Some theoretical considerations of thermal discharge in shallow lakes

Heating of freshwater lakes or streams (so called thermal pollution) is an incidental result of many industrial processes, but mainly of the production of electricity. In this paper we try to identify the areas of greatest concern in this problem. We like to start with a few introductory remarks about the similarities and contrasts to thermal pollution of seawater. The natural cycle of water is on a scale which is more than sufficient to supply man's needs; about 100,000 km³ flows downrivers each year and is adequate for



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the needs of even the most densely populated areas. Problems do occur in those parts of the world where man tries to live in semi-deserts, and in temporarily arid areas such as India where there are recurrent seasonal shortages.

Water supply problems in other areas are usually a result of using water for waste disposal too. The need for electricity is especially high in populous regions where the generation of electricity produces thermal pollution, which is only one aspect of the wider pollution and eutrophication problems caused by industrial, agricultural and other activities of these dense populations. These pollution problems affect freshwaters to a greater extent than they do the seas. Thermal pollution in particular is more serious in W.Europe (except perhaps in Britain) where freshwaters are used for cooling than in the USA where most heat is discharged into the sea — where the heat will be diluted by currents or tidal activities - or into rivers in sparsely populated regions. Even in the USA there are problems however. Eutrophication of the Great Lakes is marked and thermal pollution may make the situation worse: these forms of pollution are probably synergistic. A lot is known about the influence of temperature on growth processes of a large number of organisms. Temperature has for a long time been recognised as a major biological parameter. There is an explosion of knowledge on the influence of temperature on one species, on its life history, its growth rate, migration, spawning and on other behavioural aspects.

Several reviews exist already in the literature on the lethal effects of heat disposal and

on its influence on fish spawning and behaviour.

Much of this work involves the effect on single species, but thermal discharges may be important in changing the species composition of population, especially where this is regulated by competition, grazing, and predation.

One may know the lethal temperatures and minimum temperatures, and the minimum duration of a given temperature for egg production. And in spite of this, no prediction can be made on the *ecological* changes induced by thermal pollution in freshwater ecosystems. The reason why such predictions cannot be made is because we lack a coherent theory.

We do not even know whether or not laws controlling ecosystems exist. Rigler (1974) compared in this context predictions made by biologists with those made by physicists. Highly accurate predictions e.g. of electrical current can be based on Ohm's law, while gas pressure can be predicted from the laws of Boyle and Gay Lussac. The problems are simple as the two processes are not related. In an ecosystem, even a simple one, predictions must be made on photosynthesis of algae, egg laying of zooplankton, and survivorship of these eggs. But these processes are related. Therefore we need theories for the separate problems and a general theory linking the several chains together. It seems to me not likely that such a theory will easily if ever be discovered. One of the essential constituents of such a theory must be competition. Competition is a main feature controlling growth in a natural ecosystem. Phytoplankton species compete for their mineral constituents, zooplankton compete for their food etc. Very few, if any studies deal with the influence of temperature on groups of organisms competing with each other, and the number of possible effects and situations that may occur may often be well beyond the practical limits for study. If for example two organisms are together in a lake it will make a large difference if one or both are in their (exponential) growing or in their decline phase. Such a study should be made at least throughout a total growing season and the numbers of organisms that may be ecologically important may be quite large. It has been suggested that only the most important organisms should be studied. How does one define importance, however? Those organisms having the greatest biomass are not always the most important. Often the nuisance algae such as blue green algae have the largest biomass. Their importance lies of course in the fact that they dominate and thus the ecosystem, but one also needs

to study those natural algae that are present normally in smaller amounts but are extinguished due to their lack of adaptation to changing environment. We do not know if the early spring blooms of diatoms are unimportant for the food chains of lakes, because they appear too early for the zooplankton. It is possible that they are important because in early spring they suppress the blue green algae and through their indirect effect on the algae that follow the diatom bloom they may ultimately affect the zooplankton. To overcome the need for so many studies one might feel inclined to use data from one ecosystem for predicting changes in another one. But in doing so we must be very careful. Rivers with their ever flowing water and rapidly changing populations are clearly distinct from lakes. Tropical lakes should not be used to predict phenomena in heated temperate lakes, because their temperature depends on or is coupled with the irradiance in a tropical lake so that evolution has led to species depending on concomitant temperature and irradiance values.

In an artificially heated lake temperature and irradiance are not related; temperature no longer depends only on irradiance as a source of heat.

Organisms have a long history of evolution. In this long period of evolution organisms have found their way of living in a certain light and temperature regime, sometimes by producing species with planktonic larvae, sometimes by carrying egg sacs, sometimes by adjusting the number of reproductive cycles in a year. The variation in life histories show the answers to a large number of combinations of environmental factors.

In conclusion is seems clear that:

1. There is a great need for basic research in applied ecology. Ecosystems must be understood, before they can be used rationally.

2. There is a great need for education. Man must realise that any waste of energy is deplorable. Methods of using waste heat should be sought; electricity made from natural gas or oil should not be used for heating as the loss of energy is considerable and can easily be avoided.

3. The aquatic ecosystem should not be considered as a dustbin or a garbage collector. Nuclear, or even the larger conventional plants, should not be built on the shores of lakes.

In the following paragraph theoretical considerations are given for a study on the influence of temperature on phytoplankton and zooplankton populations, which together form the basic part of the food pyramid in the aquatic ecosystems. At present in The Netherlands a plant is being built that will dispose 300 Cal.cm⁻² day⁻¹ in Lake Bergumermeer, which has a surface area of only 5 km² and a depth of about 2 m. The natural irradiance is given in table 1.

From this table it can be seen that the

 TABLE 1 - Total solar energy at latitudes 50°
 North (in Cal.cm-2d-1)

Jan.	March	May	July	Sept.	Nov.
110	310	550	570	350	120
		······			

human heat input is equal to the natural input in March. Owing to the greater losses of heat in December and January the winter temperatures will not actually reach the March values, but they will be considerably higher than normal and ice will disappear. No estimates of possible winter temperatures seem to have been made. The lake is alkaline and rich in humic substances like most in this district and is comparable with Lake Tjeukemeer, which is the IBP site of the Limnological Institute in the Netherlands. The lake is rich in phytoplankton (Chlorophylla concentrations reach levels of about 100 mg.m⁻³ in summer).

As the energy for the whole aquatic ecosystem enters foodchains primarily via the phytoplankton and then dispersed via the zooplankton or bacteria, the theoretical effects of heat disposal on phytoplankton and zooplankton populations will be discussed in this paper. It is hoped to demonstrate the effects in future research in simplified models of populations with 2 or 3 zooplankton and phytoplankton species and to provide evidence for the theoretical effects by studying the lake itself for a 5 year period with Tjeukemeer as a baseline study.

2. Effect of temperature on photosynthesis

Before considering the influence of increased temperature on growth or photosynthesis of algae, the other factors regulating photosynthesis must be considered first.

Photosynthesis in lakes is primarily a function of depth, as light decreases exponentially with increasing depth, the function being (see fig. 1A).

$$\mathbf{Iz} = \mathbf{1}_0 \, \mathbf{e}^{-\varepsilon \mathbf{Z}}$$

where $I_0 =$ light intensity at surface

Iz = light intensity at depth = d $\varepsilon = extinction$ coefficient (1)

Z = depth

The relationship between light and photo-

$$\begin{array}{c} \begin{array}{c} \text{DEPTH} & \frac{25}{160} & \frac{50}{75} & \frac{75}{100} \\ 1 & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} \\ 1 & \frac{1}{125} & \frac{1}{25} & \frac{1}{50} & \frac{100}{100} \\ 1 & \frac{1}{125} & \frac{1}{25} & \frac{100}{50} & \frac{100}{100} \\ 1 & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} \\ 1 & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} \\ 1 & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} \\ 1 & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} \\ 1 & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} \\ 1 & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} \\ 1 & \frac{1}{16} & \frac{1}{16} & \frac{1}{16} \\ 1 &$$

Figure 1 - Relationship between photosynthesis and depth

A. Relationship between light intensity and depth

B. Relationship between light intensity and photoassimilation

- C. Summation of curves A and B (lin scale)
- D. Summation of curves A and B (log scale)

synthesis can be described by a normal saturation curve (see fig. 1).

$$A = A_{max} \frac{aI_Z}{\sqrt{1 + (a I_Z)^2}}$$
where A = photoassimilation

$$A_{max} = Light saturated photo-
assimilation
a = \frac{1}{I_k}$$
(2)

 I_k = light intensity where photosynthesis would be A_{max} if the increase of photosynthesis with light was linear.

The model has been developed by Talling (1957) and a full theoretical description has been given by Vollenweider (1965). Curve 1 B has two distinct parts: It can be shown that at low light intensities,

$$\mathbf{A} = \mathbf{A}_{\max} \cdot \mathbf{a} \mathbf{I}_{\mathbf{Z}} \tag{3}$$

so that it may be concluded that photosynthesis increases with light intensity linearly up to the light intensity value of about $\frac{1}{2}$ I_k.

At higher light intensities curve 1 B becomes $A = A_{max}$,

the photosynthesis is no longer dependent on the light intensity, but on nutrient supply, for instance the amount of available nitrogen or phosphorus.

The total photosynthesis per m^2 lake surface is the summation of the photosynthesis in the different water layers,

$$\Sigma \mathbf{A} = \mathbf{A}_{\mathbf{z}} \, \mathbf{dz} \tag{4}$$

(where ΣA = integral photosynthesis g.m⁻² · t⁻¹)

$$A_z = A$$
 at depth Z.

or the surface between the y-axis and the A-depth curve.

The mathematical solution of (4) is

$$\Sigma \mathbf{A} = \mathbf{Z}^{\mathrm{I}} \mathbf{A}_{\mathrm{max}} \tag{5}$$

where $Z^{l} = \text{depth of } \frac{1}{2} I_{k}$ (Vollenweider 1965).

From figure 1 it can be seen that the larger part of the surface lies above the line $Z = \frac{1}{2} I_k$, independent on the total depth penetration of the light as the slope of the curve is similar in optically deep or shallow lakes.

Thus the larger part of the photosynthesis is performed under nutrient limiting conditions. Only in the deeper water layers (and in the upper layers during winter) photosynthesis can be limited by the light. Between these two well defined layers a transistory phase will occur for which Takahashi and Nash (1973) suggested that temperature may have a stimulatory effect (fig. 2).

The influence of the temperature on algal growth and photosynthesis is physiologically well established. Photosynthetic rate will increase with temperature up to an optimal value. Above that temperature the photosynthetic rate will decrease and often much more steeply than below the optimum (fig. 3). Talling (1955) demonstrated that the influence on photosynthesis is different from that on growth rate probably due to the influence on respiration (fig. 4). Other studies are those of Jørgensen and Steemann-Nielsen (1965) and Thomas (1966), but very little information is available on the influence of temperature on the growth of algae under nutrient limited conditions.

Aruya (1965) worked with natural populations from a pond and showed that high optimal temperatures occur at high water temperatures (fig. 5).

A close approximation in the warmer months and discrepancy in the colder months was demonstrated indicating that in the warmer months temperature increase may have a strong inhibitive effect. From the high values for the photosynthetic rates it can be deduced that this phytoplankton population was not growing under nutrient limiting conditions.

Eppley (1972) reviewed the influence of the temperature on phytoplankton growth in the sea and found that temperature set an upper limit on the growth rate and on the rate of photosynthesis per weight of chlorophyll. The upper limit of the temperature effect on the growth rate is given in figure 6, which shows much variation in the specific growth rate. The drawn line indicates the upper limit, an approximate equation is $\log_{10}\mu = 0.0275 \text{ T} - 0.070$ where $\mu =$ doublings per day (see below). Other factors such as light and nutrient supply overrule the temperature reduction of the rates of growth (see figure 7). Temperature may have a further effect on growth rate as it also influences the rate

of the nutrient supply by mineralization

(see subsection 4). In natural lake water the influence of temperature is obviously complex although there does seem to be an upper limit set to algal growth by temperature. This effect (figure 6) could be described as a temperature limited upper growth rate, which in nature is seldom reached due to the depletion of nutrients. It could be that this effect plays a role in the transistory layer between light and nutrient limitation but very little evidence for this hypothesis is available. Takahashi and Nash (1973) studied the influence of temperature on natural populations by plotting photosynthesis at different dates against the temperature; their results are already shown in figure 2. It may be argued however, that temperature was not the only other parameter in the different samples, and that photosynthesis and temperature might both be dependent on another factor, e.g. nutrient supply which well may be dependent on the season. Algal growth is

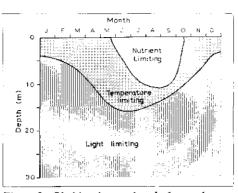


Figure 2 - Limiting factors for algal growth as function of time and place (Takahashi and Nash, 1973).

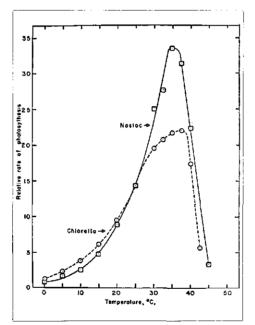


Figure 3 Temperature relations of photosynthesis in Nostoc muscorum and Chlorella pyrenoidosa (from Clendenning et al 1956).

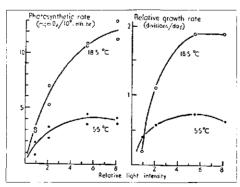


Figure 4 - Comparison of the variation, recorded under laboratory conditions, of the photosynthetic rate and the relative growth rate of cultured Asterionella population in relation to light intensity and temperatures. Each relative growth rate indicated is derived as a mean from two duplicate cultures. (Talling 1955).

regulated by mineralization as well as by photosynthesis. This aspects will be discussed in subsection 4. The temperature may have an effect on the depth of the so called compensation point, i.e. the point where the light intensity is so low that the photosynthesis is equal to the respiration. This effect which is well known in physiology, (see figure 8) means that in a lake the photosynthetic layer becomes shallower as the compensation point shifts to higher light values while the layer of (dark) 0_2 -uptake becomes deeper. It is not known how nutrient depletion will affect this phenomenon.

3. Effect of temperature on algal periodicity

Most of the primary production in lakes is performed by unicellular algae (sometimes arranged in colonies), which even in nature may reach high growth rates; division (doubling) times of once a week or even higher will often be found. The population reach their maxima in a few weeks; after that the population normally disappears equally rapidly. As an example, the periodicity of Asterionella formosa will be discussed briefly (Lund 1949, 1950) (See figure 9). Starting in February, the cell number increases exponentially following the formula: AN

$$\frac{d\mathbf{r}}{dt} = \mu \mathbf{N} \tag{6}$$

where N = number of cells $\mu =$ division per day

It seems likely that the start of growth is mainly due to the increasing light quantity (cal.day⁻¹). Although temperatures from February till May become higher as well, the growth rate remains linear if plotted on a log scale. It seems therefore likely that the growth rate is nutrient dependent as stated above for photosynthesis. As soon as silica is depleted, growth ceases; the maxima is controlled by the silica concentration in winter, or

$$\frac{\mathrm{dN}}{\mathrm{dt}} = \beta \mathrm{N} \cdot \frac{\mathrm{K} - \mathrm{N}}{\mathrm{N}} \tag{7}$$

where K = the maxima number that N can reach.

K can be calculated from the winter SiO_2 concentration (10⁶ cells = 0.14 mg SiO₂). It can be seen from figure 9 that the cells disappear in roughly the same time that they took to develop. The disappearance rate again follows an exponential relation and is therefore different from the cease of bacteria growth, which is often described by the formula: dN

$$\frac{dI}{dt} = \beta N - \gamma N^2$$
(8)

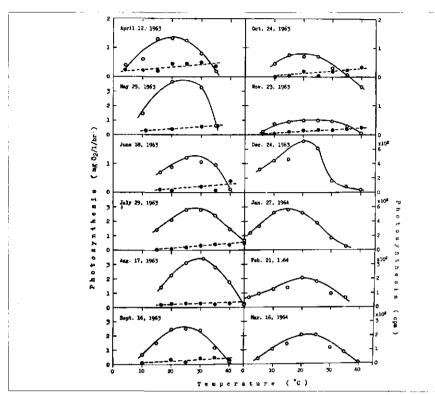


Figure 5 - Seasonal changes in photosynthesis temperature curves (solid lines) and respiration temperature curves (dashed lines) of phytoplankton from Shinjiike Pond. Photosynthesis was measured at 15 200 lux by the Winkler method from April to November and by the C¹⁴ method from December to March.

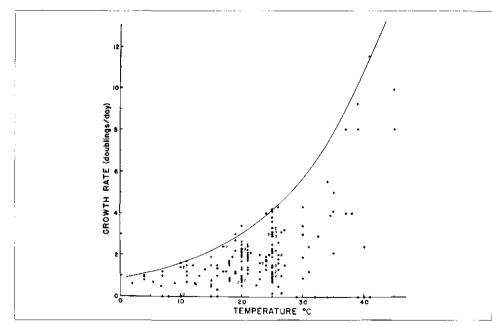


Figure 6 - Variation in the specific growth rate (μ) of photoautotrophic unicellular algae with temperature. Data are all for laboratory cultures. Growth rate is expressed in doublings/day. From Epply 1972).

Death rate of the Asterionella population must therefore be described by

$$-\frac{dN}{dt} = \delta N \qquad (9)$$

The death of the cells is caused by the combined action of high light intensity and

high temperature during the period when the algae are severely nutrient limited (Lund 1965). The fact that the disappearance must be described with equation (9) after equation (8) might be explained by assuming that cells are killed in a period that they are present in the upper water layers where light might be harmful. The number of

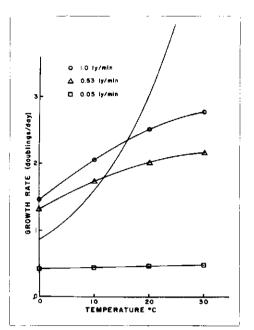


Figure 7 - Growth rate vs. temperature relationship predicted by the Baly equation as used by Riley, Stommel and Bumpus (1949). Three different levels of total radiant energy are included for the Baly equation: 1.0 (circles), 0.53 (triangles), and 0.05 ly/min (squares). The line of maximum expectation predicted by Equation (1) is drawn for comparison (no symbols).

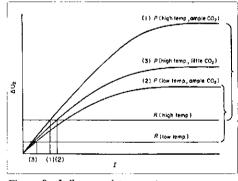


Figure 8 - Influence of temperature on compensation point (Rabinowitch, 1951).

cells killed per unit time would thus be proportionnal to the number itself and not to its second power.

After the Asterionella growth either Fragillaria or Tabellaria appear.

These have been growing at the same time but could not compete with Asterionella. Lund (1964) has explained how Tabellaria cannot compete with Asterionella due to the lower growth rate of Tabellaria, while Fragillaria, having the same growth rate cannot compete due to the low number of overwintering cells.

Competition can be described mathematically as follows:

$$\frac{\mathrm{dN}_1}{\mathrm{dt}} = \beta_1 N_1 \frac{\mathrm{K}_1 - \mathrm{N}_1 - \alpha \mathrm{N}_2}{\mathrm{K}_1} \qquad (10a)$$

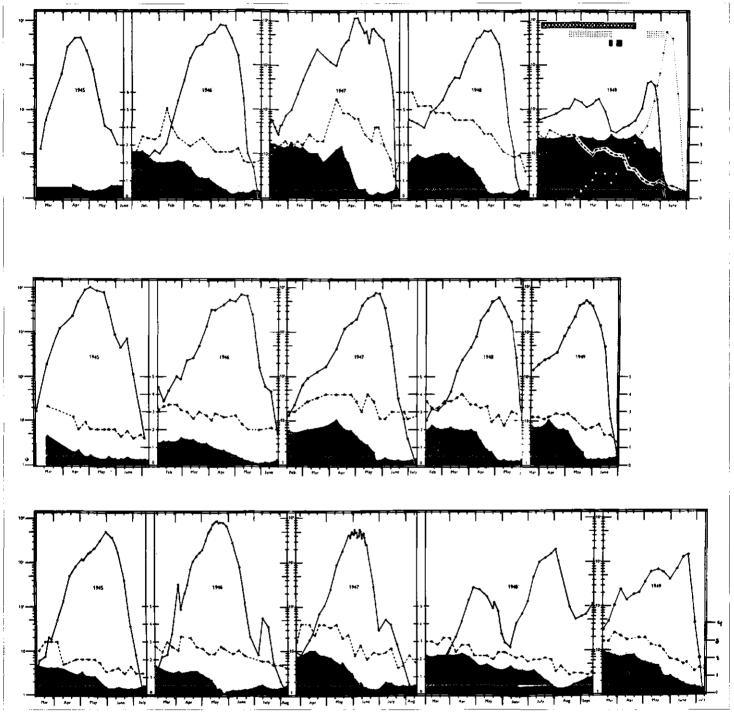


Figure 9 - Periodicity of Asterionella formosa and silica in Windermere and Esthwaite Water (Lund 1949, 19750).Solid line: number of live cells per mlUpper series: Esthwaite waterInterrupted line: nitrate nitrogen (mg.l-1 x 10)Middle series: Windermere South BasinSolid black: SiO2 conc. (mg.l-1) 0.5 mg.l-1 cross hatchedLower series: Windermere North Basin

(10b)

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = B_2 N_2 \frac{K_2 - N_2 - \gamma N_1}{K_2}$$

where α and γ are competition coefficients (Slobodkin 1961)

It can be shown that survivorship is K_1

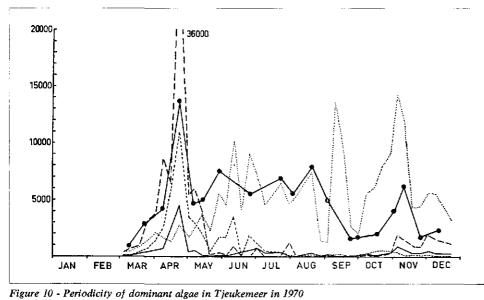
controlled by
$$\alpha$$
, β , γ and $-$.

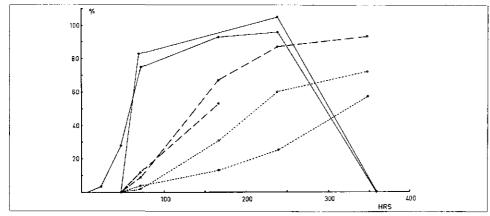
Temperature will have a more dominant effect on the outcome of this type of competition than can be explained by its influence on the growth constants themselves.

It is hoped to demonstrate these effects with simplified computer models. In shallow eutrophic lakes the normal algal successions are often as follows: after the diatoms spring bloom peaks of Chlorococcales (often *Scenedesmus* and or *Pediastrum*)

occur, which gradually will be replaced by blue greens (See figure 10).

Competition is believed to be one of the most important factors regulating this succession and it seems likely that changes in spring temperature of 2-3°C will drastically change this succession pattern: disposal of heat will have a synergistic effect to that of eutrophication.





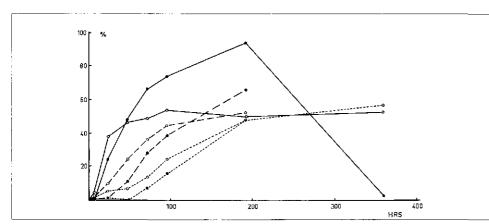


Figure 12 - Release of ammonia from 'leached' Scenedesmus cells during mineralization in lake water (0—0) or in cultures of P. boreopolis (•—••) at three temperatures; —--: $30 \,^{\circ}$ C; —---: 20° C; ----: 10° C.

4. Influence of temperature on mineralization

After the death of the algal cells they will be rapidly mineralized by bacteria (Golterman, 1973). The bacterial mineralization is strongly dependent on the temperature. In figure 11 the temperature effect on the ammonia production from dead algal cells by natural populations is demonstrated. The algal cells were killed by autolysis and suspended in lake water at different temperatures. Cells were also suspended in lake water that had been heated at 65°C to kill protozoa. It can be seen in figure 11 that protozoa did not contribute to the mineralization and that the temperature has its effect via the bacteria. In figure 12 it can be seen that a single strain of Pseudomonas sp, which digest the algal cells and releases ammonia, shows the same temperature effect as the natural population. It has been stated above that the growth rate of the phytoplankton is limited by nutrient supply. More rapid mineralization therefore automatically means a higher growth rate, but not a higher standing crop. Nevertheless the diurnal oxygen variation in eutrophic shallow lakes, which often shows large supersaturations in day time and a decreased oxygen concentration at light will show more pronounced differences. This will be due, not only to increased bacterial mineralization, but also by increased algal respiration. Both respiration and photosynthesis will increase with rising temperature, but often photosynthesis will reach its optimum at a lower temperature than will respiration (see figure 13). This effect is probably more important in the competition between different algal species than the temperature effect on photosynthesis alone. It seems likely for instance, that the optimum temperature in the P-R curve for diatoms will be exceeded by the increasing spring temperatures and that these will then approach the optimum for blue-green algae. From this and other factors the replacement of diatoms by blue greens seems to be a predictable effect of artificial heating. Sorokin (1971) warned that with increasing temperatures the aquatic habitat will not be automatically colonized by high temperature phytoplankton but probably by blue green algae and suggested rather optimistically that artificial restocking of such habitats with high-temperature algae of less nuisance species would be feasible and suggested the establishment of a collection of high temperature algal strains. Disregarding problems during the winter period it should be realized that the preparation of the inoculum for a relative small lake would involve several thousands of liters of algal cultures.

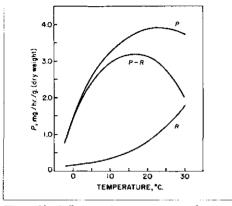


Figure 13 - Influence of temperature on photosynthesis and respiration of Ramalina farinacea (Rabinowitch 1956).

Very few — if any — data exist on the influence of increasing temperatures on competition and growth (photosynthesis respiration) of natural phytoplankton populations. This will be more difficult to study than measuring the influence of temperature on isolated samples of lakephytoplankton. Practically, the only way to study rather subtle effects is in large experimental ponds built in the lake itself, which can be kept at an elevated temperature for a long time, or by comparing an artificially heated lake with similar lakes in the same area.

5. Influence on zooplankton

The same effects on competition between zooplankton species and on net growth (assimilation — respiratory losses) of these organisms may be expected as have been described for the phytoplankton. Again, a small increase of the temperature may completely change the outcome of competition and through this change, secondary effects may affect the phytoplankton again, as many examples are now available of the specificity of grazing of the zooplankton.

A special feature with the zooplankton has to be taken into account as well; that of the influence of temperature on the life cycle of the zooplankton. During the summer, eggs develop via different nauplii and copepodite stages into fertile females, which will produce eggs again.

Temperature has a major effect on the duration of each stage. Examples are given in figures 14, 15, 16 which show how consistent this effect is. *Eudiaptomus graciloides* follows the same

type of curve in Lake Erken as Eudiaptomus gracilis in Schluchsee and Bodensee. Other examples can be found in Nauwerck's paper (1963). Furthermore it can be seen how an increase of 5° C will considerably shorten the whole life cycle

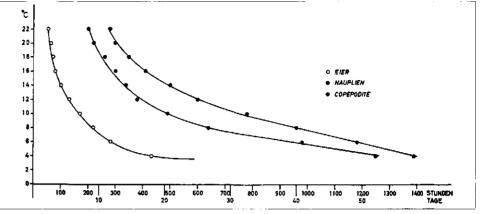


Figure 14 - Development time of different stages of Eudiaptomus gracilis (Eckstrin, cited in Nauwerck, 1963).

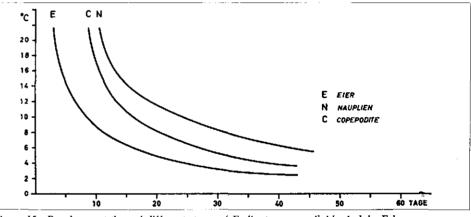


Figure 15 - Development time of different stages of Eudiaptomus graciloides in lake Erken. (Nauwerck, 1963).

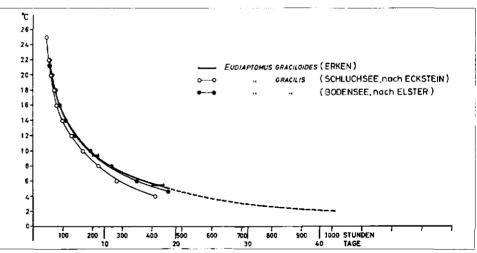


Figure 16 - Development time of different stages of Eudiaptomus gracilis and Eudiaptomus graciloides in different lakes (Nauwerck, 1963).

as the shortening of the different stages will be additive, and number of generations per year will increase. Considering the influence of temperature on primary production it does not seem likely that the primary production will be increased, so that more food for the extra generations will be present. Furthermore, as the natural periodicity of both phyto- and zooplankton will be disturbed, it seems possible that the production of specific food for smaller stages (e.g. nauplii) may take place at the wrong time. It also seems likely that in the evolution of dominant populations in a given lake, these timing effects of the food supply will be important. The fact that one

physical factor (temperature) will be changed without the naturally controlling one, (irradiance) is a pollution different from the nutritional effects of sewage for example, in which the nutrients are often in balance for algal growth, so that the whole community will be influenced to the same extent. The effect of temperature on life cycles can be more easily demonstrated than the effect of temperature on phytoplankton by comparing warm with temperate lakes because the phytoplankton will also be influenced by the different erosion patterns in tropical environments. It is known however that warm water lakes produce smaller zooplankton organisms with shorter life cycles and that higher respiration losses do indeed occur, but total productivity tends to be higher.

If the shortening of the life cycle occurs in the winter too, a rather special problem could develop. Normally the populations survive the winter as 'winter eggs' ('Dauereier). If these should start developing e.g. in December or January only a small quantity of food will be present so that the population might starve. The recruitment for a new population would then depend on migration from other lakes in the same area, where the overwintering populations were not affected. It is possible that in the Frysian district this migration would not be a problem as all lakes are interconnected through open canals, and there are no differences in elevation.

If this migration did not occur for some reason this would leave the lake with an open niche and the introduction of a new species would be possible. This introduction may have a favourable or a harmful effect (introduction of a vector for a new disease). It should be realized that several organisms that occur only in warm lakes do not occur in cooler lakes as they have no possibility of overwintering, because the water temperature falls below 4°C. Similar effects on life cycles (especially during winter) may occur for benthic organisms such as Chironomids and even on fish spawning. If this happened in conjunction with the timing effect on food production serious disturbances in several food chains would occur.

Summarizing remarks

1. Increasing temperatures may effect net growth of phytoplankton positively or negatively depending on the species. Mineralization of dead phytoplankton will occur more rapidly, and may lead to faster growth rates, but does not necessarily lead to higher biomass.

2. Larger effects may be expected on the

selection of dominant species. The influence will have a synergistic effect with eutrophication, both stimulating the production of blue green algal blooms.

3. Increasing temperatures will increase the number of generations of zooplankton per year, without increased food production. The effect on overwintering stages of the fauna may be detrimental, ultimately leaving open niches in the ecosystem. Other predator-prey relationships and competitive processes will be disturbed.

4. The above mentioned points together with better known effects such as influence on spawning and migration and other physiological or even lethal effects, make heat disposal not permissible if this causes temperature elevations larger than those occuring naturally. Attention should be given especially to winter temperatures as the tolerance of the ecosystem is smaller than during summer.

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