 μm	0.32 ± 0.12 (n=2) (a) 0.24 ± 0.01 (n=2) (b)	0.34 ± 0.05 (n= 7) (a) 0.22 ± 0.04 (n=15) (b)	
	< 30 μm		0.22 ± 0.02 (n= 5) (a) 0.18 ± 0.05 (n=19) (b)	

Table 13. Concentration (number per liter) of some zooplankton species.

Species	August 2		August 3	
	$\overline{x}$	$s_{\overline{x}}$	$\overline{x}$	$s_{\overline{x}}$
Bosmina spec. adult	0.42	0.08	0.43	0.02
Bosmina spec. juv.	0.43	0.08	0.47	0.04
Daphnia longispina big	3.90	0.36	1.09	0.08
Daphnia longispina small	0.49	0.12	0.14	0.03
Cyclops spec.	0.94	0.10	1.02	0.09
Cyclops cop.	2.59	0.21	2.39	0.07
Eudiaptomus gracilis	0.73	0.03	0.50	0.07
Eudiaptomus cop.	0.87	0.11	0.80	0.06
Naupliën	9.56	0.25	9.09	0.46
Asplanchna spec.	0.75	0.13	0.78	0.11
Conochilus unicornis	0.34	0.06	0.16	0.05
Filinia longiseta	2.74	0.15	1.67	0.15
Habrotrocha spec.	1.52	0.14	1.07	0.52
Kellicottia longispina	8.60	0.22	7.48	0.52
Keratella cochlearis	49.31	1.58	45.71	0.91
K. quadrata	0.28	0.05	0.26	0.02
Polyarthra spec.	9.38	0.25	7.76	0.17
Synchaeta spec.	0.54	0.03	0.48	0.04
Trichocerca spec.	2.07	0.18	2.41	0.11

Table 14. Number of individuals in a column (0-20 m;m^2) estimated according to two methods.

Species	Vertical Haul Daytime	Closing Net	
		Daytime	Nighttime
Eudiaptomus gracilis	14 600	45 920	45 860
Cyclops spec.	18 800	74 800	62 060
Nauplius	191 200	14 740	15 100
Daphnia longispina	87 800	69 960	79 020
Bosmina spec.	14 600	5 840	11 460
Eudiaptomus copepodites	17 400	30 100	29 700
Asplanchna spec.	15 000	17 080	16 480

Table 15. Daily production mg C per column part (0-5 m, m^2).

Depth	< 30 μm	< 150 μm	30-150 μm
0- 5 m	203	226	23
5-10 m	75	62	0

Table 16. Hourly productivity rates (mg C per column part (0-5 m; m^2) per hour), August 2, 1978 for three size class fractions.

time of day	Productivity		
	< 30 μm	< 150 μm	30-150 μm
6- 7	11.10	13.47	2.37
7- 8	18.32	22.59	4.27
8- 9	18.36	20.19	1.83
9-10	15.97	17.83	1.86
10-11	14.96	17.66	2.70
11-12	14.62	16.79	2.17
12-13	14.87	15.80	0.93
13-14	15.14	17.07	1.93
14-15	14.92	16.28	1.36
15-16	14.37	15.60	1.23
16-17	13.10	13.72	0.62
17-18	13.97	15.02	1.05
18-19	11.02	11.51	0.49
19-20	8.46	8.84	0.38
20-21	3.34	3.54	0.20
21-22	0.10	0.11	0.01
Total	202.62	226.02	23.40

Table 17. Grazing percentages ($\%.h^{-1}$) according to ^{14}C method (data dr. R. Gulati) and other relevant data (August 3,4, 1978). See also text.

Time of day		1	2	Information	1	2	P
sunrise	07 h	0.504	0.405	phytoplankton 0.291 mg C.1^{-1}	3.679	2.956	0.1>P>0.05
	09 h	0.773	0.876		5.642	6.394	
	12 h	0.733	0.420	zooplankton 0.137 mg C.1^{-1}	5.350	3.066	
noon	12-13 h	0.365	0.333	phytoplankton 0.320 mg C.1^{-1}	2.085	1.903	P < 0.01
	17 h	0.934	1.096		5.337	6.263	
	20 h	2.880	1.198	zooplankton 0.175 mg C.1^{-1}	16.457	6.845	P << 0.001
sunset	20-21 h	0.213	0.147	phytoplankton 0.363 mg C.1^{-1}	1.638	1.131	P < 0.01
	24 h	0.609	0.433		4.685	3.331	
	05 h	0.667	2.18	zooplankton 0.130 mg C.1^{-1}	5.131	16.769	P << 0.001
sunrise	?	0	0.322	phytoplankton 0.242 mg C.1^{-1}			
				zooplankton 0.125 mg C.1^{-1}			

Table 18. Grazing percentages (%.h^{-1}) for different algal species (data
Ir. A. Hulsmann, P. van Rijswijk). August 3,4, 1978.

Time of day	*A. formosa*	*C. erosa*	*C. ovata*	*C. comta*
sunrise-sunset	0.88	0.84	0.97	0.04
sunset-sunrise	0.14	0.35	1.10	0.11
sunrise-sunset	0.70	0.41	0.84	0.46

Table 19.

SPECIES	INITIAL CONC.		PRODUCTION		RESPIRATION		GRAZING		LOST		END CONC.		F
Asterionella formosa	21.38	+	11.75 (19%)	−	4.86 (41%)	−	3.73 (32%)		(27%)	=	24.54		0.5
Cyclotella comta	23.05	+	0.026 (59%)	−	≈0.001 (41%)	−	4.48			=	18.59		0.001
Cryptomonas cf. erosa	59.92	+	187.45	−	76.38 (41%)	−	21.78 (12%)		(52%)	=	149.21		2.85
Cryptomonas cf. ovata	81.62 (16%)	+	8.95 (59%)	−	3.70 (41%)	−	18.62			=	68.25		0.1
Dinobryon divergens	18.66	+	11.31 (41%)	−	4.79 (45%)	−			3.76 (14%)	=	21.42		0.55
TOTAL PHYTOPLANKTON	Σ 204.63	+	Σ 219.49 (41%)	−	Σ 89.73 (21%)	−	Σ 48.61 (4%)		Σ 3.76 (34%)	=	Σ 282.01		

Table 20. Comparison of some important data.

	May 1978	August 1978
A. formosa *D. divergens* *C. comta* *C. erosa* *C. ovata*	2 x 10^9 (declining) 1 x 10^8 (declining) 1 x 10^7 (increasing) 2 x 10^8 (stationary) 1.5 x 10^7 (stationary)	6 x 10^7 per m^3 (stationary) 4 x 10^7 (declining) 2 x 10^7 (stationary) 1.4 x 10^8 (stationary) 2.5 x 10^7 (stationary)
Carbon content (mg)	1670 - 2700 per column 0-10 m, m^2	411 - 563 (cell count C) 2000 - 3400 (Total P.O.C.)
daily production mg C.m^{-2}	285	288
grazing per day	25 mg C	49 mg C
	mean value per m^3 for 0-5 m column	
grazer community	13.000	16.000
	individuals in 0-10 m; m^2 column	

Fig. 1. The abundance of six dominant phytoplankton species at
the time of crucial research period 1978-1.

Fig. 2. Total particle volume < 30 μm on May 17, 1978, 15.45-16.00 hours (Coulter countings on June 8 (crosses) respectively June 15, 1978). (Data Kersting).

Fig. 3. The vertical distribution of three dominant zoo-
plankton species. Samples were taken on May 17,
1978 at 11.30 h (histogram on the left) and at
23.30 h (at the right). Note difference in scale.

Fig. 4a. Phytoplankton response curve (P vs I curve), fraction < 30 µm, depth range 0-10 m, sunrise May 16, 1978. Broken line: extrapolation analogous to an empirical response curve.

Fig. 4b. See legend 4a. Fraction < 150 µm.

Fig. 5a. See legend 4a. Fraction < 30 μm. Noon May 16, 1978.

Fig. 5b. See legend 4a. Fraction < 150 μm. Noon May 16, 1978.

Fig. 6. The abundance of five dominant phytoplankton species before and after the research period 1978-2.

Fig. 7. The vertical distribution of some phytoplankton species on August 3, 1978.

Fig. 8. The vertical distribution of two zooplankton species,
August 3, 1978.

Fig. 9. Productivity as a function of incubator irradiance
(P vs I curve). Phytoplankton sampled between 0-5 m
at sunrise (August 3, 1978) and divided into two
fractions (• < 150 µm, ✳ < 30 µm). Productivity
in desintegrations per minute, irradiation in
log Joule.m^{-2}.sec^{-1}. (Data B.J.G. Flik).

Fig. 10. P vs I curves of phytoplankton sampled between 5-10 m at
noon (August 3, 1978) and divided into two fractions
(• < 150 µm, * < 30 µm). Dpm means desintegrations per
minute. (Data B.J.G. Flik).

Fig. 11. A comparison of P vs I curves for noon phytoplankton
from 0-5, 5-10 and 10-20 m depth intervals. (Dpm is
desintegrations per minute).(Data B.J.G. Flik).

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THE SUBMERGED AQUATIC MACROPHYTES IN LAKE MAARSSEVEEN I: SPECIES COMPOSITION, SPATIAL DISTRIBUTION AND PRODUCTIVITY

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Introduction

So far information about the submerged vegetations of the lakes around the river Vecht area is scarce. Only a few reports are available, all referring to other, more shallow lakes. A study on the vegetation of the nearby Botshol by Westhoff (1949), which was supplemented only for the submerged plants by Vroman (1976), makes mention of the occurrence of several submerged angiosperm species as well as charophytes, but no quantitative data are given. Den Held *et al.* (1970) carried out an investigation on the emergent, floating and submerged macrophytes in the De Haak lakes, applying the method of Barkman *et al.* (1964) for the vegetation analysis. By Westhoff *et al.* (1971) the distribution of submerged macrophytes, including charophytes, is noted in the Nieuwkoop-lakes.

In Lake Maarsseveen I the distribution and abundance of the submerged and floating macrophytes were studied in order to find out a) which species were present, and b) to assess their role in the nutrient cycles of the lake.

Sampling occurred with the use of SCUBA, which has proved adventageous in ecological studies on these plants (Wood, 1963, 1975; Chapman & Clayton, 1975; Love & Robinson, 1977; Sheldon & Boylen, 1978).

All macrophytic species present were listed, and of the predominant species the seasonal changes in biomass were measured during the year. The plant cover was mapped out into main vegetation types, and their related standing crops, carbon and nitrogen values were measured.

In the present study Wetzel's (1975) definition of aquatic macrophytes is used, in which also watermosses and charophytes are included - this in contrast to Sculthorpe's (1967) definition, referring to vascular aquatic plants only.

Materials and methods

In 1976 an initial survey of the submerged macrophytes was made during the growing season. Therefore, as an alternative to the widely used transect based on distance with variable depth, every time a variable distance at the same depth

was covered. Depth and direction were adjusted by aid of, respectively, depth gauge and compass. Signals between the SCUBA-diver and boat-operator were exchanged to indicate stations. The stations were based on landmarks and distance was estimated using a topographic map. The survey was carried out from the lake's surface down to the limit of the photic zone. From 1976 to 1979 many observations were made to complete the inventory of the submerged macrophytes. Identification of the species was done with several keys (Fassett, 1975; Haslam *et al.*, 1975; Heukels and Van Ooststroom, 1970; Velddeterminatietabel 1977; Wood & Imahori, 1965).

In order to study the structures of the macrophytic communities indications are given of either the presence or absence of a species, related to depth, and the species predominance within the vegetation.

In general, a submerged vegetation is not suitable for frequency analysis since the community is either too monotonous or too intricately interwoven. The widely used method of Braun-Blanquet (1951) is not applicable since the vegetations are usually very dense and divided into several layers within the water. This method was originally developed for terrestrial plants, and it is based on an estimate of the percentage surface area covered by the vertical projection of the plants concerned. A more suitable method for the classification of submerged aquatic vegetations, based on a combination of floristic, structural and ecological data, was developed by Den Hartog & Segal (1964). This method, in general used by non-SCUBA divers, is very time-consuming since extensive sampling by means of a grub is required, in order to take the minimum area of every single species into account. SCUBA-divers can indicate accurately the parts of the lake-bottom that are overgrown, and their vegetal occupants, and, therefore, make extensive sampling superfluous.

Since the aim of the present study was more directed towards a quantification of the plant biomass than to merely vegetation analysis, no attempt was made to classify more than five main vegetation types.

As a result of the earlier mentioned first survey a) the composition of the main vegetation types and b) their sites could be determined.

Growth of the dominant species, notably two charophytes and three angiosperm species, was recorded. As parameter for growth the ash-free dry weight per plant shoot was chosen. In order to avoid confusion about the differences in age, the plants were marked with metal tags at the onset of the growing season. Monthly three tagged plants were sampled throughout the year. To estimate the related standing crops, every two months a square was harvested from the center of the vegetation, using a metal rectangular of 25 by 25 cm. The plant material was freed from periphyton, by means of rinsing them with water, and freeze-dried.

The ash content was determined at 550°C (resulting ash including carbonates) and at 980°C (carbonates removed). In addition to the ash-free dry weight, also the carbon and nitrogen contents were determined as parameters for biomass.

Results and discussion

About 50% of the shoreline of Lake Maarsseveen I is surrounded by a narrow zone of emergent plants, mainly *Phragmites australis*. This zone will be studied later on. 25% of the Lake's total surface area is occupied by a more or less dense cover of submerged macrophytes. The plants are present until a depth of 10-11 m, apparently the limit of the photic zone. In general the image of the submerged vegetation is determined by charophytes, which are only completely absent at sites with a dense cover of *Elodea* sp.

Vegetation types

The distribution of the main vegetation types, related to depth, is indicated in Fig. 1, and their stylized representation is given in Fig. 2.

In the north-western part of the lake only one single characee occurs from 3 to 11 m depth, i.e. *Chara globularis*. The same species is present also, and in the same densities, in the south-western part of the lake, from 3 to 11 m, and in the southern part, from 2 to 6 m depth, but the vegetation in these parts is mixed with *Elodea* sp., *Zannichellia palustris* and *Potamogeton perfoliatus*. Although both *Z. palustris* and *P. perfoliatus* co-determine the image of the vegetation - the former grows in tufts whereas of the latter only single plants occur with regular intervals - they do not represent a substantial amount of biomass. *Elodea*, on the contrary, contributes considerably to the biomass of this mixed vegetation. In the southern part of the lake, a small region (about 1% of the total lake area) is occupied exclusively by *Elodea* sp.: both *Elodea canadensis* and *Elodea nuttallii* are found, but *E. nuttallii* prevails. Along the major part of the southern, eastern and northern shoreline, at depths from 6 to 10 m, meadows occur, constituted either esclusively by *Elodea* sp. or charophytes. The latter are predominated by *Nitellopsis obtusa*.

Mainly along the eastern shore several *Zannichellia*-predominated patches occur, at depths from 2 to 6 m. *Potamogeton lucens* grows also in patches, but larger ones than those of *Zannichellia*, and the sites are scatterred over the lake's bottom from 2 to 7 m depth.

Submerged plant species

All submerged plant species, which are detected in the lake in the period

ranging from June 1976 to August 1979, are presented in Table 1. Included are also the species that occur often emergent or floating in other waters, but which are almost never found in this stage in the lake Maarsseveen: respectively, *Alisma* spp., *Hydrocharis*, *Nuphar* and *Utricularia*.

The bottom of the lake consists mainly out of sand, which lies bare until a depth of about 3 m in the western part of the lake. Although occupation of this region by plants might be possible, it is inhibited probably by the damaging action of swimming people.

Most angiosperms grow in the relatively shallow regions, from 3 to 5 m depth, around the outlet at the northern side, and along the southern and the southeastern side of the lake. They occur among the vegetations either predominated by exclusively *Chara globularis* or those predominated by the same species as well as *Elodea* spp., *P. perfoliatus* and *Z. palustris*. *Ceratophyllum demersum*, *Myriophyllum* sp. and *Ranunculus circinnatus* grow in tufts. Since the *Myriophyllum*-plants did not flower in the lake, these could not be identified with their species name. *Potamogeton pectinatus* and *Potamogeton pusillus* grow in patches among the earlier mentioned vegetations. *Potamogeton crispus* and *Potamogeton obtusifolius* occur only in the eastern part of the lake, where also but on three locations only, *Najas marina* is found. The latter species is considered to belong to oligohaline to mesohaline waters, exemplified by De Haak and Botshol, where the Cl^--concentrations range from 224 to 1100 $mg.l^{-1}$ (Den Held *et al.*, 1970; Vroman, 1976). In contrast, the maximum Cl^--concentration in the open water of the lake Maarsseveen is much lower, i.e. 36 $mg.l^{-1}$. This might point to seepage on the sites where the *Najas*-plants occur. *Potamogeton obtusifolius* is also a seepage indicator. Only a few single plants of *Hydrocharis morsus-ranae* and *Nuphar lutea* were found, submerged, around the water inlet. They originate probably from ditches around the lake where both species grow abundantly. *Utricularia vulgaris* occurs on several places abundantly and it forms garlands on top of the charophytic pillows (mainly *Nitellopsis obtusa*).

It is suggested that most submerged angiosperms propagate vegetatively in the lake, since only the *Elodea* spp. and *P. lucens* were seen flowering. Winter buds were found in several cases, notably *C. demersum*, *Myriophyllum* sp., *P. obtusifolius*, *P. pusillus* and *U. vulgaris*.

Of the normally emergent macrophyte *Alisma plantago-aquatica* and *Alisma gramineum*, several specimens are found, mostly submerged, and both species flowered in the lake. *A. plantago-aquatica* occurs along the whole southern shoreline and around the inlet, *A. gramineum*, however, is found only at the latter site.

Among all angiosperms discussed above, *A. gramineum*, *N. marina*, *P. lucens* and *U. vulgaris* have a small ecological amplitude, whereas *N. marina* is consider-

ed also a rare species according to Westhoff (1949). The occurrence of *P. lucens*, *P. pectinatus*, *C. demersum*, *Elodea* sp. and, more so, *N. morsus-ranae* and *N. lutea* point to a fairly high nutrient supply in the water at the southern side of the lake and especially near the outlet, whereas *P. pusillus*, on the other hand, is less tolerant in this respect (Segal, 1965).

Only a few specimens of the water moss *Fontinalis antipyretica* are found along the northern shoreline between the *Phragmites*-stems. This species is a clear water-indicator.

Charophytes occur in general in non-polluted, clear waters. In the lake Maarsseveen, several species are present and they are therefore discussed separately. Their distribution and predominance related to depth are represented in Fig. 3. Most frequently *Chara globularis* is found: it is a small, fragile plant and it predominates in the shallowest regions as well as in the deepest ones. Also in very shallow regions *Chara major* occurs, a very robust plant, that can reach heights of about 60 cm. The lower boundary of this mixed *Chara* vegetation is formed by *Chara vulgaris* and *Chara aspera*, both fairly small plant species. Among these vegetations also several angiosperms occur as is discussed earlier. *Nitellopsis obtusa*, a very tall (heights until 1 m recorded) charphyte without cortical cells, forms very dense meadows from 6 to 10 m depth, among which almost no other charophytes or angiosperms are present (*U. vulgaris* is the only exception).

Propagation of the charophytes occurs vegetatively as well as sexually in the lake. Part of the vegetation hibernates and starts to grow again in spring. Only in very cold winters when the ice reaches the bottom in the more shallow regions, the plants are frozen and removed by the movements of the ice. Then propagation might occur only by means of oöspores (Murris, 1971). Most charophytes are found fructifying abundantly. In the case of *Nitellopsis obtusa* mainly male plants are found; this species is dioecious. In general, the charophytic species and their sequence with respect to depth distribution are similar to those reported for the nearby Botshol (Heimans, 1949; Vroman, 1976). The range of their depth distribution, however, is greater.

Estimate of biomass and standing crop

The seasonal dependency in growth of the predominant species was determined by harvesting the tagged plants monthly. The quantitatively most important charophytes, notably *Chara globularis* and *Nitellopsis obtusa*, showed different growth patterns (Fig. 4). *N. obtusa* had a higher productivity, and reached its maximum biomass much earlier in the season than *C. globularis* (Table 2). In both species the carbon and nitrogen concentrations varied considerably and, consequently, al-

so their C:N ratio's. Less than half of their dry weight consisted of organic matter, which is in agreement with values reported by Westlake (1965). Up to 40% of their ash was made up by carbonates (Table 2), a common phenomenon in charophytes. As to *Z. palustris*, *P. lucens* and *Elodea* sp., these species had their maximum biomass in, respectively, July, August and September (Fig. 4). Particularly *P. lucens*-plants represent a very large biomass. *P. lucens* and *Elodea* sp. had very high productivities (Table 2), which were considerably higher than those of *Z. palustris* and both charophytic species. During the growing period the C:N ratio's were lower in the angiosperms than in the charophytes.

From the biomass data mentioned above, and the standing crop samples the extremes of the total standing crop of the main vegetations in the lake were calculated (Table 3). The *Chara* sp. vegetation is considered to be composed mainly by *C. globularis*. The *Chara* and *Elodea* meadows cover about 50% of the total region indicated in Fig. 1, both species occur in monotypic stands and account for half of the plant-occupied area. The charophyte concerned in this case is *Nitellopsis obtusa*. *Elodea* sp. grows in the same densities in the meadows and in the much larger monotypic stand in the southern region of the lake. In the mixed vegetation, *C. globularis* grows in the same densities as where it occurs in a monotypic stand, *Elodea* sp. and *Z. palustris*, however, in densities of about 1/6 and 1/4, respectively.

To assess the significance of the submerged plants to the nutrient cycles of the lake, the input to the dissolved organic matter (DOM) pool can be calculated from the differences between maximum and minimum standing crop (Table 3). Although the charophytes occupy the largest area of the lake, they do not play the most important role in the nutrient cycles concerned in this case (carbon and nitrogen). Obviously *P. lucens* contributes most to both, carbon and nitrogen cycles, the two charophytic species and *Elodea* sp. play a significant role also, whereas *Z. palustris* does not cause a large input of organic matter.

Summary

The submerged littoral zone of Lake Maarsseveen I is well-developed and it occupies about 25% of the total surface area of the lake. Several macrophytic species occur which have become more or less rare in the Netherlands, notably the angiosperms *Alisma gramineum* and *Najas marina*, and 5 charophytic species. The plant cover can be divided into 5 main vegetation types.
Although the largest area of the littoral zone is occupied by charophytes, the *Potamogeton lucens* vegetation contributes most significantly to the total DOM input of the lake. High productivities were found for *Potamogeton lucens*, *Elodea*

sp. and the charophytes, a considerably lower one for *Zannichellia palustris*.

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References

BARKMAN, J.J., H. DOING & S. SEGAL, 1964. Kritische Bemerkungen und Vorschläge
    zur quantitativen Vegetationsanalyse. Acta·Bot.Neerl., 13: 394-419.

BRAUN-BLANQUET, J., 1951. Pflanzensoziologie; 2nd ed. Vienna. 631 p.

CHAPMAN, V.J. & J. CLAYTON, 1975. Submerged vegetation of the Rotorua and Waika-
    to lakes. 3. Lake Rerewhakaiitu. Hydrobiologia, 47: 399-413.

FASSETT, N.C., 1975. A manual of aquatic plants. Madison, The University of Wis-
    consin Press, 405 p. 1rst publ. 1940.

HARTOG, C. DEN & S. SEGAL, 1964. A new classification of the water-plant commu-
    nities. Acta Bot.Neerl., 13: 367-393.

HASLAM, S.M., Ch. SINKER & P. WOLSELEY, 1975. British waterplants. Reprinted from
    "Field studies; a journal concerned with all aspects of the environment."
    p. 243-351.

HELD, A.J., DEN, J.J. DEN HELD & E.X. MAIER, 1970. Waterplanten en waterplanten-
    vegetaties in de plassen van De Haak·bij Slikkendam (Z.-H.). Gorteria, 5:
    21-35.

HEUKELS, H. & S.J. VAN OOSTSTROOM, 1970. Flora van Nederland; 16e dr. Groningen,
    Wolters-Noordhoff, 908 p.

LOVE, R.J.R. & G.G.C. ROBINSON, 1977. The primary productivity of submerged macro-
    phytes in West Blue Lake, Manitoba. Can.J.Bot., 55: 118-127.

MURRIS, H.R., 1971. Een onderzoek naar de overwintering en verspreiding van Chara-
    ceae-oösporen in de Botshol. Biol.Lab., Free University, Amsterdam, Plant
    Taxonomy (unpublished report).

SCULTHORPE, C.D., 1967. The biology of aquatic vascular plants. London, Edward Ar-
    nold (Publishers) Ltd., 610 p.

SEGAL, S., 1965. Een vegetatieonderzoek van hogere waterplanten in Nederland. We-
    tenschappelijke mededelingen van de K.N.N.V., nr. 57, Hoogwoud (N.-H.).

SHELDON, R.B. & C.W. BOYLEN, 1978. An underwater survey method for estimating sub-
    merged macrophyte population density and biomass. Aquat.Bot., 4: 65-72.

RAAM, J. VAN, 1977. Velddeterminatietabel voor de Nederlandse kranswieren. Hilversum; Gewest Gooi en Vechtstreek. Stencil, 10 p.

VROMAN, M., 1976. De verspreiding van water planten in de Botshol. In: De Noordelijke Vechtplassen; flora en fauna. Uitgave van de "Stichting Commissie voor de Vecht en het oostelijk en westelijk plassengebied". Vlaardingen, Van Dooren, p. 317-332.

WESTHOFF, V., 1949. In: Landschap, flora en vegetatie van de Botshol nabij Abcoude; onder redaktie van V. Westhoff. Uitgave "Stichting Commissie voor de Vecht en het oostelijk en westelijk plassengebied", Baambrugge, p. 43-100.

WESTHOFF, V. et al., 1971. Wilde planten; flora en vegetatie in onze natuurgebieden; onder redaktie van V. Westhoff, P.A. Bakker, C.G. van Leeuwen en E.E. van der Voo. Deel 2: Het lage land. Uitg. Vereniging tot behoud van natuurmonumenten in Nederland.

WESTLAKE, D.F., 1965. Some basic data for investigations of the productivity of aquatic macrophytes. Mem.Ist.Ital.Idrobiol, 18 Suppl.: 229-248.

WETZEL, R.G., 1975. Limnology. London, etc., Saunders, 743 p.

WOOD, R.D., 1963. Adapting SCUBA to aquatic plant ecology. Ecology, 44: 416-419.

WOOD, R.D., 1975. Hydrobotanical methods. Baltimore, University Park Press, 173 p.

WOOD, R.H. & K. IMAHORI, 1965. A revision of the Characeae; 2 parts. Weinheim, Verlag J. Cramer. 1rst part: Wood, R.D., Monograph of the Characeae, 904 p. 2nd part: Wood, R.D. & K. Imahori, Iconograph of the Characeae; with 394 icones, 1964.

Table 1. Macrophytic species detected submerged in Lake Maarsseveen I,
between June 1976 and August 1979.

Pteridophytes

Alisma gramineum Lej.
" *plantago-auqatic* L.
Ceratophyllum demersum L.
Elodea canadensis Michx.
" *nuttallii* (Planch.) St. John
Hydrocharis morsus-ranae L.
Myriophyllum sp.
Najas marina L.
Nuphar lutea (L.) Sm.
Potamogeton crispus L.
" *lucens* L.
" *obtusifolius* Mert. et Koch
" *pectinatus* L.
" *perfoliatus* L.
" *pusillus* L.
Ranunculus circinnatus Sibth.
Utricularia vulgaris L.
Zannichellia palustris L.

Bryophytes

Fontinalis antipyretica

Phycophytes

Chara aspera Deth. ex Willd.
" *globularis* Thuill.
" *major* Vaillant
" *vulgaris*
Nitellopsis obtusa (Desv. in Lois.) J.Gr.

Table 2. Productivities of the five predominant submerged macrophytic species determined from monotypic stands. For duration of the growing season 180 days was taken. Changes in the concentrations of carbon, nitrogen, total ash, carbonates and the C/N ratio. S, summer; W, winter.

Species	Productivity (mg C.m^{-2}.day^{-1})	C (% ashfree dr.wt)		N (% ashfree dr.wt)		C/N		Total ash (% dr.wt)		Carbonates (% dr.wt)	
		S	W	S	W	S	W	S	W	S	W
C. glob.	68	82.5	32.9	3.3	2.7	25.2	12.3	59.3	52.3	17.4	14.6
N. obt.	126	48.4	37.2	2.1	3.7	23.3	10.0	60.0	65.9	12.8	5.1
Elodea sp.	342	40.8	47.0	3.3	4.8	12.5	9.8	19.0	40.1	3.2	6.4
P. luc.	350	42.0	—	2.2	—	19.5	—	20.2	—	2.3	—
Z. pal.	29	42.9	—	3.3	—	13.0	—	17.5	—	1.8	—

Table 3. Distribution and extremes in standing crop of the main vegetation types in Lake Maarsseveen I. In cases where more than one species predominated the vegetation, the contributions are also given separately per species.

Vegetation type	Area colonized by macrophytes		Total standing crop (kg)					
			ashfree dr.wt.		C		N	
	m²	% of total	min.	max.	min.	max.	min.	max.
Chara sp.	64,079	8.78	274	1061	90.3	875.2	7.4	34.7
Chara and	51,097	7.00	C 22	614	8.1	297.5	0.8	12.8
Elodea meadows			E 72	1842	38.5	824.1	3.9	75.2
			94	2456	46.6	1121.6	4.7	88.0
Chara, Elodea	28,913	3.96	C 124	479	40.7	394.9	3.3	15.7
P. perf., Z. pal.			E 27	695	15.3	310.8	1.5	28.4
			Z 0	130	0	37.8	0	3.0
			151	1304	56.0	743.5	4.8	47.1
P. luc.	25,700	3.52	0	3328	0	1620.9	0	89.2
Elodea sp.	7,554	1.03	43	1070	22.7	487.3	2.3	44.5
Z. pal.	5,600	0.77	0	100	0	29.3	0	2.3
Total	182,943	25.06	562	9,319	215.6	4,877.8	19.2	305.8

Fig. 1. The distribution of the main submerged vegetation types, related to depth, over Lake

Fig. 2. Stylized representation of the main submerged vegetation types
present in Lake Maarsseveen I.

CHAROPHYTIC SPECIES

Fig. 3. The vertical distribution of the Charophytes in Lake Maarsseveen I.
a) Upper and lower limit for growth.
b) Depth at which the species predominate.

Fig. 4. The seasonal changes in plant biomass of the predominant submerged macrophytes in Lake Maarsseveen I.
●—● , ash-free dr.wt.; ▲--▲ , nitrogen; ○··○ , carbon.

PERIPHYTON ON EMERGENT MACROPHYTES IN MAARSSEVEEN, AN ENUMERATION

P.J. Roos

A. Periphyton associated with *Phragmites australis*

A.1. Available substratum (with E. de Ridder).

The zone of great emergent macrophytes in Lake Maarsseveen I consists predominantly of *Phragmites australis*. It covers more than 90%. This reed occurs in pure stands or intermingled with *Typha* spp. and/or *Carex* spp. Stands of pure *Scirpus lacustris*, at one place mixed with *Phragmites australis*, are also found. The density of *Phragmites* over the whole emergent vegetation zone, has a mean of 52.64 individuals.m^{-2}, with a 95% confidence interval between 49.68 and 55.60, based on 664 countings of 0.25 m^2. From aerial photographs, checked in the field, a total area of emergent macrophytes of 16,893 m^2 was calculated. This amounts to an estimation of 889,221 stems (95% confidence interval between 839,219 and 939,223. The mean diameter, at mid-water depth, of 398 randomly sampled stems appears to be 0.742 cm (95% confidence interval 0.740-0.744). The mean length of the submerged parts of *Phragmites* stems, based on 362 random depth recordings is 32.98 cm, with a 95% confidence interval between 30.91 and 35.05 cm. An estimation of the surface of *Phragmites*, available as a substratum for periphyton is now calculated as being about 6833 m^2 (95% confidence interval between 6044 and 7670 m^2). This holds true for the emergent reed stems. Older stems, consisting of small parts greatly varying in length, amount to about 808,272 individuals. Variation in length made reliable sampling impossible.

A.2. Structure and development of periphyton on reed-stems (with A. Post).

From August 1977 till August 1978 the periphyton in one reed stand was studied. Samples were taken every two weeks. It was to be expected from the literature that a difference could be found between periphyton from older and younger stems (Hillebrand, 1976), or between reed-stems from the peripheral and central parts of the reed stand (Meschkat, 1934). Stems were therefore collected from the outer side of the reed stand, facing open water and from the central part. From the outer zone living stems, less than one year old, and stems from the foregoing growing season were taken. The submerged parts of the stems were transported to the laboratory in PVC containers. There one square cm at every 10 cm was scraped off and examined immediately under the microscope. With the

exception of the diatoms, all organisms were identified and counted. This material was subsequently rinsed over to a cover glass and glowed for diatom examination. The glow-method was chosen in favour of the hydrogen peroxide-potassium dichromate method (Van der Werff, 1955) in order to preserve the original configuration.

The following positions of the epiphytic taxa were compared by means of statistical analysis:

> lake side vs. bank side of the stems;
>
> central stems vs. peripheral stems;
>
> stems from the foregoing growing-season vs. younger stems;
>
> upper part of the submerged stem vs. lower part.

It was found that:

Cymbella prostata and *Achnanthes* spec. occur more on the lakeside, while *Cocconeis* and *Rhoicosphaenia* prefer the bankside of the stems;

Mougeotia and *Spirogyra* occur more on peripheral stems than on central ones just like *Cymbella ventricosa*, while on the contrary *Cocconeis*, *Rhoicosphaenia* and *Gomphonema* are to be found predominantly in the central part of the reed stand;

Cymbella affinis, *Tabellaria*, *Synedra* and *Gomphonema* grow more frequently on younger stems, *C. ventricosa* more on older ones.

Striking differences were found between upper- and lower parts of the stems. Dividing the submerged part of the stem into three regions: upper, middle and lower, the algae of the order Zygnematales (*Mougeotia*, *Spyrogyra* and *Zygnema*) are found predominantly on the upper part, as do the diatoms *Cymbella ventricosa*, *Rhoicosphaenia curvata* and *Gomphonema* spp. Oedogoniales and Ulothrichales occur in greater numbers on the middle and lower parts. In the lower region, mainly in the neighbourhood of the adventive rootlets, the greatest numbers of *Batrachospermum*, *Cocconeis* spp. and blue-green algae are to be found. Seasonal changes in total numbers of individuals and of species are also obvious. The species-list is given in section D, the temporal variation is briefly discussed below.

The young sprouts that appear in May are rapidly colonised by the green algae *Oedogonium* spp. and *Bulbochaete* spp. and by diatoms. These epiphytic diatoms also occur on the cells and hairs of the green algae. These offer an additional substratum, and therefore enlarge the available substratum for diatom growth. Nevertheless, the green algae are better colonizers than the diatoms. *Oedogonium* and *Bulbochaete* reach a maximum in July, with about 60 individuals per cm^2. At the same time a minimum number of about 10000 diatoms per cm^2 is found. During

the summer *Oedogonium* and *Bulbochaete* become covered by a layer of lime. This lime becomes densely packed with diatoms of the genera *Achnanthes*, *Anomoeoneis*, *Cocconeis*, *Rhoicosphaenia* and *Synedra*. Consequently, the number of diatoms increases significantly. Also the stalks of *Cymbella lanceolata*, the tubes of *Cymbella prostrata* and the filaments of *Homoeothrix juliana* offer additional substratum. At the end of the summer the number of *Cymbella*'s and blue-green algae is still increasing. The number of individuals of *Oedogonium* and *Bulbochaete* however decreases to about 10 individuals.cm^{-2}. At the same time the number of invertebrate animals increases. Predominant among these are peritrich Ciliates, Nematodes, Oligochaets, the bivalve *Dreissena polymorpha*, the snail *Potamopyrgus jenkinsi* and several insect-larvae, especially Trichoptera and Chironomids. In December the lime formed during the summer disappears, as do nearly all green algae. At that time *Cymbella lanceolata* and *Cymbella prostrata* start with an explosive bloom, which continues to the end of the winter, resulting in densities of 3500 *C. lanceolata* and 2000 *C. prostrata* per cm^2. The total number of diatoms may rise to nearly 2,000,000 per cm^2, the half of which is situated on stalks and tubes of *Cymbella* spp. When in April most of the *Cymbella*'s disappear, the total number of diatoms decreases also abruptly. The stem, now nearly one year old, is then barely overgrown by periphyton. Soon the development of the periphyton on this stem corresponds to the settlement of epiphytes on the new sprouts.

A.3. Structure and development of periphyton on reed rootlets (with J.M. Revier).

The periphyton of the adventive rootlets consists mainly of epiphytic algae. The complete list of species is given in section D. In number of species as well as in number of individuals the diatoms are dominating. Other striking organisms are: *Homoeothrix juliana*, *Oedogonium* spp., *Bulbochaete* spp., *Asterocystis smaragdina* and a number of epiphytic protozoans, especially Vorticellids. *Homoeothrix*, and other blue-green algae, occur predominantly on the lowest adventive rootlets, Oedogoniales dominate the higher ones. Settling also occurs on epiphytic algae, with a slight preference of some organisms for certain substrates. The diatoms *Cocconeis* and *Amphora* are frequently found on *Homoeothrix*; *Achnanthes* spp. occur on this blue-green alga as well as on *Oedogonium*, *Bulbochaete* and on stalks of *Cymbella lanceolata*. Bushes of *Synedra* are often to be found on tubes of *Cymbella prostrata*. The peritrichous ciliates grow both on the rootlets and on epiphytic algae, the Vorticellids more on the rootlets, the Vaginicolids *Vaginicola* and *Cothurnia* show a preference for the algae. There is some evidence that a bloom of diatoms and multicellular algae alternates with mass-growth of Vorticellids.

The lowest rootlets are mostly free of the periphyton described above. Often however, the Zooflagellates *Codosiga utriculus* and *Salpingoeca* spec. occur on these rootlets. To a lesser extent *Bicoeca* spec. is to be found. During the period of this part of the investigation, February - June 1978, *Vorticella campanula* had a maximum in February, declining to a minimum in April. The same holds true for the other Vorticella's, which recovered after that time. During the summer *V. campanula* was scarcely met. This is in accordance with findings in an other lake in the region (Roos & Trueba, 1977). In March and April there also is a minimum in coverage of multicellular algae, but there is a luxurious growth of diatoms.

In comparison to the periphyton on the stems of *Phragmites* the greater number of faunistic elements in the periphyton of the adventive rootlets is especially noteworthy. Among the animals Vorticellids are conspicuous. *Homoeothrix juliana* which is very common on the rootlets, is to be found on the stems only in the neighbourhood of these rootlets. The diversity of green algae is greater on the stems than on the rootlets.

A.4. Distribution of the periphyton on *Phragmites* in Lake Maarsseveen I
     (with N. Bas and R. Koolma).

The situation described above is based on observations from one sampling station only. In order to check the representativity of the periphyton of this station a comparison has been made between periphyton from this locality and other localities along the same bank. Samples were taken from September till December 1978. Only the proportional contribution of the diatom genera has been taken into account. This reveals a striking difference in the ratio of the two dominant genera *Achnanthes* and *Gomphonema*. At the previously investigated locality these two genera make up 72.4% of the total number of diatoms, the *Achnanthes/Gomphonema* ratio being 6.3. The greater part of the area along the same bank, however, has a ratio of 0.5. Both genera make up 81% of the total diatom community. Along this bank there was also one sampling station with a varying composition of genera that shifted from *Achnanthes* predominance to *Gomphonema* hegemony. These findings have given rise to an extension of this investigation over the emergent vegetation of the whole lake during a longer period. This has been carried out from January till July 1979. It appears that there are localities which differ from other localities in predominance of *Achnanthes* or *Gomphonema*. This phenomenon is most evident in early winter. When in spring and summer the number of *Cymbella* spp. and of algae of the order Oedogoniales rises, all localities become *Achnanthes* dominated. At the end of the summer however,

the previously *Gomphonema* dominated localities return to their initial genus-composition. At a representative locality the *Achnanthes/Gomphonema* ratio shifts gradually from .26 in February to 8.77 in May and moves back in September, reaching a value of .50.

A.5. Comparison of *Phragmites*-periphyton from the two lakes in Maarsseveen
(with M. de Nooij).

The above mentioned investigations were carried out in Lake Maarsseveen I, which is relatively poor in nutrients. The smaller Lake Maarsseveen II has a higher degree of eutrophication. Since a differentiation based on the ratio of diatom genera proved to be to work out fruitfully, the same procedure was followed. Two localities from Lake II were compared with one locality in Lake I and mutually, during April and May 1979. In this period no significant differences in the *Achnanthes/Gomphonema* ratio are found. Comparison takes place according to Kadlubowska (1977), using Spearman's rank-correlation. This shows a high similarity between the two localities in Lake II, each of which differs significantly from the representative locality in Lake I. In all samples *Achnanthes* predominates, followed immediately by *Gomphonema* and *Fragilaria*. Differences between the two lakes are to be found in the less frequent genera. In the samples from Lake I *Cymbella* occurs always in a higher proportion than in the samples from Lake II. *Tabellaria*, always present in Lake I, although in low numbers, is not found in the samples from Lake II. *Amphora* and *Eunotia* occur in somewhat greater numbers in Lake II.

B. Diatoms associated with *Typha latifolia* (with B. Huizing).

During the winter 1978-1979 a comparison was made between the diatoms associated with *Typha latifolia* from different localities in Lake Maarsseveen I and between the diatom genera associated with *Typha latifolia* and *Phragmites* from the same station. As the "stem" of *Typha* is in fact a bundle of leaf-sheaths, the submerged part of *Typha* is not easily comparable to *Phragmites* stems. A possible difference between inner- and outer side of the leaf-sheath has to be taken into account. The list of species is given in section D. The *Achnanthes/Gomphonema* ratio on the outer side of *Typha* equals that on *Phragmites* stems from the same locality. Therefore along the bank that was studied by us, most of the *Typha* stems are comparable. The chosen bank is the same as the previously investigated area described in section A.4. The proportion of

less frequent genera is significantly lower on *Typha* than on *Phragmites*. These genera, like *Cymbella*, *Anomoeoneis*, *Asterionella*, *Diatoma*, *Fragilaria*, *Navicula*, *Synedra* and *Tabellaria* occur more frequently on the inner sides. Moreover, on the inner side of the leaf-sheath the *Achnanthes/Gomphonema* ratio has a larger value than on the outer side. The proportion of *Cocconeis* on the contrary is significantly higher on *Typha* than on *Phragmites*, which holds for the inner as well as for the outer side of the leaf-sheath. No differences are found between upper and lower regions of the submerged part of *Typha latifolia*.

C. Architecture of the periphyton.

In the description of the development of the periphyton as well as in the obscuration of differences in *Achnanthes/Gomphonema* ratio, some emphasis is laid on the presence or absence of multicellular algae and large stalks and tubes of *Cymbella* species. The presence of these structures appears to offer a considerable, temporal additional substratum. Large numbers of diatoms may occur on these structures. The following describes the situation observed in March 1977. Several *Cymbella lanceolata* stalks bear more than 250 *Achnanthes* colonies or solitary individuals. On the same stalks that attain a length of about 4 mm also more than 50 *Synedra* individuals occur, often in dense bushes. Multitudes of diatoms, especially *Achnanthes* and *Synedra*, may be present on *Bulbochaete* and *Oedogonium*. Not all algae are colonized. Apart from the above mentioned algae the blue-green alga *Homoeothrix* is overgrown by *Achnanthes*, *Cocconeis* and *Amphora*. The latter genus is lacking on the green algae. Generally, no periphyton is found on Zygnematales, *Ulothrix* and *Microspora*.

In scanning electron microphotographs of *Bulbochaete* there appears a gradient as regards overgrowth. Young cells at the top of the branches are apparently bare. Details of the cell surface are clearly visible. No diatoms are settled there. On somewhat older cells a number of bacteriae is present, together with a closed layer covering the cell surface. This layer is apparently thicker on cells at still greater distance from the top. This probably represents the mucoid matrix, the existance of which was revealed by Allanson (1973) and was required for the model of Wetzel and Allen (1970). When this matrix is present a great number of diatoms is found. However, setae of *Bulbochaete*, on which no matrix is demonstrable, are also favoured by *Achnanthes* and *Synedra*. This matrix may also play a role in the formation of a lime-crust around these algae. The lime, offering an enlargement of the available substratum, becomes densely covered by diatoms, pre-

dominantly *Achnanthes*.

The normal winter situation is characterised by an undergrowth of *Cocconeis*, *Rhoicosphaenia*, lower *Gomphonema* and *Achnanthes*. Higher up rise greater *Gomphonema* colonies, sometimes in touch with long *Cymbella prostrata* tubes. High up rise towering *Cymbella lanceolata*, older stalks of which are covered by *Achnanthes* and *Synedra*. *Achnanthes* grows more near reed surface, *Synedra* occurs predominantly in free space. The same holds true for the overgrowth of the *Cymbella* tubes. In between this wickerwork are woven the chains and guirlandes of the araphid genera *Diatoma*, *Fragilaria* and *Tabellaria*.

In summertime the supporting *Cymbella*'s are gradually replaced by multicellular green algae. In this web, of which the supporting individuals are firmly attached to the substratum, the members of the loosely interwoven colonies are tightly connected. In this way the periphyton forms a unity, not only functional, but structural as well.

D. Species list.

In the following species-list a distinction is made between periphyton occurring on *Phragmites*-stems (PS), *Phragmites*-rootlets (PR) and submerged parts of *Typha* (TS). Mollusca, Annelida and Arthropoda are not included.

Cyanophyta

Chamaesiphon spec.	PS	
Homoeothrix juliana	PS	PR
Lyngbia spec.	PS	PS
Merismopedia spec.	PS	
Oscillatoria spec.	PS	
Symploca spec.	PS	

Chlorococcales

Pediastrum boryanum	PS	PR
Pediastrum spec.	PS	
Scenedesmus acuminatum		PR
Scenedesmus spec.	PS	

Ulothrichales

Coleochaete scutata	PS	
Microspora tumidula	PS	
Microspora spec.	PS	PR
Ulothrix spec.	PS	PR
Ulothrix zonata	PS	

Chaetophorales

Aphanochaete spec.	PS	
Chaetosphaeridium pringsheimi	PS	
Chaetosphaeridium spec.	PS	
Coleochaete spec.	PS	PR
Draparnaldia spec.	PS	
Stigeoclonium spec.	PS	PR

Oedogoniales

Bulbochaete mirabilis	PS	
Bulbochaete spec.	PS	PR
Oedogonium spec.	PS	PR

Siphonocladiales

Cladophora spec.	PS	PR
Rhizoclonium	PS	PR

Zygnematales

Closterium spec.	PS	PR	
Cosmarium spec.	PS	PR	
Mougeotia spec.	PS	PR	
Staurastrum spec.	PS	PR	
Spirogyra spec.	PS	PR	
Zygnema spec.	PS	PR	

Xanthophyta

Vaucheria spec.		PR	

Centrales

Cyclotella comta	PS	PR	TS
Melosira spec.	PS		
Melosira varians	PS	PR	TS
Stephanodiscus astrea	PS	PR	TS

Pennales

Achnanthes affinis	PS		
Achnanthes clevei	PS		
Achnanthes dispar	PS		
Achnanthes lanceolata	PS		TS
Achnanthes minutissima	PS		
Achnanthes spec.		PR	TS
Amphora ovalis	PS	PR	
Amphora spec.			TS
Anomoeoneis exilis	PS		TS
Asterionella formosa	PS		TS
Caloneis amphisbaena	PS		
Cocconeis pediculus	PS		
Cocconeis placentula	PS	PR	TS
Cymatopleura elliptica	PS	PR	
Cymatopleura solea	PS	PR	
Cymatopleura spec.	PS		
Cymbella affinis	PS	PR	TS
Cymbella aspera	PS		
Cymbella cistula	PS	PR	TS
Cymbella helvetica	PS		
Cymbella lanceolata	PS	PR	TS
Cymbella microcephala	PS		
Cymbella naviculiformis	PS		
Cymbella cf. *parva*	PS		
Cymbella prostrata	PS	PR	TS
Cymbella turgida	PS		
Cymbella ventricosa	PS	PR	
Diatoma anceps	PS		
Diatoma elongatum	PS	PR	TS
Diatoma vulgare	PS	PR	TS
Epithemia sorex	PS		
Eunotia pectinalis	PS		TS
Eunotia spec.	PS	PR	
Fragilaria capucina	PS	PR	TS
Fragilaria construens	PS	PR	
Fragilaria crotonensis	PS	PR	TS
Fragilaria intermedia	PS		
Fragilaria pinnata	PS		

Gomphonema acuminatum	PS		TS
Gomphonema angustatum	PS		
Gomphonema constrictum	PS	PR	TS
Gomphonema gracile	PS		
Gomphonema intricatum	PS		
Gomphonema longiceps			TS
Gomphonema olivaceum	PS	PR	
Gomphonema parvulum	PS		
Gomphonema spec.		PR	
Gyrosigma acuminatum	PS	PR	
Gyrosigma attenuatum	PS		
Gyrosigma spec.			TS
Navicula cincta	PS		
Navicula cryptocephala	PS		
Navicula cuspidata	PS		
Navivula dicephala			TS
Navicula gastrum	PS		
Navicula gracilis		PR	
Navicula hungarica	PS		
Navicula pupula	PS		
Navicula radiosa	PS	PR	TS
Navicula rhynchocephala	PS		
Navicula spec.	PS		
Navicula tuscula	PS		
Neidium iridis	PS		
Nitzschia angustata			TS
Nitzschia dissipata			TS
Nitzschia recta	PS		TS
Nitzschia sigma		PR	
Nitzschia spec.	PS	PR	
Pinnularia spec.	PS		
Rhoicosphaenia curvata	PS	PR	TS
Stauroneis lapponica	PS		
Stauroneis phoenicenteron	PS		
Stauroneis spec.	PS		
Surirella robusta		PR	
Surirella spec.	PS		
Synedra acus	PS	PR	TS
Synedra affinis		PR	
Synedra parasitica	PS		
Synedra pulchella	PS		
Synedra rumpens	PS		
Synedra tabulata	PS		
Synedra ulna	PS	PR	
Synedra vaucheriae	PS		
Tabellaria fenestrata	PS	PR	TS
Tabellaria flocculosa	PS	PR	TS

Rhodophyta

Asterocystis smaragdina	PS	PR
Batrachospermum spec.	PS	PR

Mastigophora

Bicoeca spec.	PS	PR
Bodo spec.	PS	
Codosiga utriculus		PR
Oicomonas spec.	PS	PR

Salpingoeca spec.		PR

Rhizopoda

Actinophrys spec.	PS	
Actinophrys subalpina		PR
Amoeba spec.	PS	
Arcella spec.	PS	PR
Chlamydophrys stercorea	PS	
Pyxidicula operculata	PS	
Raphidiophrys pallida		PR
Vampyrella spec.	PS	PR

Ciliatea

Acineta tuberosa	PS	PR
Carchesium polypinum	PS	
Cothurnia spec.	PS	PR
Euplotes spec.		PR
Lacrimaria olor	PS	
Lacrimaria spec.		PR
Lacrimaria vermicularia	PS	
Lionotus spec.	PS	PR
Opercularia spec.	PS	
Podophrya spec.		PR
Stentor		PR
Vaginicola spec.	PS	PR
Vorticella campanula	PS	PR
Vorticella convallaria	PS	PR
Vorticella microstoma	PS	PR
Zoothamnium simplex		PR

Porifera

Spongilla lacustris	PS	

Cnidaria

Hydra spec.	PS	PR

Rotatoria

Adineta spec.	PS	
Brachionus spec.	PS	PR
Collotheca spec.		PR
Conochilus spec.	PS	
Ptygura spec.		PR
Sinantherina socialis	PS	

Nematoda

Prodesmodora spec.	PS	

Gastrotricha

Chaetonotus spec.		PR

E. References

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.

HILLEBRAND, H., 1976. De meercellige wieren van de Botshol. In: Bakker *et al.*, ed., De Noordelijke Vechtplassen. Stichting voor de Vecht en het Oostelijk en Westelijk Plassengebied.

KADLUBOWSKA, J.Z., 1977. Einfache Methode zum quantitativen Vergleich von Saprobiocoenosen. Arch.Hydrobiol.beih.Ergebn.Limnol., 9: 113-116.

MESCHKAT, A., 1934. Der Bewuchs in den Röhrichten des Plattensees. Arch.Hydrobiol., 27: 436-517.

ROOS, P.J. & F.J. TRUEBA, 1977. Epiphytic protozoans on reed rootlets from Dutch water. Hydrobiologia, 54: 241-245.

VAN DER WERFF, A., 1955. A new method of concentrating and cleaning diatoms and other organisms. Verhandl.Intern.Verein.Theoret.Angewand.Limnol., 12: 276-277.

WETZEL, R.G. & H.L. ALLEN, 1970. Functions and interactions of dissolved organic matter and the littoral zone in lake metabolism and eutrophication. In: Z. Kajak & A. Hillbricht-Ilkowska, eds., Productivity problems of fresh waters. Warszawa, PWN Polish Scientific Publishers, 333-347.

MACROFAUNA IN THE BOTTOM AND THE LITTORAL VEGETATION

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Introduction

A study of macro invertebrates was started in 1977 with preliminary investigations in different types of vegetation, along different shores and with a number of artificial substrates. The first objective was to find the best approach for a quantitative inventory. The bottom fauna has been investigated with a Peterson grab in a number of stretches from the shore to the deepest part of the lake. In 1978 we carried out a programm of inventory in the littoral vegetation and the bottom, the results of which are briefly reported here. In 1979 three types of natural vegetation were sampled for biomass estimation. This part is under study. As the results of the 1978 investigations are still in a reporting phase, we shall indicate some of the main findings that can give a first insight in the structure of the macrofauna cenoses to be found in the lake.

Methods

a. Natural vegetation. Scuba divers took samples from the littoral vegetation with a specially constructed handnet with an opening of approximately 1200 cm^2. The vegetation consisted predominantly of *Potamogeton lucens* (June-November). In dependence of the season the samples had to be taken near the shore at 1.5 m depth or further to the centre of the lake with a maximal depth of 8 m. For comparing the results in a quantitative way the volume of the plant material was assessed by measuring the water displacement (law of Archimedes). The numbers of organisms have been counted and expressed as numbers per standard sample of 230 ml of vegetation.

b. Artificial plants. In the littoral some lines of artificial plants were attached just above the bottom. At depths of 3, 6, 11 and 16 m 4 plants were placed. Moreover, in the open water zone outside the vegetation belt at a depth of 6, 11 and 16 m a few units of three plants were placed. In these units the plants are connected above each other (Fig. 1). At the moment of sampling the artificial plants were enveloped with nets. All manipulations were executed by scuba divers. The surface of each artificial plant is 0.31 m^2.

c. Bottom. The bottom fauna has been sampled with a Peterson grab on depths

of 3, 6, 9, 11, 16, 21 and 27 m. At each depth 5 grasps were taken. The organisms
have been calculated as numbers per grasp per depth, which comprises a surface
area of 400 cm^2.

Results

We found a total number of species of about 180. Of these 131 species were
found on the natural vegetation (21 exclusively), 112 species on artificial
plants (14 exclusively) and 120 species in the bottom samples (26 exclusively).
The natural vegetation and the artificial plants had 96 species in common. In
Table 1 some figures have been given for numbers of species and, for the natural
vegetation, of specimens in the different months of investigation.
In all cases an increase in species numbers towards the end of the year can be
observed, especially in the natural vegetation. Here a similar increase in num-
bers of organisms per volume of plant material occurred. Because of the late
start in growth of the natural vegetation the colonization of the artificial
plants took place at least one month earlier. The bottom fauna is partly consti-
tuted of animals living on detritus in the shallow part. The animals living in
the deeper parts of the lake are less influenced by the season.

In Table 2 the numbers of species within taxa of different levels is given
per method of sampling and as total numbers as well. A number of species was
captured once or a few times and in very low numbers. This was due to the sam-
pling methods enabling quick-swimming organisms to escape. For some of these
species the unsuitability of the sampled substrates must have been another fac-
tor. The caddis larva *Anabolia nervosa* for example can be found at the stony
shore where the water is turbulent and rich in oxygen. The species has been
found only once in the bottom samples and none were observed in the natural veg-
etation or on the artificial plants. Another caddis larva however, *Mystacides
longicornis*, was found in most samples. We present the numbers per sampling
method in the months of collection in Table 3. This species was encountered in
the littoral with a frequency of 70% out of 37 samples. The increase in numbers
during the season is beautifully demonstrated here. As the flight period of
this species is from June-September, the high numbers in autumn constitute the
next years generation.

The most numerous organisms in the littoral vegetation were by all means the
snail *Potamopyrgus jenkinsii*, the bivalve *Dreissena polymorpha* and larvae of the
chironomid *Endochironomus albipennis*. The latter species did not occur in the
bottom fauna samples, but the numbers on artificial plants were very high. From

Table 4 the enormous numbers of individuals found can be read. It is evident that the above mentioned organisms constitute a very important part of the food chain in the littoral. As for *Dreissena* there is a direct line to birds such as coots and ducks.

The bottom fauna samplings demonstrate the relation between the occurrence of organisms and depth. In Fig. 2 we plotted the number of species (total, arithmatic mean) of the bottom fauna for each sampled depth. There is a sharp bend in the curve around 10 m of depth. At this depth the maximal extension of the littoral vegetation is reached. Moreover, the metalimnion is formed at a depth of 8 (June) to 11 m (Autumn). The bottom samples in the epilimnion contain quite a number of species that populate the detritus. Therefore numbers increase after June as can be seen in Fig. 3. In the hypolimnion seasonal influence on the species composition can hardly be discerned. The numbers of specimens may increase during the year, just as is found in the natural and artificial vegetation (for example the molluscs in Table 4). However, this does not hold for all species. In Fig. 4a the numbers of specimens of tubificid worms (bottom samples) with hair chaetae are given. These organisms are characteristic for the bottom fauna. Their numbers are not influenced by the "autumn growth" effect. On the other hand the Tubificidae without hair chaetae (Fig. 4b) show an increase in numbers from June to October and a decrease in December on their preferred depth of 16 m. So there is a remarkable difference in distribution between these two groups of worms. It is suggested that the Tubificidae with hair chaetae are adapted to the weak mud in the deeper parts of the lake, where those without hair chaetae sink down into the mud. Such distribution patterns in relation to the depth have been analyzed for all species. A clear vertical distribution in the biocenoses is apparent. The three different sampling methods have proved to supply each other perfectly.

Most species belong to a group with a distribution pattern that can be described as decreasing in numbers from surface to deeper parts, either in gradually diminishing numbers or according to a steep curve. In other groups stable numbers are present until a depth of 6 m or even 11 m is reached before the decrease starts. Apart from these patterns sometimes an increase in numbers with progressing depth can be observed (Fig. 4a). Also a maximal number at a certain depth, for instance at 16 m can be present (Fig. 4b).
Additional information is derived from cluster analysis. On the basis of the quantitative species composition all samples have been compared. These data are being worked up at the moment. The first results seem most promising. Comparing all samples of the three methods a division in four clusters was obtained. The

main division shows two clusters, one consisting of bottom samples from 9 m and deeper including the artificial plants at the 16 m depth, and one of the vegetation samples together with the "shallow water" samples from bottom and artificial plants. In this last category a seasonal influence dominates the further division.

Some general conclusions

The littoral vegetation starts its development only in June and reaches its richest expansion in autumn. By that time the organic debris from these plants start to play an important role for detritivorous organisms. The quantitative development of the fauna in the littoral is highest in autumn and early winter. The bottom fauna in the hypolimnetic parts of the lake is less dependent on the season. The experiments with artificial plants have shown that most species are present at the time when no littoral vegetation can be observed. The absence of substrate in the form of vegetation with epiphyton as a major food resource keeps the numbers low in spring and early summer.

Acknowledgements

Table 1. Numbers of species and specimens in different months.

1978	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Natural vegetation								
number of species		46	61			87	107	
number of specimens/230 ml		80	648			2231	3136	
idem without *Dreissena*		55	600			868	1031	
Artificial plants (species)	42	74			87	90		
Bottom (species)		45	89			75		89

Table 2. Numbers of species in total and per method.

	total	nat. veg.	artific.	bottom
SPONGILLIDAE	1	1	-	-
HYDROZOA	4	4	4	-
BRYOZOA	2	2	-	1
OLIGOCHAETA				
Naididae	10	9	5	4
Tubificidae	14	9	1	12
Lumbriculidae	1	-	-	1
TURBELLARIA	6	3	6	2
HIRUDINEA	7	5	5	6
NEMERTINI	1	1	1	-
GASTROPODA + *Dreissena*	18	10	14	12
LAMELLIBRANCHIATA				
Pisidium	8	1	2	8
CRUSTACAEA	4	4	3	2
HYDROCARINA	33	27	20	24
INSECTA				
Ephemeroptera	6	6	5	3
Odonata	2	1	1	1
Hemiptera	1	-	1	1
Megaloptera	1	-	1	1
Neuroptera	1	-	1	-
Trichoptera	16	11	11	10
Lepidoptera	3	3	1	1
Coleoptera	4	3	2	1
Chironomidae	35	30	27	28
other Diptera	2	1	1	2

Table 3. Numbers of *Mystacides longicornis*.

1978	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Natural vegetation (N/230 ml)		1.8	1.9			119	39	
Artificial plants (N/plant)	22.7	5.3			20.5	42		
Bottom (N/grab)		2.2	1.9			5.5		13.2

Table 4. Numbers of the most abundant species of macro organisms.

1978	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Potamopyrgus jenkinsii								
Nat. veg. (N/230 ml)		26.4	9.3			70.4	284.4	
Art. pl. (N/plant)	13.3	11.6			39.5	25.8		
Bottom (N/grab)		6.4	29.5			32.2		120.6
Dreissena polymorpha								
Nat. veg. (N/230 ml)		4.2	3			1404	2105	
Art. pl. (N/plant)	6.7	21			1562	2695		
Bottom (N/grab)		9.3	22.2			85.5		175
Endochironomus albipennis								
Nat. veg. (N/230 ml)		1.9	554			9.4	10.2	
Art. pl. (N/plant)	37	6.5			73.1	41.4		

Fig. 1. Position of artificial plants with nets.

Fig. 2. Number of species of the bottomfauna in relation to the depth.

Fig. 3. Number of species of the bottomfauna in relation to the depth
for four sampling dates.

Fig. 4a. Number of specimens of Tubificidae with hair chaetae in relation to the depth for four sampling dates.

4b. Idem of Tubificidae without hair chaetae.

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INTERRELATIONS BETWEEN MACRO- AND MICROFAUNA IN THE LITTORAL ZONE

C. Davids

Introduction

My contribution to the present report consists of a description of a number of small-scale investigations that could not have been realized but for the efforts of our technical assistants and students during the past two years. These investigations, together with others to be carried out in future years will ultimately lead us to the understanding of the ecological factors that determine the appearance of exactly that combination of animal species, now present in the littoral zone of Lake Maarsseveen I.

In the initial phase of such a field of research, inventories, studies on species distribution according to depth and on the fluctuations in numbers in time will be predominant. The preliminary contribution by DAVIDS and WEGENER SLEESWIJK, an inventory of the testaceans in the lake, is also to be considered as a part of the description of the structure of the littoral zone.

In order to obtain the above mentioned purpose, a good deal of research into autecological and population-dynamical problems is needed.
Among the macrofauna, the most important taxonomic groups studied now are the chironomids (viz. contribution by DAVIDS, KOUWETS and SCHREYER) and the water mites (viz. contribution by DAVIDS, DE GROOT and MOL). Among the microfauna, the following groups can be mentioned: Cladocera, Copepoda and Ostracoda. A contribution on the Ostracoda is shortly to be published (SLUYS, Hydrobiol.Bull., in press).

It seems that the water mites make up the most important group of predators in Lake Maarsseveen I, together with some species of chironomids and copepods. Their preys probably consist of representatives of almost all taxonomic groups.

Items that will be studied, both in the field and in the laboratory, are predator-prey relations, dynamics of populations, parasitic relations (between water mite larvae and insects), interspecific competition and annual cycles of species. Results are to be translated toward the situations in the field. A study by DAVIDS, HEYNIS and WEEKENSTROO (Hydrobiol.Bull., in preparation) can be regarded as a first step in the realization of this program.

In order to obtain a correct estimation of the results of these studies, it will sometimes be necessary to compare data from Lake Maarsseveen I with those from other lakes, a.o. Lake Maarsseveen II.

Moreover, the mutual exchange of organic and anorganic material between the pe-
lagial and littoral zones in Lake Maarsseveen I must be considered. Apart from
the natural sedimentation, also filter feeders will deposit a fair amount of
organic material. It is, for instance, well-known that more chironomid larvae
occur between banks of the bivalve *Dreissena polymorpha* than on localities
where these banks are lacking. The contribution by DAVIDS and TEN WINKEL deals
with the part played by *D. polymorpha* in the development of the layer of bottom-
sediment.

TESTACEANS (RHIZOPODA, TESTACEA) FROM THE BOTTOM SEDIMENTS OF
LAKE MAARSSEVEEN I AND II.

C. Davids and Corien Wegener Sleeswijk

Presented are the results of a preliminary study on the comparison of the
testacean associations in the two Maarsseveen lakes. The samples were taken on
comparable depths in the two lakes, viz.:
a̱. Beyond the emerged vegetation (1 m). ḇ. Beyond the zone of vegetation (sub-
littoral), lake I 8 m; lake II 5 m. c̱. Below the thermocline, lake I 12 m; lake
II 10 m. ḏ. In the deeper part of the produndal, lake I 20 m; lake II 15 m.
Scuba divers collected 3 litres of the superficial mud layer on each of the in-
dicated depths. The collecting bottles had an extra opening to let the air es-
cape out of the bottle, so water and mud could enter smoothly. The sampling
date for Lake I was July 30th 1979 and for Lake II August 6th 1979.
Each sample was concentrated by sieving through a net with meshes of 30 μm. The
samples were stored for one or two days in bottles. In this period the mud had
deposited and the testaceans had congregated in the superficial mud layer. By
pipetting off this layer one can collect most of the amoebae from the original
3 litres sample.
The material was preserved and from each depth 50 specimens were counted. For
this purpose the testaceans in one drop were counted under the microscope and
next we examined as many drops as necessary in order to find the desired 50
specimens. Mostly we needed 20 drops (5-52) to complete this number. The data
are summarized in Table 1.
    It was not always possible to identify to the species level, so a part of
the testaceans has been identified to the genus. The following remarks can be
made concerning the various species found.
Especially on the depth of 20 m in Lake I we found specimens very close to *Dif-
flugia amphora* Leidy, but we are not quite sure.
Arcella rotundata var. *aplanata* Defl. is mentioned once for the dutch fauna by
A.G. Vorstman (1956) in a Meyendel report.
Among specimens belonging to the genus *Centropyxis*, we were able to identify a
number as *Centropyxis aculeata* Ehr.: but since these identifications combined
with the counting method are very difficult, we are not sure of the exact num-
bers.
Once we found *C. delicatula* Pen.; possibly more specimens collected belong to
this species. For these reasons we tabulated all the *Centropyxis* specimens to-

gether. Once we found *Euglypha aspera* Pen.; the specimen was so similar to the description of Penard that we are sure of our identification. The species is new to the dutch fauna. *Cyphoderia trochus* Pen., a very rare species of the dutch fauna, was found once by DE GROOT (personal communication). *Campascus minutus* Pen. is new to the dutch fauna.

Comparing the samples from Lake II we see a great similarity between the results of the several depths, while in Lake I differences exist between the associations of 8 and 12 m on one hand and 1 and 20 m on the other. The latter two are comparable with the results of Lake II.

The area around the thermocline (8 m and 12 m) in Lake I is characteristic because of the presence of rather large quantities of *Corythion, Cyphoderia* and *Campascus*. Minor differences between Lake I and II are the presence of larger numbers of *Difflugia oblonga* and *Euglypha laevis* in Lake II than in Lake I.

In Lake I we found 22 species belonging to 10 genera and in Lake II 17 species belonging to 6 genera.

When comparing the species composition of the two lakes and considering the fact that different distribution areas for testaceans can be distinguished in Lake I, we conclude that Lake II is more polluted than Lake I. This is in agreement with other studies.

There are only a few data from other deep lakes. PENARD (1905 and previous papers) collected from depths of 20 up till 50 m especially in Lac Léman. ŠTĚPÁ-NEK (1968) collected in the Bodensee 653 specimens from 4 up till 251 m (12-73 specimens per depth). Both authors found *Difflugia* on any depth in similar numbers, just as we did. We found much larger numbers of *Arcella* than were found in the Bodensee. *Arcella* and *Centropyxis* were not found in Lac Léman. Just like ŠTĚPÁNEK we did not find *Centropyxis* in the deeper parts of the lake (this genus being most abundant above the thermocline). There is agreement concerning the numbers of *Euglypha* between Lake I and the Bodensee. In Lake II *Euglypha* is more abundant than in the lakes just mentioned. Also concerning the distribution of *Cyphoderia* similarity exists between Lake I and the Bodensee. ŠTĚPÁNEK found *Cyphoderia* between 10 and 30 m, we did so between 8 and 20 m.

LITERATURE

PENARD, E., 1905. Les Sarcodinés des Grands Lacs. Genève.

STEPANEK, M., 1968. Die Rhizopoden des Tiefenschlammes im Bodensee. Arch.Hydrobiol., Suppl. 33: 442-450.

Table I. The testaceans with their numbers collected on different depths of the Lakes Maarsseveen I and II.

depth	Lake I				Lake II			
	1 m	8 m	12 m	20 m	1 m	5 m	10 m	15 m
Difflugia acuminata Ehr.	1			1	1	1	1	1
" *corona* Wallich	2				1	1	1	
" *elegans* Pen.			1		1			
" *gramen* Pen.	4		1	1	2	1	2	2
" *lobostoma* Leidy	2		1	2	1	1	3	5
" *oblonga* Ehr.	1		2	2	7	18	13	14
" spp.	10	2	6	17	10	4	3	4
Lesquereusia modesta Rhumbler			1					
Arcella conica Defl.						1		1
" *discoides* Ehr.	1		3	2	3		3	3
" *gibbosa* Pen.		2	3	1	2	4	2	3
" *hemisphaerica* Perty	6	3	10	9	1		8	5
" *rotundata* var. *aplanata* Defl.					1			2
" *vulgaris* Ehr.		1		2				1
" spp.	3	3	2	2	2	1	1	3
Centropyxis spp.	19	1		2	11	12	6	1
Cryptodifflugia oviformis Pen.				3		2		1
Euglypha aspera Pen.				1				
" *laevis* (Ehr.)	1		1	2	7	4	7	3
Trinema enchelys (Ehr.)				1				1
Corythion cf. *dubium* Taránek		13						
" *pulchellum* Pen.		1		1				
Cyphoderia ampulla (Ehr.)		20	9	1				
" *laevis* Pen.			9					
" *trochus* Pen.			1					
Campascus minutus Pen.		4						

CHIRONOMIDS (CHIRONOMIDAE, DIPTERA) FROM LAKE MAARSSEVEEN I

C. Davids, F. Kouwets and M. Schreyer

Chironomids occur in large numbers in the benthic zone of Lake Maarsseveen I and play an important part in the food-web within the lake. Moreover there are several relationships between chironomids and water mites. The larvae of the majority of the water mite species from Lake Maarsseveen I are parasitic on chironomids. Besides this, the adult stages of several mite species are predacious on chironomid larvae. For these reasons it is worthwhile to study the chironomid associations of Lake Maarsseveen I, the abundance of the separate species and their bionomics.

In 1978 the third author (M. Schreyer) collected and identified the chironomid larvae that were sampled on different substrates. The imagines were collected and identified in 1979 by the second author (F. Kouwets).

Chironomid larvae

This investigation is a part of the general survey of the macrofauna in Lake I, presented in this volume separately by HIGLER. HIGLER also describes the sampling methods, which include the use of artificial plants.

Apart from in Lake I, samples were also taken in the peat bog area near Lake Maarsseveen I.

The results of the sampling on the various substrates have been presented in Table 1. Identification of the specimens is based mainly on the monography of Moller Pillot (1978-1979).

Imagines

The imagines were collected by sweeping a net along the vegetation and the shrubs around the field station. One of the disadvantages of this method is that we are not sure whether or not all the specimens originate from the lake, but for certain reasons we did not use floating cages for collecting purposes.

On every fortnight, from May up till October 1979, we collected several hundreds of chironomids. The total number of collected specimens was 12,292. These were anaesthesized by means of aethylacetate and subsequently preserved in alcohol 70%. A list of species is presented in Table 2.

Chironomids harbouring water mite larvae were observed for the first time in the end of May, and were from then on continuously found until the end of

the sampling period. The identification of these parasitizing water mite larvae
has not yet been completed.

Once in the night of July 3th 1979 collecting was done by means of a light
trap. On this occasion, the chironomids that alighted on the screen behind the
light were collected separately from those that gathered round the lamp and were
caught by the sweep-net. The results of these catches were compared with the one
obtained on the previous day by means of the regular sampling method.
During the day 678 chironomid specimens were caught, belonging to 45 species. At
night we collected from the screen 453 specimens, belonging to 28 species. In
this sample especially females of *Cricotopus sylvestris* were abundant (131 speci-
mens). From the air round the lamp we collected 911 specimens belonging to 29
species. Also this sample contained many (103) females of *C. sylvestris*, but
even more females of *Procladeus choreus* (106) and of *Phaenospectra flavipes* (118).
The latter two species therefore are strongly attracted by the light, but do not
alight on the screen. The number of chironomids caught in the daytime has been
included in Table 2.

Special remarks on the larvae (see Table 1).

The species *Pogonocladius consobrinus*, *Potthastia longimana*, *Parakiefferiel-
la bathophila* have their main distribution area in alpine and subalpine lakes in
Scandinavia and Austria. *Potthastia longimana* occurs also in the so-called
"Eifelmaaren" in western Germany (BRUNDIN, 1949; THIENEMANN, 1954). Very little
is known on the distribution ecology of *Pogonocladius consobrinus*. The main dis-
tribution area should be northern Europe (MOLLER PILLOT pers. comm.). BRUNDIN
(1949) has found the species in lakes in eastern Greenland.
Potthastia longimana is a species that prefers small ,well aerated and swiftly
flowing waters and also highly oxygenated parts of lakes (THIENEMANN, 1954).
Parakiefferiella bathophila is a common species of subarctic lakes in Lapland,
it is much less common in central Europe.

The group of the Tanytarsini as well as the species belonging to the genus
Chironomus often constitute a rather large part of the benthal fauna of lakes.
We obtained indications (see Table 1) that in Lake I the Tanytarsini in general
mainly inhabit the sandy soil of the littoral zone, *Chironomus* species inhabit
the profundal zone from a depth of 16 up to 30 m. Tanytarsini and *Chironomus*
spp. are often found to compete in lakes where the groups occur together (THIE-
NEMANN, 1954). The data shown in Table 3 also seem to indicate this.

It appears further from Table 1 that several species mainly inhabit the sub-
mergent vegetation and are all but absent from bottom samples. Many species of

the Orthocladiinae are mining species, which accounts for their presence in the natural submergent vegetation. When compared with non-mining species they occur in low numbers. Filterfeeders make use of the submerse vegetation exclusively as a substrate. This is illustrated by the fact that species belonging to this group also occur in large numbers on the artificial plants. This is shown for *Endochironomus albipennis* and *Glyptotendipes* spp., and to a lesser extent for *Microtendipes* group *chloris*.

Something more can be said about the identity of the specimens belonging to *Microtendipes* gr. *chloris*. On Fig. 1A the distribution of larval length in the course of the year is shown. When comparing this diagram with the data on the relative abundance of the imagines of *M. pedellus* (Fig. 1B) (in percentages of the total numbers of specimens per sample) we can draw the following preliminary conclusions: 1. that the larvae most probably belong to the species *M. pedellus*; 2. that this species has two generations per year. According to the data of Moller Pillot (1978-1979) *M. pedellus* is on the wing between early May and the second half of October, with peaks in July and in September. In our data these maxima appear in August and October.

Special remarks on the imagines (see Table 2).

Camptocladius stercorarius, *Pseudorthocladius filiformis* and *Smittia* spp. have terrestrial larvae. *Limnophyes globifer*, *Metriocnemus atratulus*, *M. tristellus* and *Paraphaenocladius impensus* possibly have terrestrial larvae or larvae that live in the border area between land and water. The bi-monthly percentages of *Procladius choreus* among the samples remained stationary during the whole period. 59 (15%) male specimens were infested with water mite larvae.

The relative abundance of *Ablabesmyia monilis* in the samples showed also very little variation with the exception of the sample of 14th August when the number of specimens was very low.

Krenopelopia nigropunctata and *Zavrelimyia melanura* are known to occur in springs (MOLLER PILLOT, 1978-1979). The latter species is new for the Dutch fauna.

Cricotopus spp. were collected especially from the middle of June up till the middle of July.

Chironomus anthracinus was very common in the beginning of May (70% of the sample),in July-August the species appeared again but in much smaller numbers than in May. *Chironomus cingulatus* was especially collected in the beginning of July. *C. plumosus* has been found throughout the sampling period. The larvae of *Demeyerea rufipes* and *Xenochironomus xenolabis* live in freshwater sponges. *Endochironomus tendens* was especially collected in August, and *Glyptotendipes paripes*

and *Limnochironomus lobiger* mainly occurred in June.

Limnochironomus nervosus and *L. tritomus* are difficult to distinguish from each other. These species were infested rather frequently with water mite larvae.

Microtendipes chlorus was only collected in May. *M. pedellus* was common throughout the collecting period (in August up to 40% in the samples, see Fig. 1A and B and comments above). The mean infestation rate by water mite larvae was 7% of the 1179 ♂♂ collected.

Parachironomus arcuatus occurred throughout the collecting period, especially in June. *P. cinctellus* is new for the Dutch fauna (LEHMANN, 1970). The larva of *Parachironomus* sp. 1 (see Table 1) possibly belongs to *P. cinctellus*.

Stictochironomus sticticus made up 40% of the sample taken in the end of May, but in the other samples the species was present only incidentally.

Tribelos intextus was found in the largest numbers in the second half of May. The largest numbers of *Tanytarsus bathophiles* were found in May and in July-August. A high infestation rate by mites was found in the second half of the summer (up to 40%). *T. lestagei* was especially found at the end of the summer season. The infestation rate by mites was very high (up to 70%). The species occurs in lakes with a complete O_2 saturation (REISS & FITTKAU, 1971).

Literature

BRUNDIN, L., 1949. Chironomiden und andere Bodentiere der südschwedischen Urgebirgsseen. Ein Beitrag zur Kenntnis der bodenfaunistischen Charakterzüge schwedischer oligotropher Seen. Rep.Inst.Freshwat.Res.Drottningholm, 30: 1-914.

LEHMANN, J., 1970. Revision der Europäischen Arten (Imagines ♂♂) der Gattung *Parachironomus* Lenz (Diptera, Chironomidae). Hydrobiologia, 33: 129-158.

MOLLER PILLOT, H.K.M., 1978-1979. Larven der Nederlandse Chironomidae (Diptera). Nederl.Faun.Meded., 1: 1-105.

PINDER, L.C.V., 1978. A key to adult males of British Chironomidae. Freshw.Biol. Assoc.Scient.Publ. No. 37 (Vol. 1 and 2).

REISS, F. & E.J. FITTKAU, 1971. Taxonomie und Ökologie europäisch verbreiteter *Tanytarsus*-Arten (Chironomidae, Diptera). Arch.Hydrobiol./Suppl.,40: 75-200.

THIENEMANN, A., 1954. *Chironomus*. Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. Die Binnengewässer,XX: 1-834.

Table 1. List of collected larvae of chironomids on different substrates in Lake
Maarsseveen I and in the peat bog area. Numbers indicate percentages.
+ less than 0.5%; *not collected as imago (see Table 2).

	Substrate			
Species	artificial plants	bottom	natural vegetation	peat bog area
TANYPODINAE				
Coelotanypodini				
Clinotanypus nervosus				+
Macropelopiini				
Procladius sp.	2		1	+
Pentaneurini				
*Ablabesmyia longistyla**		+	+	+
Ablabesmyia monilis/A. phatta	3	+	+	4
*Guttipelopia guttipennis**				+
ORTHOCLADIINAE				
Orthocladiini				
Cricotopus sp.	+	+	2	7
Microcricotopus bicolor	+		+	1
*Pogonocladius consobrinus**			1	
*Potthastia longimana**	+	+	+	
Prodiamesa olivacea		+		
Psectrocladius ex gr. *dilatatus**	1		1	+
*Psectrocladius simulans**	1	+	1	+
Psectrocladius ex gr. *psilopterus*	2	+	2	+
Metriocnemini				
Corynoneura sp.	+	+	+	+
Parakiefferiella bathophila	+	+	1	+
CHIRONOMINAE				
Chironomini				
Chironomus ex gr. *plumosus*	+	2		+
Chironomus ex gr. *thummi* s.l.	19	28	+	1
Cryptochironomus sp.*	1	6	1	+
Cryptocladopelma ex gr. *laccophila**		+		
Cryptotendipes sp.	+	1	+	
Demicryptochironomus vulneratus	1	2	+	
Limnochironomus ex gr. *lobiger*		+	2	1
Limnochironomus ex gr. *nervosus*	+	5	1	2
Limnochironomus ex gr. *tritomus*	6	1	3	2
Endochironomus albipennis	31	1	56	29
Endochironomus tendens				1
Glyptotendipes cf. *caulicola**				4
Glyptotendipes sp.1	3	+	1	22
Harnischia sp.		2	+	
Microtendipes ex gr. *chloris*	24	15	18	9
Parachironomus ex gr. *arcuatus*	2	+	4	2
Parachironomus sp.1	1	+	+	
Phaenopsectra sp.	+	+	2	+

Table 1. (Continued)

| | Substrate | | | |
Species	artifi-cial plants	bottom	natural vegeta-tion	peat bog area
Polypedilum ex gr. *bicrenatum*	1	2	1	+
Polypedilum ex gr. *nubeculosum*	1	7	+	+
Polypedilum ex gr. *sordens*	+	+	+	10
Stictochironomus sp.		8	+	+
Tribelos intextus	+	4	+	2
Xenochironomus xenolabis				+
Zavreliella marmorata *				+
Tanytarsini				
Cladotanytarsus sp.	1	3	1	+
Paratanytarsus sp.	+	1	+	
Tanytarsus sp.	2	2	2	1
	100%	100%	100%	100%
Total number of specimens	4408	3978	4460	3897

Table 2. List of chironomid imagines collected by sweep-net around the field sta-
tion at Lake Maarsseveen I from May till October 1979. The total number
of chironomids was 12 292. •rather common, ••common, •••very common
(more than 1%, 5% and 10% of the total amount respectively). The nomen-
clature is after Pinder (1978), except for *Tribelos intextus* where Mol-
ler Pillot (1978-1979) is followed.

TANYPODINAE

Coelotanypodini
    Clinotanypus nervosus (Meigen)
Macropelopiini
    ••*Procladius choreus* (Meigen)
    P. simplicistylus Freeman
    Psilotanypus lugens (Kieffer)
    P. ruforittatus (van der Wulp)
Pentaneurini
    •*Ablabesmyia monilis* (L.)
    A. phatta (Eggert)
    Krenopelopia nigropunctata (Staeger)
    Zarrelimyia melanura (Meigen)
    Z. spec. 1
Tanypodini
    Tanypus punctipennis Meigen

ORTHOCLADIINAE

Orthocladiini
    Cricotopus (Cricotopus) albiforceps (Kieffer)
    C. (C.) festivellus (Kieffer)
    C. (C.) flavocinctus (Kieffer)
    •*Cricotopus (Isocladius) intersectus* (Staeger)
    C. (I.) sylvestris (Fabricius)
    Microcricotopus bicolor (Zetterstedt)
    Paratrichocladius rufiventris (Meigen)
    Psectrocladius sordidellus (Zetterstedt)
Metriocnemini
    Camptocladius stercorarius (Degeer)
    Corynoneura edwardsi Brundin
    Limnophyes globifer Brundin
    Metriocnemus atratulus (Zetterstedt)
    M. tristellus Edwards
    Parakiefferiella bathophila (Kieffer)
    Paraphaenocladius impensus (Walker)
    Paratrissocladius spec. 1
    Pseudorthocladius filiformis (Kieffer)
    Smittia leucopogon (Meigen)
    S. pratorum (Goetghebuer)

CHIRONOMINAE

Chironomini
    Camptochironomus pallidivittatus (Malloch)
    ••*Chironomus anthracinus* Zetterstedt
    •*C. cingulatus* Meigen
    C. luridus Strenzke
    C. obtusidens Goetghebuer

Table 2. (Continued)

    C. plumosus (L.)
    C. riparius Meigen
    Cryptochironomus spec. 1
    C. spec. 2
    Cryptocladopelma virescens (Meigen)
    C. viridula (L.)
    Cryptotendipes spec. 1
    Demeijerea rufipes (L.)
    Demicryptochironomus vulneratus (Zetterstedt)
    Einfeldia dissidens (Walker)
    E. longipes (Staeger)
    E. pagana (Meigen)
    Endochironomus impar (Walker)
    E. lepidus (Meigen)
   •*E. tendens* (Fabricius)
    Glyptotendipes cf. *mancunianus* (Edwards)
    G. pallens (Meigen)
   •*G. paripes* (Edwards)
    Harnischia curtilamellata (Malloch)
    Kiefferulus tendipediformis (Goetghebuer)
    Leptochironomus tener (Kieffer)
    Limnochironomus lobiger (Kieffer)
    L. nervosus (Staeger)
    L. notatus (Meigen)
   •*L. pulsus* (Walker)
    L. tritomus (Kieffer)
  •*Microtendipes chloris* (Meigen)
 •••*M. pedellus* (Degeer)
  •*Parachironomus armatus* Goetghebuer
    P. cinctellus Goetghebuer
    P. digitalis (Edwards)
    P. frequens Malloch
    P. monochromus (van der Wulp)
    P. parilis (Walker)
    P. tenuicaudatus (Malloch)
    Pentapedilum sordens (van der Wulp)
  •*Phaenopsectra flavipes* (Meigen)
    Polypedilum cultellatum Goetghebuer
    P. nubeculosum (Meigen)
    P. scalaenum (Schrank)
    P. spec. 1
    Stenochironomus gibbus (Fabricius)
 •••*Stictochironomus sticticus* (Fabricius)
  •*Tribelos intextus* (Walker)
    Xenochironomus xenolabis (Kieffer)
Tanytarsini
    Cladotanytarsus nigrovittatus Goetghebuer
    Paratanytarsus laetipes (Zetterstedt)
    P. tenuis (Meigen)

Table 2. (Continued)

Stempellina bausei (Kieffer)
•• *Tanytarsus bathophilus* Kieffer
T. *eminulus* (Walker)
T. *excavatus* Edwards
T. *gregarius* Kieffer
T. *holochloris* Edwards
T. *inaequalis* Goetghebuer
•T. *lestagei* Goetghebuer
T. *pallidicornis* (Walker)
T. *usmaensis* Pagast
T. *verralli* Goetghebuer

Table 3. *Chironomus* spp. and Tanytarsini: numbers collected by
bottom sampler on different depths in Lake Maarsseveen I.

	Depth						
	3 m	6 m	9 m	11 m	16 m	21 m	27 m
Chironomus spp.	80	22	24	127	297	301	248
Tanytarsini	103	139	9	4	5	7	1

Fig. 1 A. Length frequency distribution of *M. pedellus* larvae on different sampling dates in 1978.

B. The proportions of *M. pedellus* imagines in chironomid samples taken by sweep-net during summer 1979.

THE WATER MITE FAUNA OF LAKE MAARSSEVEEN I

C. Davids, Ch. de Groot and A. Mol

Introduction

Water mites are our main field of study. Important subjects are for in-
stance their role in the food web and the parasitic relationships of the lar-
vae with insects.

It is necessary that our first object of research will be the species associa-
tions, the distribution in the lake and the abundance of the different species.
Once possessing such basic knowledge we can plan our further studies.
The following collection methods have been used.

a. Collecting by dip net along the shores.

b. Collecting by dip net, handled by scuba divers, in the littoral zone.

c. Collecting whole plants from various depths which were brought to the sur-
   face surrounded by nets. Natural as well as artificial vegetation was sam-
   pled this way.

d. Collecting by bottom sampler.

e. Collecting stones by dip net in exposed areas.

f. Collecting by underwater light traps in the littoral and profundal zones.

The methods mentioned sub c, d and e have been applied by the third author (A.
MOL). They are described in detail in the contribution of HIGLER elsewhere in
this volume.

The light trap used by us (DAVIDS and DE GROOT) is 30 cm in diameter and 15 cm
in height. It consists of four plexiglass funnels placed in a circle. The open-
ing in each funnel is a square with sides of 1 cm. It is constructed in such a
way that no light can escape upwards. In the centre of the trap is placed a
chemoluminescent light source. It consists of a sealed outer polyethylene tube
containing a liquid reagent and a tubular glass ampoule containing a second
liquid reagent. It is activated by flexing the polyethylene cylinder to break
the glass ampoule, allowing the two reagents to mix. The tube is then shaken
vigourously, and the chemoluminescent reaction is almost instantaneous. The
emission spectrum for the light source shows that the highest intensity is at
a wave-length of 516 nm. About 80% of the total emission lies between 480 nm
and 548 nm ("green") (see BARR, 1979). This author provides more practical de-
tails a.o. on the correlation between the temperature and the intensity and on
the decay in intensity of the light source.

The species of water mites of the two lakes compared

In 1977, we carried out some pilot sampling in the Lakes Maarsseveen I and II. This was done five times by dip net, in the period April-August and one time (August) by light trap. By these methods, we collected 30 species in Lake I and 19 species in Lake II during 1977, from which we concluded that the richer water mite fauna is present in Lake I. In 1978 we collected mainly by light trap and incidentally by scuba diving, exclusively in Lake I. In 1979 we did the same but results of this year are not yet available, apart from some incidental data which are included in Table 1. The general list of species in Lake I consists of all available data of these three years.

From the results of 1977, it became evident that the following species are very common in Lake II: *Hydrodroma despiciens* (640 collected specimens, against 8 specimens from Lake I), *Piona coccinea coccinea*, *P. stjoerdalensis* and *Unionicola crassipes*. Of these the two *Piona* species are very rare in Lake I, while *U. crassipes* is very common in both lakes. Characteristic among the list of species from Lake I (Table 1) are both species from deep lakes (*Arrenurus nobilis*, *Piona paucipora*, *P. coccinea imminuta*) and species common in lowland streams and unpolluted waters (*Hygrobates trigonicus*, *Piona longipalpis*) (see also DA-VIDS, 1979). *Piona pusilla disjuncta*, a new (sub)species for the Dutch fauna, was hitherto only known from a lake in Pomerania (VIETS, 1930). For another number of species (*Piona paucipora*, *Arrenurus biscissus* and *A. nobilis*) Lake Maarsseveen I is the only known finding-place in the Netherlands (DAVIDS, 1979).

Table 2 and 3 give indications about the abundance of the different species. It appears from these multiple data that a number of mite species occurs very frequently in Lake I. One of these dominant species is *Unionicola crassipes*, which together with *U. minor* forms the group of the so-called sponge-mites, because they have an obligatory relationship with freshwater sponges (Spongillidae). The eggs are laid in the sponge tissue and also the transformation stages (proto- and tritonymph) need the sponge so the mites do emerge from and re-enter the sponge during deutonymphal and adult stages.

It has become apparent to us that *U. crassipes* is present throughout the lake in large numbers. On the other hand, the distribution of the freshwater sponges is by no means uniform, as has been observed by scuba diving and by other means. In 1978, *Spongilla lacustris* completely covered the gauze partition of the swimming pool, the wooden palisade in the yachting-harbour and the moorings of the working platform; on the latter it occurred up to a depth of about 10 m. Also, the sponge *Ephydatia fluviatilis* was found in large quantities (about 25% of the total sponge mass) in the harbour. Contrary to our observations of 1978 we found

in 1979 a fair amount of *S. lacustris* also on dead reed-stems and dead branches near the ditch connecting the lake with the peat-bog area. Anyway, for the moment we must assume that the mites, after leaving the sponges, will swarm over the whole area of the lake.

Distribution of the species in depth

The purpose we had when using light traps in 1978 was twofold:
a. to establish on what depth the various species occur,
b. to obtain information on the rate in which water mites leave the bottom, in
     other words to find out which species appear regularly in the pelagial zone.
During 7 nights between May 1st and the end of October we used the underwater light trap on various depths. Each night the trap was placed on the bottom on 5 different depths along an imaginary line perpendicular to the shore. The trap remained during 30 minutes on each depth. The total catching period of three hours and 30 minutes mentioned in Table 2 is the sum of units of 30 minutes catching time during these seven nights.
The data presented in Table 2 need little further comment. By far the largest numbers of species and specimens in the 4th column (deeper than 10 m) were found between 10 and 12 m. The species found deepest was *Unionicola crassipes* (27 m). Our list of species (Table 1) and of species distribution in depth (Table 2) show a great similarity with data given by VIETS (1924 and 1930) for the lakes in northern Germany and by KOWALIK (1977) for a deep lake in Poland. When the catching results by light trap (Table 2) and by dip net are compared it is evident that several species that were numerous in the net were not attracted by the light (see also Table 3). This holds true for *Arrenurus albator*, *Brachypoda versicolor*, *Hygrobates longipalpis* and *Piona longipalpis*. On the other hand, it is likely that *Mideopsis orbicularis* is restricted to the bottom to such an extent, that this species is hardly caught by dip net (see also Table 3), but it is found in the light trap in large numbers.
Since the various mite species apparently differ in their reactions to the light, one must consider the data on the vertical distribution for each species separately. A comparison between the species would be incorrect, as long as the intensities of the reactions to the light for the different species are unknown.
The number of species present decreases with increasing depth (Table 2). This is also shown in Fig. 1, that represents the data obtained by the 3rd author with other collecting methods. The figure suggests that the artificial vegetation attracts more water mites and offers them sufficient shelter, with the re-

sult that more specimens remain in deeper layers than would do so without this substrate. This seems to be a plausible explanation of the differences found on greater depth between the results of collecting by means of bottom sampler and of artificial vegetation, beside the fact that these sampling methods are fundamentally different.

The occurrence of water mite in the pelagial zone

This problem was investigated by using two light traps simultaneously, one of which rested on the bottom and the other floated at a vertical distance of 0.75 to 3.00 m straight above the first one. The number of specimens caught in the floating traps was only a fraction of that caught in the traps on the bottom (107 against 2413 specimens). These specimens belong mainly to a few species, that are regarded as good swimmers, viz. *Forelia variegator* (8 in floating trap, against 93 in bottom trap), *Piona* spp. (46 against 635), *Unionicola* spp. (27 against 538). By contrast, only one specimen was found in floating traps of the species *Arrenurus crassicaudatus* and *Mideopsis orbicularis*, of which respectively 242 and 308 were caught on the bottom. Species belonging to the first category, although clearly bound to the bottom or the substrate are able to leave this zone incidentally. The second group consists of species that are strictly confined to the bottom.

The statements presented above are corroborated by observations on the behaviour of *Arrenurus*, *Piona* and *Unionicola* species in aquaria, that are discussed elsewhere in this volume.

Distribution according to habitat

In Table 3 the data, obtained by the collecting methods c, d and e (see above) are shown. Sampling among the natural vegetation was also partly done by scuba divers. This was carried out in the following zones: among the reeds up to 1 m; on sandy soil, *Elodea* and *Chara* 1 to 1.50 m; on *Potamogeton* 1.50 to 3 m; on dense *Elodea* and *Chara* vegetation 3 to 6 m; on diffuse *Elodea* and *Chara* vegetation 6 to 10 m.

The most exposed parts of the shore are protected by rubble, among which a number of stones were collected and examined. Moreover, more stones and tiles were placed in this zone and examined after an exposure time of several weeks.

By these methods *Mideopsis orbicularis* and *Arrenurus crassicaudatus* were found mainly on the bottom, which is in agreement with light trap results. It is not clear, why several other species were caught in smaller numbers than could be expected. Of the bottom-dwelling species *Unionicola crassipes* for instance,

only a few specimens were caught by the sampler. Probably this must be ascribed to the collecting method. *U. crassipes* was collected in considerable numbers on the artificial plants, even on greater depths (e.g. 122 specimens on 11 m depth). On the natural vegetation almost all species occur that are known from the lake (no further comment in the third column in Table 3 is needed).

In the zone exposed to wave action, *Hygrobates longipalpis* and, to a lesser extent, *H. trigonicus* and *Atractides ovalis* occur in large numbers when compared with those found on other substrates. Both these species are also known from brooks and apparently prefer moving water and well aerated habitats.

The results gathered by the different methods described in this paper give already a good impression of the water mite fauna and the distribution of the mites in the lake. The data of 1979 from light trap samples as well as those collected by scuba divers in the different vegetation types will complete our present view.

Literature

BARR, D., 1979. Water mites (Acari, Parasitengona) sampled with chemoluminescent bait in underwater traps. Int.J.Acar., 5: 187-194.

DAVIDS, C., 1979. De watermijten (Hydrachnellae) van Nederland. Levenswijze en voorkomen. Wet.Med.K.N.N.V., nr. 132: 1-78.

KOWALIK, W., 1977. Occurrence and distribution of water mites (Hydracarina) in the near-bottom zone of Piaseczno Lake. Ann.Univ.Mariae Curie-Sklodowska Section C, 32: 323-344 (in Polish).

VIETS, C., 1924. Die Hydracarinen der norddeutschen, besonders der holsteinischen Seen. Arch.Hydrobiol., Suppl. 4: 71-179.

VIETS, C., 1930. Quantitative Untersuchungen über die Hydracarinen der norddeutschen Seen. Arch.Hydrobiol., 22: 1-71.

Table 1. List of water mite species of Lake Maarsseveen I.

Arrenurus albator (O.F.M.)
     "   *biscissus* Lebert
     "   *buccinator* (O.F.M.)
     "   *crassicaudatus* Kramer
     "   *globator* (O.F.M.)
     "   *latus* Barrois et Moniez
     "   *nobilis* Neuman
     "   *perforatus* George
     "   *securiformis* Piersig
     "   *sinuator* (O.F.M.)
     "   *tricuspidator* O.F.M.
     "   *truncatellus* (O.F.M.)
Atractides ovalis Koenike
Axonopsis complanata (O.F.M.)
Brachypoda versicolor (O.F.M.)
Eylais extendens (O.F.M.)
Forelia liliacea (O.F.M.)
     "   *variegator* (Koch)
Frontipoda musculus O.F.M.
     "   *globosa* (De Geer)
Hydrochoreutes krameri Piersig
     "   *ungulatus* (Koch)
Hydrodroma despiciens (O.F.M.)
Hygrobates longipalpis (Hermann)
     "   *trigonicus* Koenike
Limnesia fulgida Koch
     "   *maculata* (O.F.M.)
     "   *undulata* (O.F.M.)
Limnochares aquatica (L.)
Midea orbiculata (O.F.M.)
Mideopsis orbicularis (O.F.M.)
Neumania deltoides (Piersig)
     "   *limosa* (Koch)
     "   *vernalis* (O.F.M.)
Oxus strigatus (O.F.M.)
Piona coccinea coccinea (Koch)
   "   "   *imminuta* (Piersig)
   "   *conglobata* (Koch)
   "   *longipalpis* (Krendowsky)
   "   *paucipora* (Thor)
   "   *pusilla* (Neuman)
   "   *pusilla disjuncta* Viets
   "   *rotundoides* (Thor)
   "   *stjoerdalensis* (Thor)
   "   *variabilis* (Koch)
Unionicola aculeata (Koenike)
     "   *crassipes* (O.F.M.)
     "   *minor* (Soar)

Table 2. Distribution in depth of water mites in Lake I, collected with chemoluminescent bait on several dates during the summer of 1978. Each column represents a catching period of 3 hours and 30 minutes.

Species	depth			
	0-2 m	2.5-5 m	5.5-10 m	> 10 m
Arrenurus albator	4			
" *biscissus*	7	7	1	
" *crassicaudatus*	76	90	66	12
" *latus*	19		1	
" *nobilis*			3	
" *securiformis*	11			
" *sinuator*	17			
" *truncatellus*	27			
Brachypoda versicolor	3	4		
Forelia liliacea	1	6		1
" *variegator*	12	20	58	11
Hydrochoreutes ungulatus	1	4		
Hygrobates longipalpis	7	1		
Limnesia maculata	20	92	122	1
" *undulata*	4	11		
Mideopsis orbicularis	65	118	123	3
Neumania deltoides	33	33	19	9
Piona coccinea imminuta	31	15	72	85
" *paucipora*	77	261	137	27
" *pusilla*	8	13	7	5
" *rotundoides*	33	38	18	2
" *variabilis*	11			
Unionicola crassipes	136	77	94	69
" *minor*	63	65	48	13
Total	657	855	769	239

Table 3. Water mites from Lake Maarsseveen I collected in 1978 from different habitats. Numbers indicate percentages; + less than 0.5%. The total number of specimens per habitat is given at the bottom.

Species	bottom	artificial plants	natural vegetation	stones in exposed areas
Arrenurus albator	+		1	1
" *biscissus*	7	1	2	1
" *crassicaudatus*	16	4	7	3
" *globator*				+
" *latus*			+	
" *perforatus*	1	+	+	
" *securiformis*	1	+	+	1
" *sinuator*			+	
Atractides ovalis			1	6
Axonopsis complanata			+	2
Brachypoda versicolor		3	6	2
Forelia liliacea	4	+	1	
" *variegator*	4	7		
Frontipoda musculus			+	
Hydrochoreutes krameri	+		+	
" *ungulatus*		2	1	+
Hydrodroma despiciens		+	+	
Hygrobates longipalpis	1	2	26	52
" *trigonicus*	2	+	1	3
Limnesia fulgida			+	+
" *maculata*	9	1	3	2
" *undulata*	7	2	14	
Limnochares aquatica			+	+
Midea orbiculata	+		+	
Mideopsis orbicularis	34	18	16	9
Neumania deltoides	1	+	1	
" *limosa*	3	+	+	
" *vernalis*	+		+	
Oxus strigatus			+	1
Piona coccinea s.s.	1	2	+	
" *conglobata*			+	1
" *longipalpis*	1	1	1	
" *paucipora*	3	1	+	
" *rotundoides*	5	1	4	1
" *stjoerdalensis*	+		+	
Unionicola crassipes	1	54	14	12
" *minor*			+	
	100 %	100 %	100 %	100 %
Total number	390	458	1040	302

Fig. 1. Numbers of water mite species plotted against the depth. The solid
circles represent the numbers collected by bottom samples. The open
circles represent those collected on artificial plants.

FOOD SELECTION BY THE FRESHWATER MUSSEL *Dreissena polymorpha* PALLAS.

C. Davids and E. ten Winkel

In Lake Maarsseveen I the numbers of *Dreissena polymorpha* are on a very high
level. These filter feeders influence the phytoplankton biomass by their filter-
ing activity and they will play a significant role in the benthic biocoenosis
a.o. by depositing pseudofaeces (material rejected by gills and palps) and fae-
ces (STAŃCZYKOWSKA, 1978). Faeces and pseudofaeces are very important for growth
of bacteriae and are valuable food resources for benthic invertebrates e.g. chi-
ronomid larvae (IZEKOVA & LVOVA- KACANOVA, 1972).

The aim of the present research was to determine the abilities of food se-
lection of the mussels. For this purpose we determined the fraction (percentage)
of each algal species in the lake plankton (P) and that of the stomach and in-
testine together (E). The ratio E/P is then a measure for the intake of that
particular alga or its rejection by the mussel. When for a certain alga E/P < 1,
this species is possibly rejected by the mussel and will occur for a larger
part in the pseudofaeces. When E/P > 1, there is possibly a positive selection.
The ciliary mechanism within the stomach transports certain algae directly to
the intestine and others to the digestive diverticula. The ratio's of algae in
stomach (S) and intestine (I) can be calculated as is indicated above. The S/I
ratio's indicate which species become digested and which possibly will leave
the intestine unharmed.
The value of the S/I ratio is more questionable than the E/P ratio's, because
we know next to nothing about the time which the different algae need to pass
the stomach or intestine.

The work started in the autumn of 1978. On every sampling date twenty mus-
sels were killed immediately after collecting and the contents of stomach and
intestine were fixed in Lugol. The percentages of the algae in the mussel and
in the plankton were calculated from in general more than 400 specimens per
sampling site, nevertheless there were high standard deviations, especially
for the smaller percentage values. However, by repeating the experiment on var-
ious days we got the same or comparable results.
We worked with spherical algae and with diatoms. Working with diatoms has the
advantage that by chemical manipulation of the contents of stomach and intes-
tine only the diatom valves will remain and can be counted easily. The disad-
vantage is their non-spherical shape, so selection by diameter can not be de-
termined clearly in this way. The problem with other algae is the difficulty

to calculate reliable percentages because of the food mass within stomach and intestine.

In Table I data are given about the diatoms. From preliminary results in 1978 we got the impression that algae with a diameter of 20 μm are highly preferred and that algae larger than about 50 μm are rejected. So we divided the diatoms in two groups, with axes shorter and longer than 40 μm.

It is clear from Table I that the ratio of the smaller diatoms is larger within the mussel than in the lake plankton. Possibly, a majority of the larger diatoms is rejected. The same calculation can be made for two common diatom species, one small and one large sized e.g. *Stephanodiscus astraea minutula* (diam. 20 μm) and *Asterionella formosa* (90-100 x 2 μm). The data are given in Table 2 together with the cell densities within the lake plankton. It is obvious again that the ratio of the smaller one (*Stephanodiscus*) is larger within the mussel than in the lake plankton. These data indicate that small algae are preferred to larger ones. This is in agreement with the literature data. For instance MORTON (1971) concluded from the filtering rate of *Dreissena polymorpha* a preference for small algae (in his case *Chlamydomonas*).

However, when we consider separate algal species with approximately equal diameters, there seems to be a different level of preference within one size class. In Fig. 1 the E/P ratio's for spherical algae obtained in several experiments are shown. On the various dates the species composition of the algae was different. Hence it was not possible to calculate E/P ratio's for certain algal species on every sampling date because of their small amount. When two algal species of about the same size are compared, it appears that *Trachelomonas volvocina* is highly preferred above *Melosira* (Fig. 1). From Fig. 1 we see also that *Phacotus lenticularis* is not taken by the mussel (E/P < 1).

Besides this we see in Fig. 1 the same phenomena as we did in Table 1 and 2, namely that in general the smaller algae are preferred above the larger ones. So it is likely that on the gills and palps besides a selection on size there is also a possible selection of chemical nature ("taste").

A problematical alga is *Cryptomonas*. We did not include it in Fig. 1, because sometimes it could be found in the stomach and sometimes not. We never found *Cryptomonas* in the intestine. *Cryptomonas* is present in the lake plankton throughout the year in concentrations of 100-400 cells per ml and must be one of the main food resources of the mussel. Apparently *Cryptomonas* is crushed in the stomach soon after entering it and digested.

Apart from observations on mussels collected in the field our conclusion about *Cryptomonas* is also based upon laboratory experiments. We had two algal cultures available, *Asterionella formosa* (90 x 2 μm) and *Cryptomonas ovata*

(20 x 12 μm), so it was possible to make mixtures in various concentrations of the two species. In the experiments we used *Asterionella* in concentrations of 430, 2100, 4300 and 8600 cells per ml, and *Cryptomonas* in a constant concentration of 600 cells per ml. Mussels were introduced in the mixtures and sacrificed after 1 hour. In all concentrations of *Asterionella* used, we found within the stomach of the mussel one *Asterionella* cell against 400-600 *Cryptomonas* cells. The pseudofaeces contained only *Asterionella* cells. In this situation the mussel apparently is able to reject nearly all *Asterionella* cells. In nature we found far more *Asterionella* cells in the stomach, however in a lower ratio than in the lake plankton.

In natural plankton, too many particles of different size and nature prevent such a clear demonstration of selectivity. These experiments under controlled circumstances therefore have strongly corroborated our hypothesis that *Cryptomonas* is one of the highly favoured algae.

The comparison of the contents of the stomach with that of the intestine is questionable as is indicated before. Nevertheless if we consider the given percentages in Table 1 and 2 and we calculate from these data the S/I ratio's, it will be clear that the largest particles can be found more in the intestine than in the stomach. Apparently the ciliary mechanism in the stomach transports the larger particles directly to the intestine. The same phenomenon was observed for organisms embedded in gelatinous material (e.g. *Chroococcus*). It is known that cladocerans excrete such organisms without damaging them. In our study *Chroococcus* and *Phacotus* were found more frequently in the intestine than in the stomach of the mussel. Cells of these types will pass the whole gut unharmed and obviously these undigestable bodies are recognized somehow and rejected by selection.

The algae that are significant as food, can be found in larger ratio's in the stomach than in the intestine. We found for instance high S/I values for *Trachelomonas volvocina*. It seems that algae with gelatinous or cellulose walls can not be used as food, contrary to certain thin-walled algae or brittle ones like most diatoms (e.g. *Asterionella*).

The compound of the pseudofaeces is not uniform. Certain pieces of pseudofaeces produced by one mussel may contain only several large algae, while subsequently emitted pieces may only consist of small algae. Also, pieces containing nothing but *Chroococcus*-like algae can be found.Different selection areas on gills and palps must be responsible for this phenomenon. This observation prevents us from calculating the percentages of the algae in the pseudofaeces and comparing them with the ratio's in natural plankton or with algal ratio's in the stomach and intestine.

In *Dreissena polymorpha* the processes of selection are very complicated on the gills and palps, combined with the pumping rate, as well as in the stomach. Moreover they are variable and without any doubt influenced by subtle changes in the environment, as temperature and the amount and composition of the food. In this respect, we got the impression that in late autumn at low algal densities the selectivity level is lowered and more large sized algae can be found in the gut than in summertime.

LITERATURE

IZEKOVA, E.J. & LVOVA-KACANOVA, A.A., 1972. Sedimentation of suspended matter by *Dreissena polymorpha* Pallas and its subsequent utilization by Chironomidae larvae. Pol.Arch.Hydrobiol., 19: 203-210.

MORTON, B., 1971. Studies on the biology of *Dreissena polymorpha* V. Some aspects of filter-feeding and the effect of micro-organisms upon the rate of filtration. Proc.malac.Soc.Lond., 39: 289-301.

STAŃCZYKOWSKA, A., 1978. Occurrence and dynamics of *Dreissena polymorpha* (Pall.) (Bivalvia). Verh.Internat.Verein.Limnol., 20: 2431-2434.

Table 1. The percentages of diatoms in two size classes in the stomach and intestine of *Dreissena polymorpha* and in the lake plankton are given. The E/P ratio's for both size classes of diatoms are calculated.

Dates 1979	Diatoms smaller than 40 µm				Diatoms larger than 40 µm			
	stomach %	intestine %	plankton %	E/P	stomach %	intestine %	plankton %	E/P
III- 7	11	6	6	1.4	89	94	94	1.0
III-21	12	18	11	1.4	88	82	89	1.0
IV- 6	83	71	47	1.6	17	29	53	0.4
IV-17	71	63	53	1.3	29	37	47	0.7
V-29	93	53	29	2.5	7	47	71	0.4

Table 2. The percentages of *Stephanodiscus astraea minutula* in the stomach and intestine of *D. polymorpha* and for the lake plankton are given. The same is done for *Asterionella formosa*. The sum of the percentages for both diatom species together is 100. So the values for *A. formosa* can be calculated from the values of *S. astraea*. The numbers of cells per ml in the lake plankton are also indicated.

Dates 1979	S. astraea					A. formosa	
	stomach %	intestine %	plankton %	nr. ml. plankton	E/P	E/P	nr. ml. plankton
III- 7	7	6	7	15	1.0	1.0	230
III-21	11	14	3	50	4.8	0.9	1250
IV- 6	71	85	35	15	2.3	0.3	28
IV-17	64	69	35	18	1.9	0.5	25
V-29	95	69	26	150	3.2	0.3	510

Fig. 1. Relationship between the food selection of *Dreissena polymorpha* (E/P
ratio, see text) and planktonic algae of different size. ● Nov. 24,
1978; ○ March 21, 1979; ▲ April 6, 1979; △ April 17, 1979.

THE ECOLOGY OF *BITHYNIA LEACHI* (SHEPPARD, 1823) (GASTROPODA:

PROSOBRANCHIA) IN THE LITTORAL ZONE OF THE LAKES MAARSSEVEEN

W.J.R. de Wijs and E. van den Broek

Observations in previous years (see Keulen, internal report 1979) indicated that the prosobranch snail *Bithynia leachi* is common in Lake II and occurs fairly regularly in Lake I. Very little is known of the biology of this species in Western Europe.

In the period from April 12th to November 20th 1979, samples were taken from both lakes, generally every fortnight, at permanent collecting stations: two in Lake I, four in Lake II. If possible, at each station the following substrates were examined: stones, polythene bags, wood, and large emergent macrophytes, both alive and decaying. The most suitable macrophytes were: *Phragmites*, *Typha*, *Carex*, *Sparganium*; these will in the following be indicated as "reed". Sampling was done at a depth between 0 and 50 cm, and four species of prosobranchs were collected. The results of the study are summarized very briefly.

1. Relative abundance of *B. leachi*. See tables I and II.

2. Population dynamics: growth.

Growth is indicated by the change in relative abundance of size classes (length of shell in mm) throughout the observation period. In Fig. 1 this pattern is represented for Lake II where the population of *B. leachi* is apparently undisturbed. This is concluded from the general trend in the pattern which can be described briefly as follows.

From April through June: general increase in size.

End of June, first weeks of July: size class distribution becomes bimodal; diminished frequency of large-sized animals; appearance of a new generation.

From second half of July through September: the old generation disappears and is no longer present after the middle of August. The new generation increases quickly in size.

From October through November: growth has stopped, general population structure as in April.

The most striking deviations from this pattern found in Lake I are:

a. Reduction of size in the older generation (see below).

b. Prolonged appearance of the older generation in the samples.

c. Appearance of new generation about four weeks retarded.

3. Population dynamics: numbers.

The numbers given are the total numbers found in Lake II. These are calculated as the numbers of snails found per minute of searching time (i.e. corrected collecting time) and therefore can be considered proportional with density. Presentation is given in Fig. 2.

4. Preference for type of substrate.

Since the various types of substrate will have a different algal flora, a preference for one of the categories of substrate by the prosobranchs will be influenced by a preference for a certain type of food.

Table III shows the mean numbers of *B. leachi* per minute searching time, averaged during a) the whole investigation period, b) the oviposition period (samples of 22-V, 6-VI, 19-VI and 3-VII).

"Reed" seems to be the less preferred substrate. Stone as a substrate was often much less available than the other substrate types which is the probable cause of the great standard deviation. Nevertheless the densities per substrate type varied almost parallel throughout the research period with one exception: plastics were clearly preferred during the oviposition period (last week of May - last week of June), see Table III.

5. Preference for food.

Examination of faeces of animals that were fixed immediately after collection, showed that in spring (May 7th) algal substances, especially diatoms, dominated and that in autumn (October 23rd) vegetable detritus was abundant besides pennate diatoms and remains of fungi.

During choice experiments in petri dishes it appeared that the diatoms *Asterionella formosa* and *Fragilaria crotonensis* were preferred as food to *Chlorella vulgare* and, to some extent, to detritus from the littoral of Lake I.

6. Oviposition.

The rate of oviposition was determined by counting the number of eggs per egg mass as well as the number of eggs per female. Table IV shows that the values for both parameters decreased strongly after the end of May, probably caused by increasing senility of the parent. Apart from the season, the temperature was important: the higher the temperature, the higher the number of eggs laid during a certain period. No significant differences in oviposition were found between

animals taken from Lake I and Lake II, or between animals kept in water from Lake I and Lake II.

7. Influence of temperature on egg development rate.

It is illustrated by Fig. 3a that eggs laid at room temperature and kept in tanks at different temperatures, showed a maximal survival at 22°C. For the surviving eggs, the period between laying and hatching was clearly dependent on temperature (Fig. 3b). It would seem that the high mortality of the eggs placed at temperatures other than room temperature, is caused by a temperature shock, and not by the damaging influence of an unsuitable temperature in itself.

8. Interactions between *B. leachi* and the other prosobranchs (see Table I).

Among the gastropods of the littoral zone in Lake II, *B. leachi* is the most numerous species (according to Keulen (1979 l.c.) about 50% of the collected gastropods are *B. leachi*). In Lake I, however, its numbers are very small in comparison with those of other snails. In this lake, *Potamopyrgus jenkinsi* is very abundant, especially from July through September. Since *B. leachi* and *P. jenkinsi* occur in the same habitat and are about equal in size, the hypothesis is put forward that the two species compete, and that in Lake I *B. leachi* is partly suppressed by *P. jenkinsi*.

Since the population pattern of *B. leachi* in Lake II can be considered as normal and undisturbed, deviations from this pattern as found in Lake I are probably caused by the presence of *P. jenkinsi*. These are:

a. In Lake I the density (number per minute searching time) of *B. leachi* falls steeply from June 19th onward, i.e. when *P. jenkinsi* becomes abundant.

b. In Lake I the parent generation disappears much later from the samples and oviposition occurs much (= about four weeks) later as well.

c. Specimens from Lake I are significantly smaller (see Table V), as was also observed in 1978 by Keulen (1979, l.c.).

This apparent success of *P. jenkinsi* when compared with *B. leachi* in Lake I can partly be explained by certain properties of the former species that place it in a more favourable position. On several of these properties, observations were carried out.

The average speed of movement of *P. jenkinsi* (more than 3 m per hour) was about twice that of *B. leachi* (and of *B. tentaculata*). This enables *P. jenkinsi* to find favourable feeding sites before other prosobranchs do.

P. jenkinsi was nearly always observed on the upper side of the substrate, which is more exposed to light and will probably have a more dense algal growth

than the underside, which is occupied by *Bithynia* spp.

Predation by cyprinid fish was studied in the laboratory. Medium-sized fishes (about 12 cm in length) rejected far more *P. jenkinsi* than *B. leachi* of a certain size. It seems that the shells of *P. jenkinsi* are much harder and more difficult to crush by means of the pharyngeal teeth of the predators than those of *Bithynia* spp. This means that *P. jenkinsi* is better protected against the smaller fish that occur in the littoral zone than *B. leachi* and can expose itself at a lesser risk. Moreover, the species is ovoviviparous and its eggs are therefore well-protected also.

The problem why *P. jenkinsi* does not occur in large numbers in Lake II falls beyond the scope of the present investigation.

Summarizing it can be stated that *B. leachi* shows a normal, undisturbed population pattern in Lake II; that the population of *B. leachi* is suppressed in Lake I by *P. jenkinsi*; and that this suppression is possible because *P. jenkinsi* has a number of properties that favour this species when in competition with *Bithynia leachi*.

Table I. Numbers of counted specimens of the four prosobranch species collected in the Lakes Maarsseveen in the period April 12th - November 20th 1979.

	Lake I	Lake II
Bithynia leachi (Sheppard, 1823)	552	2404
B. tentaculata (L., 1758)	543	69
Potamopyrgus jenkinsi (Smith, 1889)	thousands [1])	34
Marstoniopsis scholtzi (Schmidt, 1856)	120	1

[1]) During the early summer *P. jenkinsi* increased tremendously in Lake I which made counting impossible.

Table II. Proportion of *B. leachi* of all collected *Bithynia* specimens.

	1978 (Keulen)	1979 (De Wijs)
Lake I	35.9%	59.9%
Lake II	93.0%	97.2%

Table III. Choice of substrate of *B. leachi* in Lake II: mean, (sd). Further explanation: see text.

period	n	polythene bags	stone	wood	"reed"
a	13	6.01 (3.25)	4.88 (4.72)	4.01 (2.25)	2.65 (1.66)
b	4	8.89 (3.67)	1.45 (1.41)	5.04 (1.96)	2.65 (1.32)

Table IV. Oviposition of *B. leachi* in 7 days periods in glass jars.

number of eggs	period	n	range	mean	sd	t
per mass	April-May	22	4.43-8.15	6.13	0.89	12.6 p<<0.001
	June-July	21	1.85-4.30	3.17	0.62	
per female	April-May	22	16.0-49.2	32.7	10.5	6.4 p <0.001
	June-July	21	2.4-25.4	16.4	5.8	

Table V. Shell height in mm of specimens of *B. leachi*. Both lakes compared.

	n	range	mean	sd	t
Lake I	497	0.8-6.0	3.17	1.03	5.03 p < 0.001
Lake II	2167	0.8-6.7	3.45	1.12	

FIG.1 SIZE DISTRIBUTION OF *BITHYNIA LEACHI* IN PERCENTAGES OF TOTAL; LAKE II.

FIG. 2. NUMBERS OF B.LEACHI PER MINUTE OF SEARCHING TIME IN LAKE II.
SUMMARIZED FROM ALL CATEGORIES OF SUBSTRATE.

FIG 3A RELATION BETWEEN TEMPERATURE AND MORTALITY OF EGGS
OF B LEACHI

FIG 3B. RELATION BETWEEN TEMPERATURE AND TIME OF
HATCHING OF EGGS OF B.LEACHI
SHOWN ARE MEAN, RANGE AND STANDARD
DEVIATION LINE FITTED BY EYE

EGGS LAID AT ROOM TEMPERATURE ON SLIDES AND KEPT AT CONSTANT TEMPERATURES

HELMINTHOLOGICAL INVESTIGATIONS IN THE TWO MAARSSEVEEN LAKES:
INFECTIONS OF GASTROPODS BY LARVAL DIGENEA.

Elisabeth van den Broek

Introduction

The first attempt to characterize large water bodies on the basis of their
parasitofauna has been made by Wisniewski (1958). An important aspect of such
water bodies is their trophic level. This character clearly determines the com-
position of its biocoenosis, which also means the availability of suitable hosts
for successive stages of parasitic animals and the position of each host species
within the food-web of the biocoenosis. Apart from such biotic factors, the oc-
currence of parasitic helminths (Monogenea, Digenea, Cestoda, Nematoda, Acantho-
cephala) in a lake is influenced by abiotic factors, such as the ranges of tem-
perature and salinity.

Parasitic helminths often have various successive stages, for each of which
a different type of host may be required. In most cases, the first larval stages
are aquatic and they generally develop in invertebrates. Subsequent larval and
adult stages may occur within the water body (e.g. in fishes) or outside it
(e.g. in amphibians or birds). Wisniewski based his opinion that "the character
of a water body influences and determines its parasitofauna" on comparative stu-
dies of the parasitofauna in several Polish lakes. The most important of these
studies was a large-scale investigation in a big, shallow, eutrophic lake (Lake
Druzno) by a team of helminthologists. Within three years, all species of poten-
tial vertebrate and invertebrate hosts were examined for the presence of stages
of helminths (Wisniewski, 1958).

Later studies on this theme, but confined to fish parasites only, have been
carried out especially in Britain. Chubb (1970) stated that the trophic level
of large British lakes influences the composition of the fish fauna and, through
this, the composition of the parasitofauna. Kennedy (1975) discussed results of
more recent work by various authors on this subject.

One of the aspects studied by Wisniewski (1958) in Lake Druzno was the oc-
currence of larval Digenean Trematodes. Since in this group the first stages
develop in molluscs, mainly in gastropods, information on Digeneans involved in
the biocoenosis of a lake can be obtained by dissecting snails. The cercarial
stage (see diagram) is the most suitable for identification. As many studies on
digenean life cycles have been published, it is often possible to indicate to

which systematical group a given cercarial form, even an undescribed one, be-
longs. In many cases this further indicates in which group of definitive hosts
(vertebrates) the adult form of the Digenean occurs. In this way, by collecting
snails and their parasites in a lake, one obtains additional information on the
vertebrates occurring there, either permanently or temporarily.

The aim of the present study is to compare the larval Digeneans in the two
Maarsseveen lakes, which are of a markedly different trophic level. Research
started in spring 1977, and will be continued for several years, during which
various species of possible snail hosts will be successively studied. The re-
sults and conclusions presented here are preliminary, since a limited number of
snail species has been examined thus far in suitable numbers.

Material and methods

Pulmonate and prosobranchiate snails were collected from stones, polythene
bags, vegetation and other substrates in the litoral zone of both Lake I and II.
Sampling stations, at suitable spots, were visited several times throughout the
summer season. In Lake I these stations were situated on the South West bank,
in Lake II on the North East bank.

In 1977, five samples were taken from Lake I and four from Lake II in the
period between May 27th and October 11th. All collected snails were dissected
and examined. In 1978, the sampling period was between March 2nd and August 15th
(eight times in both lakes, at a varying number of stations in each lake).
During this period Mr. S.M. Keulen concentrated on the Digenean fauna of the
prosobranchs *Potamopyrgus jenkinsi*, *Bithynia leachi* and *B. tentaculata*. Mean-
while I dissected small numbers of *Planorbis (Anisus) vortex*; the latter study
is to be continued throughout the summer season of 1979.

Results

The tables I and II show the numbers of snails dissected in the various
years and the infections by larval Digeneans.

The total number of species of cercariae found in 1977 was 13 (from five
host species), in 1978 this was 15 (from five host species). Several of the
forms found in 1978 are probably new. Keulen will publish a description of these
forms elsewhere.

Snails may also act as intermediate hosts for encysted cercariae, the meta-
cercariae (see diagram, and tables I and II). Keulen described the metacercariae
found by him in detail (internal report, 1979).

Discussion

The differences between the Lakes I and II regarding their molluscan fauna are mainly quantitative (see also: De Wijs and Van den Broek, this volume, table I).

By far the most dominant gastropod species in Lake I is *Potamopyrgus jenkinsi*. During summer this mollusc is present in huge numbers. This species seems to play no vital part in the life cycle of any digenean. In Lake II, *Bithynia leachi* seems to be most abundant, and this species harbours stages of various digeneans.

As regards the cercariae, our data are not yet complete enough to construct a general picture of the cercarial fauna in both lakes. No sampling has as yet been carried out in early autumn, a period when the cercarial fauna is general-ly most diverse and abundant.

In Lake I we found a series of single infections by four species of Psilo-stomid cercariae in *Bithynia tentaculata*. This group consists of various spe-cies, the adults of which live in birds, especially in Anatids.

A striking feature in Lake II is the occurrence, in various snail species, of a group of Xiphidiocercariae that mature in frogs. The most common species of this group (see Fig. 1) also occurred occasionally in Lake I.

In both lakes, Monostomid cercariae occur regularly. Final hosts of these digeneans are mainly Anatids and Coots. We found three cercarial species of this type. One of these is rather common in *Planorbis vortex* and was found dur-ing the whole period of investigation.

Up till 15th June 1979 we have found twice as many cercarial species in Lake I as in Lake II (19 and 9 respectively). The two lakes had five species in common.

A preliminary comparison between the two lakes as regards the definitive host of the cercariae is given in table III. Since especially the large Lym-naeids, which are important hosts for a wide range of cercariae, have hardly been studied (see tables I and II), the picture now presented may change con-siderably in the future.

It appears that the digenean species from homoiothermic hosts are compara-tively numerous in both lakes. In the eutrophic Lake II, the digeneans of fish are scarce and those of amphibians are well represented. In the oligo-mesotro-phic Lake I, more Digeneans of fish occur, and those of birds dominate. If we consider the frequency of occurrence of the species from the bird (and mammal) group, it appears that from the eleven species found in Lake I, seven have been found only once, five of which belong to the Psilostomid cercariae. During win-

ter, large flocks of Anatids visit the lake (Roos and students, pers.comm.), and it is very probable that these birds, which breed in Eastern and Northern Europe, are the definitive hosts of these Philostomids. Their cercariae were mainly found in spring and early summer. In Lake II, only one bird species out of four has been found once. This species is reported to be fairly common in snails in Polish lakes (Niewiadomska, pers.comm.). It seem therefore that the hibernation of so many birds on Lake I causes an important contribution to the cercarial fauna of this lake. It is, of course, not certain that the life cycles of these digeneans can be completed here.

The study of the metacercariae from the snails seems to corroborate these conclusions. In the life cycle of digeneans the metacercariae must be eaten by the definitive host where they can develop into egg-producing adults. Metacercariae are therefore mainly found on or in plant or animal species that serve as food for the definitive hosts. Thus, the occurrence of metacercariae in a given host species may indicate its position within the food web of a biocoenosis.

Vertebrate predators of the snails studied by us are probably mainly fishes, and to a lesser extent various species of birds. Keulen was unable to identify his metacercariae, but he could distinguish several types. The majority of these types seem to belong to digenean species that mature in birds. On the other hand, the number of infections by a metacercaria that probably would mature in fish was about 75% of the total number of infections found by Keulen. Also, it appears from tables I and II that the infection percentages of the snails by metacercariae are highest in Lake I, although the number of metacercarial types found is equal in the two lakes.

Summarizing these results the preliminary conclusion is drawn that the digenean fauna in Lake I is rather varied, and highly influenced by the presence of large numbers of hibernating birds. In Lake II, where fewer species were found, the composition of the digenean fauna seems to be more stable.

As a result of his studies in Lake Druzno, Wisniewski (1958) stated that the predominance of bird parasites is characteristic for large eutrophic lakes. Esch (1971), who compared the parasitofauna of fish and gastropods between a large oligotrophic lake and a smaller eutrophic one in Michigan, U.S.A., agreed with this conslusion. In the former lake, Esch found many species that complete their life cycle in predatory fish, and in the latter the species maturing in birds were dominant. The results of the investigations on parasites of fish and of snails clearly showed the same trend.

Among the Maarsseveen lakes, it is the oligotrophic one in which the bird

parasites dominate. It can be argued that this picture may change when the investigations are continued for several years, and more groups of snails will be involved. In my opinion, however, human activities must have a considerable influence on the composition of the parasitofauna of these two lakes. As regards the vertebrate hosts of the digeneans, birds will be driven away by recreants during summer, and probably be attracted by large, quiet water bodies during winter. In order to stimulate angling, various species of fish have been introduced, and this process will continue. Amphibians may be exterminated when recreation pressure becomes more heavy, especially round Lake II. It would appear that the majority of the aquatic invertebrate species is far less influenced by human activities. But since both lakes are man-made and very young, long-term research might reveal changes of their fauna, in particular of the parasitofauna, which cannot now be predicted.

Literature

CHUBB, J.C., 1970. The parasite fauna of British freshwater fish. In: Aspects of Fish Parasitology, Symp.Brit.Soc.Parasitology, 8: 119-144.

ESCH, G.W., 1971. Impact of ecological succession on the parasite fauna in Centrarchids from oligotrophic and eutrophic ecosystems. American Midland Naturalist, 86: 160-168.

KENNEDY, C.R., 1975. The natural history of Slapton Ley Nature Reserve. VIII. The parasites of fish, with special reference to their use as a source of information about the aquatic community. Field Studies, 4: 177-189.

WISNIEWSKI, W.L., 1958. Characterization of the parasitofauna of an eutrophic lake. Acta Parasitologica Polonica, 6: 1-64.

Table I. Infections by larval digeneans in snails in Lake Maarsseveen I.

Snail species	year	number dissected	infected by cercariae		infected by metacercariae	
			number	percentage	number	percentage
Bithynia spp. [1])	1977	138	19	14.0	18	13
Bithynia leachi	1978	88	7	8.0	27	31
Bithynia tentaculata	1978	187	9	4.8	27	14
Potamopyrgus jenkinsi	1977	66	0	0	3	5
idem	1978	133	0	0	0	0
Physa fontinalis	1977	17	0	0	1	6
idem	1978	56	1	1.8	26	46
Lymnaea stagnalis	1977	8	3	37.5	0	0
Lymnaea palustris	1977	28	2	7.0	3	11
Lymnaea peregra	1977	19	4	21.0	2	11
Planorbis carinatus	1977	22	0	0	0	0
Planorbis (Anisus) vortex	1977	40	5	12.5	0	0
idem	1978	36	4	11.1	3	8
idem	1979 [2])	24	2	8.3	0	0

[1]) in 1977 the identification of the two species was not reliable

[2]) up to 16-VI-1979

Table II. Infection by larval digeneans in snails in Lake Maarsseveen II.

Snail species	year	number dissected	infected by cercariae		infected by metacercariae	
			number	percentage	number	percentage
Bithynia spp. [1]	1977	97	0	0	1	1
Bithynia leachi	1978	305	60	20.0	9	3
Bithynia tentaculata	1978	20	1	5.0	1	5
Potamopyrgus jenkinsi	1977	0			0	0
idem	1978	1	0	0	0	0
Physa fontinalis	1977	15	2	13.3	0	0
idem	1978	67	1	1.5	3	5
Lymnaea stagnalis	1977	5	0	0	0	0
Lymnaea palustris	1977	19	2	10.6	0	0
Lymnaea peregra	1977	55	0	0	3	6
Planorbis (Anisus) vortex	1977	25	3	12.0	0	0
idem	1978	50	7	14.0	0	0
idem	1979 [2]	66	16	24.2	0	0

[1] in 1977 the identification of the two species was not reliable

[2] up to 16-VI-1979

Table III. Composition of the cercarial fauna of the Lakes Maarsse-
veen, based on groups of definitive hosts (Vertebrates).

Definitive host a	number of cercarial species in	
	Lake I	Lake II
fish	4	1
amphibian	1	3
bird (or mammal)	11	4
unknown	3	1
total	19	9

Diagram: succession of various stages in the life cycle of a Digenean
Trematode (generalized).

P.J.R.

100 μm

a

100 μm

b

Fig. 1. *Pleurogenes claviger* (Rudolphi, 1819), larval stages from *Bithynia leachi*.
a. Cercaria.
b. Sporocyst, containing embryos and developing cercariae.

APPENDIX

Chemical Analyses

Samples for chemical analyses were taken each month in the years 1976, 1977 and 1978. In 1975 also some samples were taken. The samples were taken from a depth of about 0.5 meters near the rafts in both Lakes Maarsseveen. The analyses were performed by the "Waterleidingbedrijf Midden-Nederland".

LAKE MAARSSEVEEN I

	75/ 6/12	75/ 7/11	75/ 8/ 8	75/ 9/11	75/11/ 6	75/12/ 9	76/ 2/ 5
Conductivity microS.cm-1	370.00	340.00	340.00	350.00	370.00	370.00	370.00
pH	8.20	8.30	8.10	8.20	7.80	7.80	8.00
KMnO4 unfiltrated mg/L	21.00	23.00	45.00	24.00	22.00	24.00	28.00
KMnO4 filtrated mg/L	13.00	14.00	22.00	17.00	19.00	12.00	21.00
Chloride mg/L	35.00	34.00	36.00	35.00	35.00	34.00	34.00
Nitrite mg NO2/L	0.02	0.01	0.03	0.03	0.02	0.01	0.01
Nitrate mg NO3/L	1.60	1.00	1.00	0.80	1.30	2.30	2.30
Sulfate mg SO4/L	21.00	18.00	16.00	22.00	16.00	13.00	13.00
Bicarbonate mg HCO3/L	175.00	175.00	160.00	160.00	170.00	175.00	170.00
Phosphate mg PO4/L	0.04	0.01	0.01	0.01	0.01	0.02	0.02
Ammonium mg NH4/L	0.26	0.45	0.20	0.26	0.25	0.23	0.15
Organic Ammonium mg NH4/L	0.35	0.35	0.30	0.06	0.10	0.40	0.35
Iron mg/L	0.02	0.03	0.03	0.01	0.01	0.01	0.01
Calcium mg/L	60.00	55.00	54.00	49.00	57.00	59.00	59.00
Sodium mg/L	23.00	19.00	23.00	19.00	17.50	17.50	17.50
Potassium mg/L	2.80	3.00	2.70	2.20	2.50	2.40	2.00
Total Hardness °D	9.60	9.20	8.70	8.50	9.20	9.60	9.40
Bicarbonate Hardness °D	8.10	8.10	7.30	7.30	7.70	7.80	8.00

	76/ 3/ 5	76/ 4/ 5	76/ 4/28	76/ 5/26	76/ 6/24	76/ 8/18	76/ 9/14
Conductivity microS.cm-1	390.00	360.00	360.00	380.00	360.00	350.00	360.00
pH	8.10	8.20	8.20	7.70	8.20	8.40	8.20
KMnO4 unfiltrated mg/L	38.00	30.00	25.00	17.00	25.00	30.00	25.00
KMnO4 filtrated mg/L	25.00	22.00	18.00	12.00	23.00	24.00	17.00
Chloride mg/L	35.00	34.00	34.00	40.00	70.00	38.00	37.00
Nitrite mg NO2/L	0.01	0.01	0.01	0.01	0.02	0.01	0.01
Nitrate mg NO3/L	1.50	0.80	0.90	1.70	1.00	1.10	0.10
Sulfate mg SO4/L	15.00	12.00	15.00	16.00	15.00	16.00	12.00
Bicarbonate mg HCO3/L	175.00	175.00	170.00	175.00	185.00	155.00	165.00
Phosphate mg PO4/L	0.02	0.01	0.01	0.04	0.04	0.02	0.05
Ammonium mg NH4/L	0.35	0.26	0.28	0.35	0.25	0.27	0.33
Organic Ammonium mg NH4/L	0.30	0.24	0.35	0.40	0.21	0.31	0.35
Iron mg/L	0.11	0.03	0.02	0.05	0.01	0.01	0.02
Calcium mg/L	59.00	57.00	57.50	62.00	61.00	54.00	55.00
Sodium mg/L	18.50	16.50	17.00	15.50	15.50	19.50	15.50
Potassium mg/L	2.00	1.90	1.90	2.10	2.00	2.00	3.00
Total Hardness °D	9.40	9.10	9.00	9.90	9.70	8.80	8.80
Bicarbonate Hardness °D	8.00	8.00	7.80	8.10	7.70	7.00	7.60

LAKE MAARSSEVEEN I

	76/10/12	76/11/9	76/12/7	77/2/2	77/3/2	77/3/29	77/4/27
Conductivity microS.cm-1	370.00	370.00	380.00	360.00	370.00	380.00	350.00
pH	8.10	7.90	7.90	7.90	7.90	7.90	8.00
KMnO4 unfiltrated mg/L	35.00	10.00	15.00	20.00	20.00	23.00	18.00
KMnO4 filtrated mg/L	21.00	6.00	6.00	15.00	13.00	16.00	16.00
Chloride mg/L	37.00	37.00	36.00	35.00	35.00	37.00	37.00
Nitrite mg NO2/L	0.02	0.01	0.01	0.01	0.01	0.01	0.01
Nitrate mg NO3/L	0.90	1.00	1.90	1.50	1.60	2.20	2.20
Sulfate mg SO4/L	5.00	8.00	20.00	10.00	10.00	16.00	15.00
Bicarbonate mg HCO3/L	170.00	170.00	175.00	185.00	180.00	180.00	180.00
Phosphate mg PO4/L	0.03	0.02	0.02	0.12	0.03	0.02	0.02
Ammonium mg NH4/L	0.31	0.35	0.10	0.22	0.34	0.25	0.34
Organic Ammonium mg NH4/L	0.43	0.40	0.48	0.10	0.23	0.30	0.21
Iron mg/L	0.05	0.10	0.14		0.06	0.14	0.07
Calcium mg/L	58.00	55.00	61.00	63.00	60.00	60.00	63.00
Sodium mg/L	17.00	17.00	17.00	15.50	16.50	17.00	16.50
Potassium mg/L	2.10	2.20	1.90	2.40	2.10	2.10	1.90
Total Hardness °D	8.50	8.90	9.80	10.10	9.70	9.70	10.00
Bicarbonate Hardness °D	7.80	7.80	8.10	8.40	8.40	8.40	8.10

	77/5/25	77/6/22	77/7/22	77/8/17	77/9/14	77/10/11	77/11/9
Conductivity microS.cm-1	360.00	360.00	350.00	350.00	340.00	380.00	380.00
pH	8.10	8.30	8.30	7.80	8.20	8.00	8.00
KMnO4 unfiltrated mg/L	22.00	19.00	16.00	14.00	16.00	17.00	16.00
KMnO4 filtrated mg/L	19.00	11.00	11.00	9.00	13.00	11.00	8.00
Chloride mg/L	34.00	37.00	37.00	36.00	36.00	37.00	36.00
Nitrite mg NO2/L	0.02	0.01	0.01	0.02	0.01	0.01	0.02
Nitrate mg NO3/L	2.70	1.20	1.30	0.80	0.70	1.20	0.90
Sulfate mg SO4/L	25.00	16.00	18.00	16.00	17.00	14.00	15.00
Bicarbonate mg HCO3/L	175.00	185.00	170.00	165.00	165.00	175.00	175.00
Phosphate mg PO4/L	0.01	0.46	0.01	0.02	0.02	0.02	0.01
Ammonium mg NH4/L	0.23	0.10	0.35	0.35	0.30	0.20	0.20
Organic Ammonium mg NH4/L	0.40	0.55	0.40	0.23	0.24	0.30	0.21
Iron mg/L	0.05	0.07	0.02	0.02	0.05	0.16	0.07
Calcium mg/L	60.00	61.00	60.00	58.00	59.00	60.00	63.00
Sodium mg/L	17.00	17.50	17.00	17.00	18.00	16.50	16.50
Potassium mg/L	2.30	2.30	2.30	2.20	2.20	2.10	1.90
Total Hardness °D	9.80	9.70	9.60	9.40	9.40	9.90	10.00
Bicarbonate Hardness °D	8.10	8.40	7.80	7.60	7.60	8.10	8.10

LAKE MAARSSEVEEN I

	77/12/14	78/1/19	78/2/21	78/3/30	78/4/26	78/5/25
Conductivity microS.cm-1	380.00	380.00	380.00	390.00	380.00	380.00
pH	8.10	8.20	8.10	8.10	8.30	8.20
KMnO4 unfiltrated mg/L	16.00	17.00	15.00	17.00	16.00	18.00
KMnO4 filtrated mg/L	10.00	7.00	7.00	5.00	6.00	6.00
Chloride mg/L	36.00	36.00	36.00	35.00	36.00	36.00
Nitrite mg NO2/L	0.01	0.01	0.01	0.01	0.01	0.03
Nitrate mg NO3/L	1.10	1.60	1.00	1.30	1.60	1.60
Sulfate mg SO4/L	14.00	17.00	13.00	19.00	18.00	18.00
Bicarbonate mg HCO3/L	175.00	175.00	180.00	180.00	180.00	180.00
Phosphate mg PO4/L	0.02	0.03	0.15	0.06	0.04	0.04
Ammonium mg NH4/L	0.08	0.14	0.25	0.18	0.30	2.00
Organic Ammonium mg NH4/L	0.23	0.30	0.30	0.20	0.40	0.30
Iron mg/L	0.16	0.21	0.08	0.07	0.06	0.04
Calcium mg/L	60.00	62.00	62.00	61.00	63.00	61.00
Sodium mg/L	17.50	15.00	16.00	19.00	15.50	18.50
Potassium mg/L	2.00	2.00	2.50	1.80	1.60	1.90
Total Hardness °D	9.60	9.80	10.00	9.80	10.10	9.70
Bicarbonate Hardness °D	8.10	8.10	8.40	8.20	8.10	8.30

	78/6/22	78/8/16	78/9/15	78/10/10	78/11/8	78/12/14
Conductivity microS.cm-1	370.00	370.00	380.00	370.00	380.00	370.00
pH	8.30	8.40	8.10	8.00	7.90	7.90
KMnO4 unfiltrated mg/L	18.00	18.00	20.00	16.00	24.00	15.00
KMnO4 filtrated mg/L	9.00	13.00	8.00	6.00	14.00	9.00
Chloride mg/L	36.00	37.00	37.00	36.00	37.00	37.00
Nitrite mg NO2/L	0.01	0.01	0.01	0.01	0.01	0.01
Nitrate mg NO3/L	1.20	0.70	0.60	0.70	1.20	1.40
Sulfate mg SO4/L	15.00	16.00	25.00	20.00	20.00	17.00
Bicarbonate mg HCO3/L	170.00	160.00	170.00	170.00	170.00	180.00
Phosphate mg PO4/L	0.02	0.04	0.01	0.02	0.02	0.09
Ammonium mg NH4/L	0.18	0.30	0.20	0.13	0.11	0.20
Organic Ammonium mg NH4/L	0.00	0.25	0.13	0.20	0.12	0.30
Iron mg/L	0.03	0.04	0.05	0.03	0.08	0.09
Calcium mg/L	59.00	58.00	60.00	60.00	61.00	63.00
Sodium mg/L	15.50	18.00	18.50	19.50	19.50	17.50
Potassium mg/L	1.70	1.80	1.70	1.80	1.60	1.80
Total Hardness °D	6.70	9.40	9.70	9.60	9.80	9.90
Bicarbonate Hardness °D	6.70	7.30	7.70	7.70	8.10	8.30

LAKE MAARSSEVEEN II

	75/ 6/12	75/ 7/11	75/ 8/ 8	75/ 9/11	75/11/ 6	75/12/ 9	76/ 2/ 5
Conductivity microS.cm-1	510.00	520.00	530.00	590.00	600.00	550.00	540.00
pH	9.00	9.20	9.50	9.10	7.60	7.40	7.60
KMnO4 unfiltrated mg/L	60.00	60.00	70.00	45.00	47.00	43.00	43.00
KMnO4 filtrated mg/L	30.00	35.00	40.00	17.00	25.00	34.00	34.00
Chloride mg/L	72.00	84.00	91.00	95.00	88.00	64.00	64.00
Nitrite mg NO2/L	0.24	0.38	0.11	0.26	0.10	0.07	0.07
Nitrate mg NO3/L	5.80	3.50	1.00	2.10	5.90	11.00	11.00
Sulfate mg SO4/L	49.00	63.00	52.00	56.00	57.00	48.00	48.00
Bicarbonate mg HCO3/L	140.00	115.00	115.00	135.00	175.00	165.00	165.00
Phosphate mg PO4/L	0.92	1.50	0.87	1.90	1.40	0.60	0.60
Ammonium mg NH4/L	0.35	0.80	0.18	0.54	1.30	0.50	0.50
Organic Ammonium mg NH4/L	1.00	1.30	0.65	0.88	1.60	0.65	0.65
Iron mg/L	0.05	0.01	0.07	0.04	0.01	0.08	0.08
Calcium mg/L	70.00	69.00	61.00	63.00	69.00	68.00	68.00
Sodium mg/L	47.00	54.00	55.00	61.00	50.00	36.00	36.00
Potassium mg/L	8.80	8.50	8.50	8.00	7.00	7.50	7.50
Total Hardness °D	11.30	11.50	10.60	10.90	11.30	11.30	11.30
Bicarbonate Hardness °D	6.40	5.30	5.30	6.30	8.00	7.60	7.60

	76/ 3/ 5	76/ 4/ 5	76/ 4/28	76/ 5/26	76/ 6/24	76/ 6/24	76/ 8/18
Conductivity microS.cm-1	530.00	530.00	600.00	790.00	850.00	850.00	840.00
pH	7.60	7.80	8.20	7.80	7.90	7.90	9.30
KMnO4 unfiltrated mg/L	55.00	45.00	55.00	35.00	45.00	45.00	40.00
KMnO4 filtrated mg/L	40.00	35.00	40.00	23.00	35.00	35.00	30.00
Chloride mg/L	60.00	65.00	83.00	135.00	150.00	150.00	180.00
Nitrite mg NO2/L	0.05	0.22	0.75	0.47	0.60	0.60	0.01
Nitrate mg NO3/L	6.90	6.10	7.50	8.30	9.00	9.00	14.00
Sulfate mg SO4/L	49.00	33.00	54.00	66.00	61.00	61.00	84.00
Bicarbonate mg HCO3/L	165.00	165.00	190.00	205.00	200.00	200.00	98.00
Phosphate mg PO4/L	0.45	0.40	1.50	1.70	7.00	7.00	2.20
Ammonium mg NH4/L	0.45	1.40	0.18	6.20	6.50	6.50	0.14
Organic Ammonium mg NH4/L	0.50	0.65	1.10	6.00	7.00	7.00	0.90
Iron mg/L	0.18	0.06	0.03	0.15	0.14	0.14	0.03
Calcium mg/L	65.00	69.00	70.00	85.00	84.00	84.00	81.00
Sodium mg/L	36.00	26.00	49.00	70.00	80.00	80.00	105.00
Potassium mg/L	6.80	7.00	8.30	9.50	11.00	11.00	10.00
Total Hardness °D	10.50	11.10	11.50	13.90	13.80	13.80	13.50
Bicarbonate Hardness °D	7.60	7.40	8.70	9.50	9.20	9.20	4.50

LAKE MAARSSEVEEN II

	76/ 9/14	76/10/12	76/11/ 9	76/12/ 7	77/ 3/ 2	77/ 3/29	77/ 4/27
Conductivity microS.cm-1	790.00	810.00	790.00	750.00	610.00	630.00	560.00
pH	8.20	7.70	7.50	7.50	7.60	7.60	7.70
KMnO4 unfiltrated mg/L	35.00	30.00	13.00	20.00	50.00	50.00	35.00
KMnO4 filtrated mg/L	19.00	25.00	7.00	9.00	25.00	26.00	11.00
Chloride mg/L	160.00	155.00	135.00	125.00	88.00	89.00	105.00
Nitrite mg NO2/L	0.90	0.40	0.60	0.18	0.17	0.07	0.25
Nitrate mg NO3/L	1.20	16.00	5.40	16.00	12.00	9.00	4.70
Sulfate mg SO4/L	77.00	75.00	67.00	66.00	66.00	59.00	56.00
Bicarbonate mg HCO3/L	165.00	160.00	180.00	185.00	175.00	175.00	175.00
Phosphate mg PO4/L	4.40	4.30	5.20	4.80	1.80	1.80	3.60
Ammonium mg NH4/L	0.90	0.55	2.50	3.00	0.38	0.75	0.70
Organic Ammonium mg NH4/L	0.70	0.65	0.55	0.50	0.65	0.60	0.45
Iron mg/L	0.01	0.02	0.26	0.21	0.32	0.12	0.07
Calcium mg/L	85.00	82.00	75.00	83.00	77.00	80.00	80.00
Sodium mg/L	86.00	85.00	79.00	70.00	48.00	47.00	57.00
Potassium mg/L	9.00	10.00	11.00	9.50	8.70	8.00	8.00
Total Hardness °D	13.80	13.40	12.40	13.50	12.90	13.00	12.90
Bicarbonate Hardness °D	7.60	7.30	8.40	8.40	8.10	8.10	8.10

	77/ 5/25	77/ 6/22	77/ 7/22	77/ 8/17	77/ 9/14	77/10/11	77/11/ 9
Conductivity microS.cm-1	560.00	580.00	630.00	630.00	610.00	690.00	650.00
pH	7.90	7.70	8.70	7.50	7.70	7.70	7.60
KMnO4 unfiltrated mg/L	45.00	30.00	30.00	25.00	26.00	30.00	27.00
KMnO4 filtrated mg/L	35.00	20.00	14.00	14.00	15.00	14.00	11.00
Chloride mg/L	76.00	105.00	120.00	115.00	105.00	110.00	105.00
Nitrite mg NO2/L	0.27	0.50	0.60	0.45	0.45	0.45	0.25
Nitrate mg NO3/L	9.10	11.00	12.00	12.00	7.00	11.00	4.00
Sulfate mg SO4/L	53.00	56.00	65.00	62.00	60.00	56.00	56.00
Bicarbonate mg HCO3/L	175.00	170.00	145.00	165.00	175.00	170.00	175.00
Phosphate mg PO4/L	1.20	5.30	3.90	3.60	3.50	3.80	3.60
Ammonium mg NH4/L	5.30	2.20	2.20	0.55	0.90	0.70	0.70
Organic Ammonium mg NH4/L	0.60	0.30	0.55	0.33	0.50	0.50	0.45
Iron mg/L	0.09	0.11	0.05	0.10	0.09	0.16	0.07
Calcium mg/L	75.00	75.00	83.00	75.00	75.00	74.00	80.00
Sodium mg/L	41.00	57.00	64.00	67.00	59.00	58.00	57.00
Potassium mg/L	7.30	8.30	9.00	8.00	7.50	7.70	8.00
Total Hardness °D	12.10	12.20	13.50	12.30	12.20	12.20	12.90
Bicarbonate Hardness °D	8.10	7.80	6.70	7.60	8.10	7.80	8.10

LAKE MAARSSEVEEN II

	77/12/14	78/1/18	78/3/1	78/3/30	78/4/26	78/5/25
Conductivity microS.cm-1	580.00	560.00	560.00	540.00	520.00	590.00
pH	7.60	7.80	7.70	7.80	8.20	7.80
KMnO4 unfiltrated mg/L	45.00	45.00	40.00	45.00	45.00	35.00
KMnO4 filtrated mg/L	35.00	19.00	11.00	16.00	24.00	16.00
Chloride mg/L	80.00	72.00	67.00	59.00	60.00	75.00
Nitrite mg NO2/L	0.95	0.30	0.12	0.27	0.23	0.45
Nitrate mg NO3/L	6.00	7.60	8.40	8.30	3.40	10.00
Sulfate mg SO4/L	57.00	56.00	56.00	57.00	58.00	60.00
Bicarbonate mg HCO3/L	165.00	175.00	175.00	170.00	175.00	180.00
Phosphate mg PO4/L	4.60	2.00	1.50	1.90	2.60	1.70
Ammonium mg NH4/L	1.20	1.60	1.10	0.50	0.40	0.18
Organic Ammonium mg NH4/L	0.40	0.55	0.80	0.50	0.70	0.50
Iron mg/L	0.34	0.33	0.14	0.16	0.09	0.08
Calcium mg/L	73.00	75.00	74.00	72.00	76.00	75.00
Sodium mg/L	42.00	39.00	34.00	36.00	30.00	44.00
Potassium mg/L	7.50	8.50	7.50	7.20	6.50	8.30
Total Hardness °D	12.00	12.00	12.10	11.60	12.20	12.30
Bicarbonate Hardness °D	7.60	8.10	8.00	7.90	8.00	8.30

	78/6/21	78/8/16	78/9/13	78/10/10	78/11/6	78/12/12
Conductivity microS.cm-1	620.00	580.00	580.00	610.00	590.00	570.00
pH	8.70	9.10	7.90	7.60	7.50	7.30
KMnO4 unfiltrated mg/L	35.00	35.00	35.00	30.00	35.00	35.00
KMnO4 filtrated mg/L	14.00	10.00	16.00	21.00	22.00	21.00
Chloride mg/L	84.00	89.00	89.00	86.00	86.00	76.00
Nitrite mg NO2/L	0.90	0.08	0.13	0.05	0.02	0.01
Nitrate mg NO3/L	8.30	6.50	7.00	7.80	12.50	9.50
Sulfate mg SO4/L	61.00	61.00	54.00	59.00	57.00	58.00
Bicarbonate mg HCO3/L	165.00	130.00	175.00	175.00	175.00	180.00
Phosphate mg PO4/L	3.00	3.00	3.10	2.90	2.80	1.60
Ammonium mg NH4/L	0.85	0.30	1.00	1.10	1.00	0.40
Organic Ammonium mg NH4/L	0.75	0.90	0.75	0.40	0.65	0.70
Iron mg/L	0.09	0.03	0.07	0.09	0.07	0.20
Calcium mg/L	77.00	72.00	71.00	74.00	74.00	73.00
Sodium mg/L	48.00	53.00	53.00	48.00	50.00	46.00
Potassium mg/L	8.30	7.50	7.30	7.80	7.00	7.80
Total Hardness °D	12.60	11.90	11.80	12.20	12.20	11.90
Bicarbonate Hardness °D	7.60	6.00	8.00	8.10	8.10	8.30