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Growth of Oscillatoria agardhii in a hypertrophic brackish-water bay

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The growth and temporal variation of the blue-green alga *Oscillatoria agardhii* Gomont was studied during four summers in a hypertrophic brackish-water bay. The alga had a pronounced biomass maximum in early summer. During the exponential phase of growth, the specific growth rate of *O. agardhii* was determined by water temperature. The course of the biomass was explained by the difference between the specific growth rate of the alga and the dilution rate of the bay. When the specific growth rate exceeded the dilution rate, pronounced biomass accumulation occurred. When the specific growth rate was smaller than the dilution rate, a slow wash-out of *O. agardhii* was observed. Limitation of *O. agardhii* by nitrogen or phosphorus did not occur during the exponential phase of growth, but may have operated later in the summer.

Key words: blue-green algae, temperature, nutrients, hypertrophy, eutrophication.

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INTRODUCTION

The blue-green alga *Oscillatoria agardhii* Gomont is known from eutrophic and hypertrophic waters around the world (Cornelius & Bandt 1933, Cedercreutz 1934, Edmondson 1967, Ahlgren 1970, Gibson et al. 1971, Berger 1975, Skulberg 1978a), and it is also common in polluted inner waters in bays and inlets of the Baltic (Häyrén 1921, 1933, 1937, Välikangas 1926, Melin & Lindahl 1973, Niemi 1973, 1979, Melvasalo & Viljamaa 1977, Alasaarela 1979). It is generally considered planktonic, but it may also live on or close to the bottom sediments (Kappers 1977). *O. agardhii* has been described as a nuisance species in many studies, both because of bloom formation, and because it is a potential source of the muddy odour compounds that impart off-flavours to water and fish (Tabachek & Yurkowski 1976, Persson 1979). In the present study area, *O. agardhii* has been shown to be a source of muddy odour in fish (Persson 1978, 1979, 1980, 1981).

The present study is part of the author's research on the etiology of muddy odour in natural waters (see above). Its aim is to explain the growth and temporal variation of *O. agardhii* in an extremely eutrophic brackish-water bay on the south coast of Finland in terms of hydrological, physical and chemical parameters. Elucidation of the growth of this alga is important to understanding muddy odours in the fish of the area, and may suggest practical measures for abating or forecasting this nuisance. The phytoplankton dynamics and other algal species occurring in the phytoplankton of the area will be discussed in a forthcoming study (P.-E. Persson, in preparation).

STUDY AREA

The study area (Fig. 1) was a shallow (mean depth 0.7 m), dilute brackish-water bay (area 2.6 km²) known as Kaupunginselkä (Stadsfjärden) Bay, situated on the south coast of Finland, at Porvoo (Borgå), c. 50 km E of Helsinki (Helsingfors). It lies at the mouth of the River Porvoonjoki (Borgå å), but is partly separated from the river mouth by the road embankment built in 1950—53 between the mainland and the islet of Sikosaari (Svinö). Discharge data for the river, measured at Vakkola (9 km

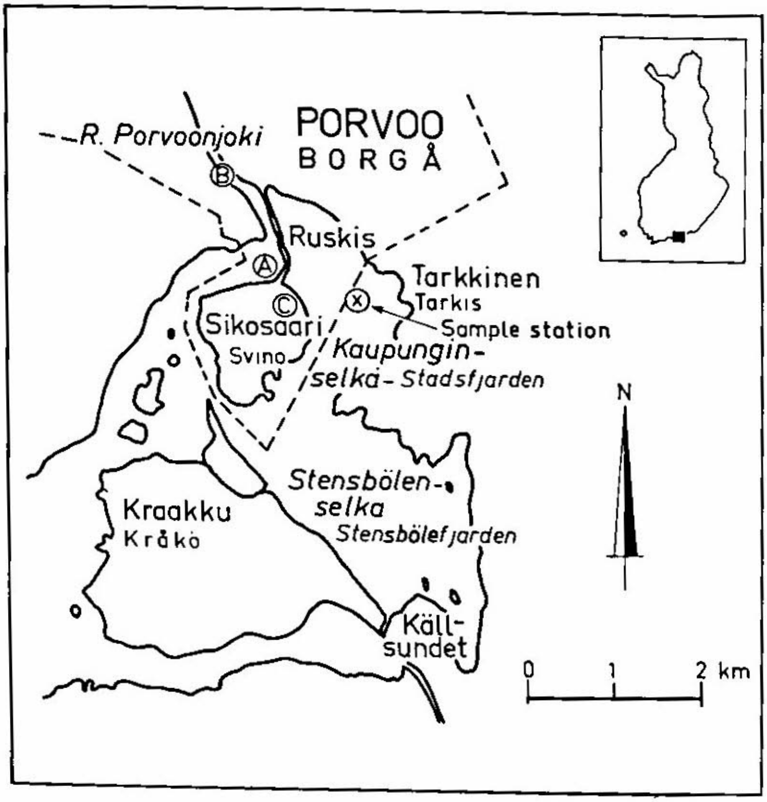

Fig. 1. The study area, Kaupunginselkä Bay at Porvoo, on the south coast of Finland (60°22'30" N, 25°42' E).

upstream), were supplied by the Hydrological Bureau, National Board of Waters, Finland. During the study, the mean monthly discharge of the river varied between 1.9 m^3s^{-1} and 28.5 m^3s^{-1}. In 1976, 1977 and 1979 the highest discharge rates during the period of study were recorded in May, but in 1978 the highest discharge occurred in September. The discharge rate during the period of study was higher in 1977 and 1979 than in 1976 and 1978. The river water mainly enters the bay through the southernmost opening in the embankment (A in Fig. 1). On the basis of the morphometry of the river close to its mouth, and the morphometry of the channel at A, it was estimated that about 20 % of the river flow entered the bay. This value was used together with the monthly mean discharge rates to calculate the theoretical average residence times of the water in the bay (Table 1).

Table 1. Theoretical residence times (monthly means in days) of the water in Kaupunginselkä Bay at mean sea water level

	May	June	July	Aug.	Sep.
1976	8.7	21.9	50.2	31.9	55.4
1977	4.0	21.5	8.6	12.1	—
1978	10.9	39.0	43.9	31.9	5.3
1979	3.7	34.0	6.8	10.2	—

The town of Porvoo (founded in 1346) has a population of c. 20 000. It is served by a chemical wastewater treatment plant, in operation since 1974. The treated wastewater is discharged close to the river mouth (at B in Fig. 1). The eastern shore of Kaupunginselkä Bay is occupied by the village of Tarkkinen (Tarkis; population 300), which was connected to the sewage plant in Porvoo in 1980. The catchment area of Kaupunginselkä Bay also contains agricultural land. In the innermost part of the bay is the bird sanctuary of Ruskis (mainly *Larus ridibundus*, 8 000 individuals; data from the Finnish Ministry of Agriculture and Forestry). During 1962—1969 sewage sludge and waste oil were dumped at two sites on Sikosaari (at C in Fig. 1). Part of the sludge ran off directly into the bay.

Nutrient load. — During the study the land-based nutrient load of the bay originated from the river, the town of Porvoo, the settlements on the shore, diffuse sources, and the bird sanctuary at Ruskis. Values for the load from the Porvoonjoki were obtained from the regression lines of the load, calculated from the nutrient concentrations, on the river discharge. Data on the water quality, sampled 2 km from Vakkola, were supplied by the Helsinki Water District. The load from the sewage treatment plant at Porvoo was calculated from data supplied by the municipal Water and Sewage Works.

Table 2. The estimated total land-based nutrient loads of Kaupunginselkä Bay at Porvoo during the study

	May	June	July	Aug.	Sep.
total nitrogen, kg d^{-1}					
1976	850	406	229	298	212
1977	987	264	721	658	—
1978	545	259	244	285	960
1979	889	269	572	443	—
total phosphorus, kg d^{-1}					
1976	43	25	16	18	15
1977	81	20	64	36	—
1978	29	13	12	15	53
1979	70	17	43	32	—

The load from diffuse sources was estimated from data in Persson (1975), and the contribution by the bird sanctuary from the data of Gould & Fletcher (1978). The results of the calculations are summarized in Table 2. Of the land-based nitrogen load, 70.2—93.3 % originated from the Porvoonjoki, and of the phosphorus load, 75.0—95.7 %. These figures indicate that the river discharge was the main variable in the land-based nutrient load of the bay. However, the total nutrient load was also influenced by changes in the sea water level. The nutrient concentrations in the surrounding sea areas were lower than those of the bay (Erkkilä 1977, 1978, 1979, Erkkilä & Takatalo 1980) and when the sea water level was rising, a complex pattern of dilution probably occurred. When the water level was declining (water volume of the bay diminishing), the effect of the river load was presumably more pronounced. Since the contribution from the surrounding sea areas to the nutrient load of the bay was difficult to estimate, it is not included in Table 2. Neither does Table 2 take account of potential internal nutrient sources in the bay.

Previous studies. — Previous studies on Kaupunginselkä Bay are those of Häyrén (1944) and Persson (1977, 1978, 1979). From Häyrén (1944) and the accounts of local inhabitants, it is evident that the water of the bay was clean and clear throughout the 1920s and 1930s. The major changes in water quality apparently occurred in the late 1950s and early 1960s. The main factors responsible for its deterioration were the building of the embankment to Sikosaari, which impaired water circulation, and the general increase in loading resulting from the introduction of water closets and detergents, and aggravated by the dumping at Sikosaari in 1962—1969. By the 1970s the bay had become hypertrophic and polluted (Persson 1975).

During the present study, the innermost parts of the bay contained large stands of *Phragmites communis*, interspersed with *Typha angustifolia* and *Scirpus tabernaemontani*. *Nymphaea candida* occurred near the shore areas, and patches of *Potamogeton* spp. were observed in the bay. Close to the sampling station (Fig. 1) was a small stand of *Phragmites communis*, but no other macrophytes were observed in its vicinity.

MATERIAL AND METHODS

Water samples were taken from Kaupunginselkä Bay during the summers of 1976, 1977, 1978 and 1979. Since the bay is shallow and of regular morphometry, one sampling station was considered adequate (Fig. 1). In 1978, sampling was performed at three additional stations in the bay, but since little variation (less than 10 %) was observed between the results from the different stations, the additional sampling was discontinued, and will not be further discussed. The sampling frequency during the study is shown in Table 3. Samples were taken more frequently in early summer in order to follow the development of the early summer peak of *O. agardhii*. The total number of water samples for physico-chemical analyses was 49, and the total number of phytoplankton samples was 57.

The depth at the sampling station varied between 0.7 and 1.2 m, depending on the sea water level. The water samples were taken at half the depth of the water column (i.e. at 0.3—0.5 m) with a 2-l Ruttner sampler. The sampler was equipped with a mercury thermometer, and the upper cover of the sampler was painted white, so that the Secchi disk transparency and water temperature could be determined at sampling. Conductance (γ_{25}), and the total nitrogen (tot. N) and total phosphorus (tot. P) concentrations were determined in the laboratory by the standard methods used in Finland (Erkomaa et al. 1977).

Phytoplankton samples were taken at the prevailing Secchi disk transparency, which usually varied between 0.10 and 0.25 m. The samples were preserved with formalin and counted using the Utermöhl (1958)

Table 3. Sampling interval (days) during the study

	sampling interval water	sampling interval phytoplankton
1976		
May — June	7	7
July — September	7—21	7—21
1977		
May — June	7	3—6
July — August	14	14
1978		
May — June	7	2—7
July — September	14	7—14
1979		
May — June	7—21	7—21
July — August	12—30	12—30

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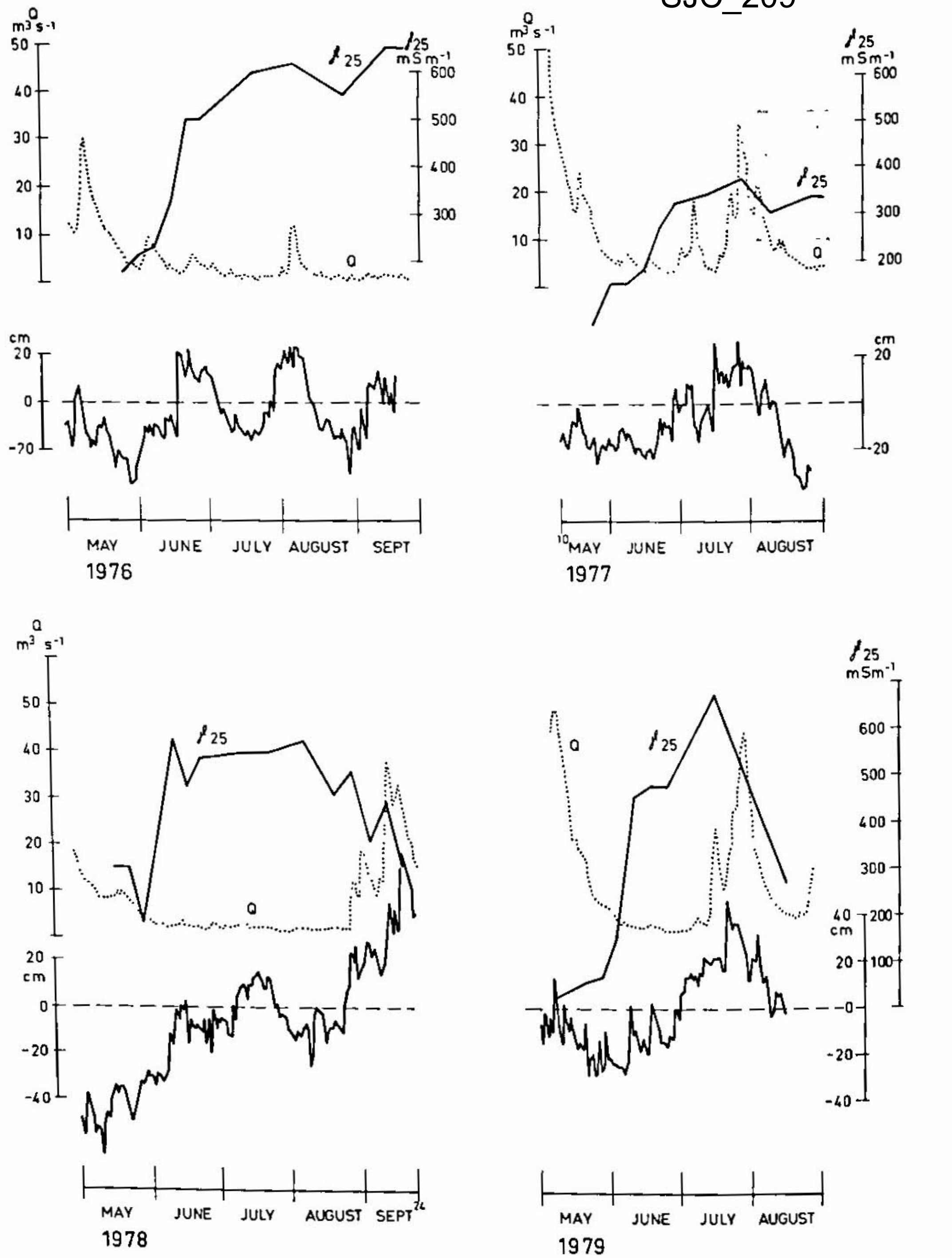

Fig. 2. Sea water level, discharge of R. Porvoonjoki (Q) and conductance of the water (γ_{25}) in Kaupunginselkä Bay during the study. Discharge data, measured at Vakkola, from the Hydrological Bureau, National Board of Waters, Finland. Sea water levels calculated as arithmetic means of the mareograph readings (daily means) in Helsinki and Hamina, supplied by the Institute of Marine Research, Helsinki.

technique. From all samples, 500 individuals (counting units as defined by Naulapää 1972) were counted from randomly chosen fields, which should give estimates of the total number of organisms with an accuracy around ± 10 % (Lund et al. 1958). The volumes of individual species were taken from Naulapää's tables. The cell size of *O. agardhii* is known to vary, however, depending on the physiological state of the alga (Kokyrtsa 1975, van Liere 1979).

In the following, statistical significance is indicated by the commonly used notation; n.s. = not significant ($P > 0.10$, (*) = nearly significant ($0.05 < P < 0.10$), * = significant ($0.01 < P < 0.05$), ** = very significant ($0.001 < P < 0.01$), and *** = highly significant ($P < 0.001$).

RESULTS

1. Physical and chemical characteristics

The conductance (salinity) of the water in the bay was influenced by the discharge of river water and the sea water level (Fig. 2). It had a negative correlation with stream discharge (r = –0.300*), being lower in the years with high discharge rates (1977 and 1979) than in the years with low rates (1976 and 1978; Table 4). Thus, although the variations in the sea water level brought about a complex pattern of water exchange in the bay, the river still seemed to exert a powerful influence on the general water quality characteristics.

The mean tot. P concentrations showed no variation between the years of study (Table 4), although the seasonal pattern varied (Fig. 4). The tot. N concentrations and the N/P ratios had higher values during years of low stream discharge (N/P ratios of nutrient load also higher, Table 2). Tot. N and tot. P were intercorrelated (r = 0.374*), probably reflecting the land-based load pattern (Table 2). Tot. P also correlated with temperature (r = 0.361*), the concentrations being higher during the summer, i.e. during periods of low discharge and comparatively long residence time of the water in the bay (Table 1).

The Secchi disk transparency was extremely low in all four summers (Fig. 3), exhibiting a slight increasing trend from spring to autumn. In early spring, the turbidity of the water was mainly caused by inorganic particles carried in during the spring maximum of stream discharge, while in summer the turbidity was caused by high phytoplankton biomasses.

Table 4A. Annual means of biomasses of total phytoplankton and O. agardhii, water temperature, conductance, tot. N, tot. P and N/P ratio of the water in the study area

Analysis of variance	F	$d.f._1$, $d.f._2$
Biomass of		
— total phytoplankton	2.24 n.s.	3, 53
— *O. agardhii*	4.44**	3, 53
— *O. agardhii* (%)	1.64 n.s.	3, 53
Water temperature	0.05 n.s.	3, 42
Conductance	4.20*	3, 43
Tot. N	3.35*	3, 35
Tot. P	0.09 n.s.	3, 38
N/P	2.44 n.s.	3, 35

Table 4B. Significance of differences between annual means of biomasses, conductance, tot. N, tot. P and N/P ratio, calculated by Scheffe's method. Means not followed by the same subscript differ at P < 0.10

	1976	1977	1978	1979
Biomass of				
— total phytoplankton mg l^{-1}	37.6_a	44.7_a	55.6_a	27.8_a
— *O. agardhii* mg l^{-1}	9.0_a	16.8_{ab}	21.6_b	6.6_a
– *O. agardhii* %	32.0_a	23.2_a	33.8_a	23.8_a
Conductance mS m^{-1}	460_a	267_b	430_a	300_{ab}
Tot. N mg l^{-1}	1.98_{ab}	1.61_{ab}	1.97_b	1.32_a
Tot. P µg l^{-1}	222_a	243_a	231_a	220_a
N/P	9.2_a	7.4_a	8.3_a	6.1_a

2. General characteristics of the phytoplankton

After the break-up of the ice cover, occurring in late April or early May, small chrysomonads predominated in the phytoplankton, whose total biomass was small (less than 5 mg l^{-1}) compared with the mean biomasses recorded in the area (Table 4). In May, a biomass maximum of *Diatoma elongatum* was observed. In late May and early June small green algae (*Ankistrodesmus falcatus*, *Chlamydomonas* spp., *Scenedesmus* spp., *Tetraëdron minimum*) became abundant. By mid-June *O. agardhii* had usually reached a pronounced biomass maximum. At about the same time, *O. limnetica* appeared in large numbers and it remained common during the rest of the summer. With

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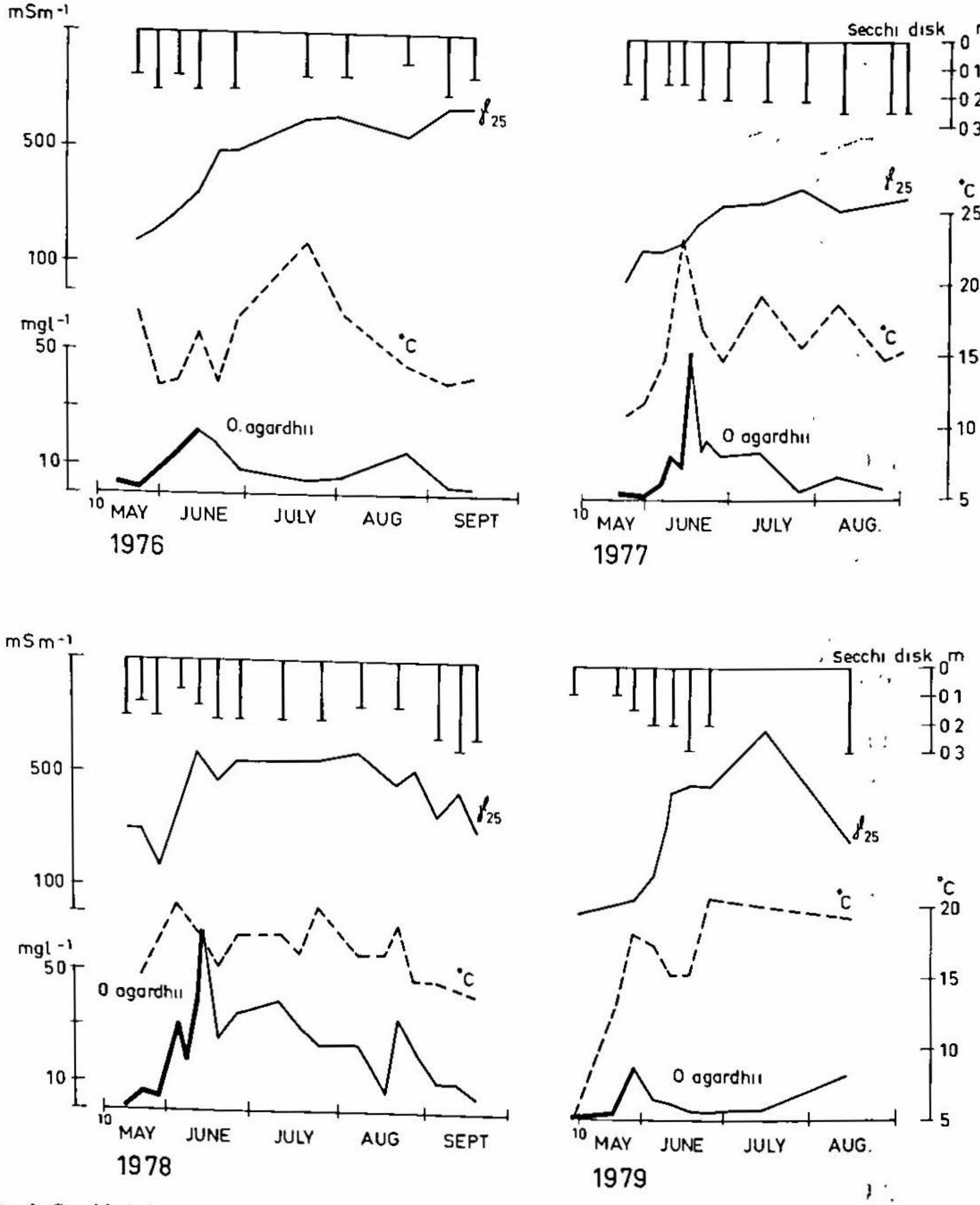

Fig. 3. Secchi disk transparency, conductance, water temperature and biomass of *O. agardhii* in the water of Kaupunginselkä Bay. The thick part of the biomass curve denotes the period of exponential growth of *O. agardhii*.

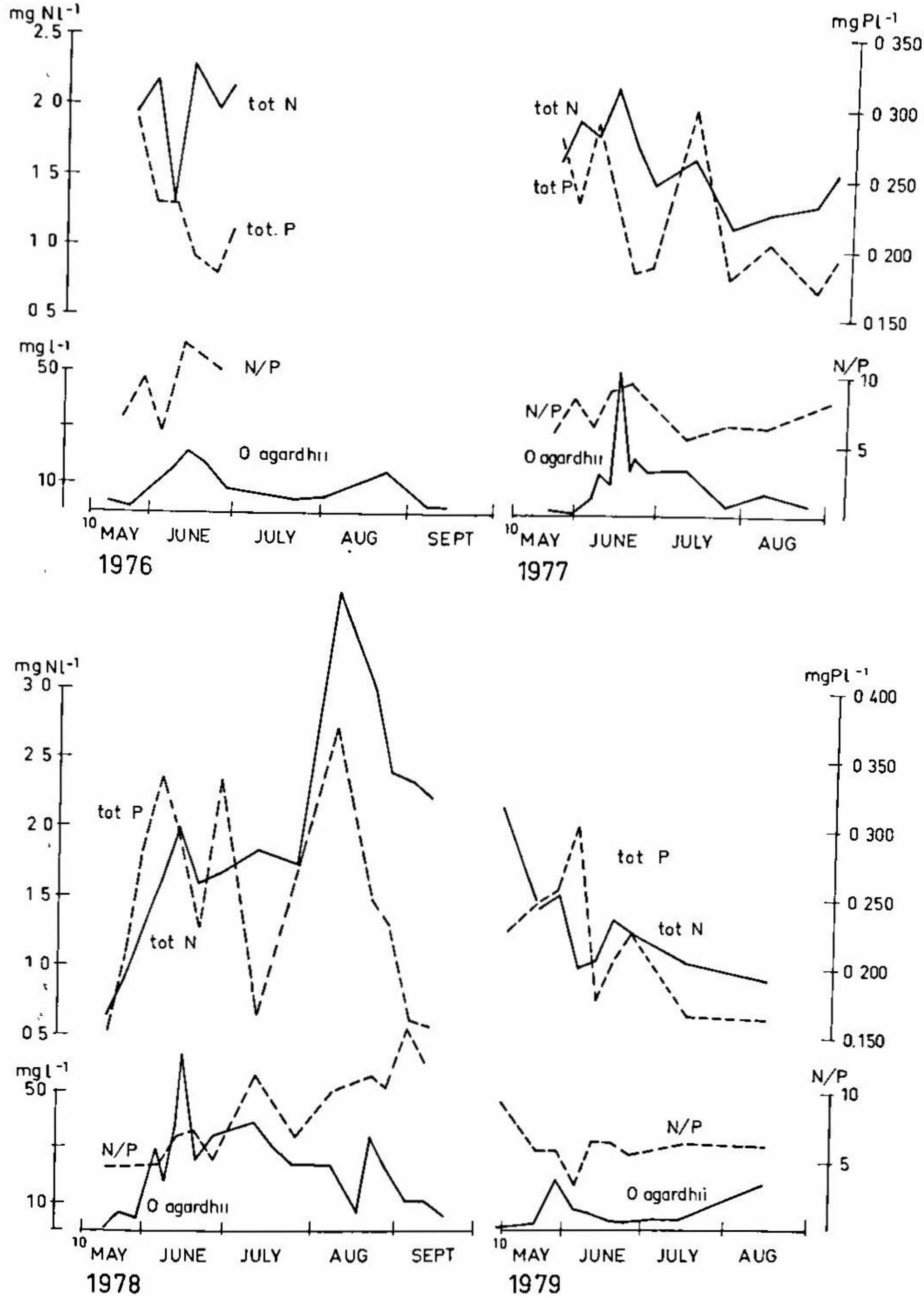

Fig. 4. Tot. N, tot. P, and N/P ratios of the water, and biomass of *O. agardhii* in Kaupunginselkä Bay.

the exception of 1978, a biomass minimum was observed in July. In August a second blue-green algal bloom occurred (*Anabaena* spp., *Aphanizomenon flos-aquae, O. agardhii, O. limnetica*). In 1979, *Nitzschia* spp. were also abundant in August. The biomass of blue-green algae decreased in September, when green algae and diatoms became abundant. In October, small chrysomonads were again abundant.

3. Growth of Oscillatoria agardhii

The course of the biomass of *O. agardhii* in the study area is shown in relation to some physical and chemical parameters in Figs. 3 and 4. The early summer maxima of this alga occurred while the conductance and temperature of the water were rising and the Secchi disk readings were low (Fig. 3). The relationships with tot. N, tot. P and N/P seem less clear (Fig. 4). In 1976, 1977 and 1979 the early summer maxima of *O. agardhii* occurred while tot. P was rising. The peaks in 1977 and 1978 concurred with an increase in tot. N, whereas the tot. N concentrations were declining during the peak in 1979. It is difficult to find any meaningful relationship between the occurrence of *O. agardhii* and the N/P ratios.

The mean biomass of *O. agardhii* was higher in 1977 and 1978 than in 1976 and 1979 (Table 4). The percentage of *O. agardhii* in the phytoplankton biomass seemed to vary in the same way as the freshwater discharge, conductance, tot. N and N/P ratios in the bay, showing somewhat higher values in 1976 and 1978 than in 1977 and 1979, though the differences were not statistically significant. The absolute (mg l^{-1}) and relative (% of total) biomasses of *O. agardhii* were strongly correlated (r = 0.742***), and so were the biomass of *O. agardhii* and the total phytoplankton biomass (r = 0.686***). However, the correlation between the relative biomass of *O. agardhii* and the total phytoplankton biomass was much weaker (r = 0.265*), indicating that the concept of "relative biomass" accentuates the difference between the total phytoplankton (other algal species) and *O. agardhii*. The relationships revealed by Table 5 in respect of the relative biomass indicate that water temperature was the most important environmental factor explaining the biomass variation of *O. agardhii* in the study area. The biomasses of total phytoplankton and *O. agardhii* correlated with all the factors studied, so that the phytoplankton dynamics observed in the area appear to be the outcome of a complex interaction between hydrological, physical and chemical parameters.

Table 5. Correlations between phytoplankton and environmental parameters in the study area during the summers of 1976-1979

	Biomass of		Relative (%) biomass of *O. agardhii*
	total phytoplankton	*O. agardhii*	
Discharge of river water	—0.361**	—0.265(*)	—0.200 n.s.
Tot. N	0.490**	0.387*	0.173 n.s.
Tot. P	0.436**	0.346*	0.141 n.s.
N/P	0.245 n.s.	0.245 n.s.	0.200 n.s.
Water temperature	0.283(*)	0.361*	0.300*
Conductance	0.316*	0.316*	0.141 n.s.

The negative relationship between freshwater discharge and phytoplankton evident in Table 5 may be interpreted in two ways. It may reflect a predominance of brackish-water plankton in the area, which is also suggested by the positive correlation between conductance and biomass, or it may indicate that phytoplankton is washed out of the bay. There was in fact a correlation (r = 0.633*) between the mean monthly biomass of *O. agardhii* and the residence time of water in the bay (Table 1).

The factors influencing the build-up of *O. agardhii* biomass in early summer were examined by comparing the biomass-based specific growth rates (d^{-1}) of the alga during the exponential phase of growth (indicated by thick lines in Fig. 3) with the prevailing water temperatures and the dilution rate of the bay (d^{-1}, Table 6). In 1976 and 1979, when the biomass peaks of *O. agardhii* were comparatively low, the specific growth rate of the alga was slightly lower than the dilution rate of the bay, and in fact, the pattern of occurrence of *O. agardhii* in these years resembles slow wash-out in a chemostat (Fig. 3). In contrast, in 1977 and 1978 the growth rates of *O. agardhii* were distinctly higher than the dilution rates, resulting in high

Table 6. Growth characteristics of O. agardhii during the exponential phase of growth related to the dilution rate and the water temperature of the study area

	Dilution rate of the bay[a) b)] (d^{-1})	Specific growth rate[b)] of *O. agardhii* (d^{-1})	Temperature prevailing around maximal biomass increase (°C)	Peak biomass[b)] of *O. agardhii* (mg l^{-1})	Mean biomass[b)] of *O. agardhii* (mg l^{-1})	Mean temperature[b)] (°C)
1976	0.094	0.082 (r=0.841(*))	13.8	21.7	10.0	14.7
1977	0.081	0.170 (r=0.888**)	18.9	52.4	11.4	15.0
1978	0.047	0.153 (r=0.931**)	18.7	64.3	23.2	17.2
1979	0.207	0.191 (r=0.994(*))	18.2	18.2	7.2	12.0

a) corrected for volume changes caused by variations in sea water level.
b) during exponential phase of growth, i.e. 17.V.—15.VI. 1976; 23.V.—17.VI.1977; 18.V.—15.VI.1978; 8.—29.V.1979 (see Fig. 3).

biomasses throughout most of the summer. The specific growth rates of *O. agardhii* were determined by the water temperature (Table 6). During the exponential phase of growth its biomass correlated with water temperature (r = 0.540*) and the conductance of the water (r = 0.735*), but no correlation was found with tot. N, tot. P or N/P.

DISCUSSION

1. Temperature, hydrology and growth

The relationships shown in Table 6 resemble those prevailing in a chemostat (Ahlgren 1979, van Liere 1979). In fact, a higher growth rate of the alga compared with the dilution rate of the bay should result in accumulation of biomass. According to the difference between the growth rate of *O. agardhii* and the dilution rate of the bay in 1977, biomass accumulation of c. 30 mg l^{-1} should have been found by the time of the biomass peak of the alga (52.4 mg l^{-1}). In 1978, the theoretical peak was c. 50 mg l^{-1} and that actually found 64.3 mg l^{-1}.

In chemostat experiments, van Liere (1979) noted a positive relationship between temperature and the specific growth rate of *O. agardhii* in both his own data and the data of Foy et al. (1976). Ahlgren (1978) found higher growth rates of *O. agardhii* at higher temperatures in batch cultures, but lower growth rates at higher temperatures in chemostat cultures. However, the difference in growth rates in her chemostat cultures was not great.

In the polluted harbour area around Helsinki, Välikangas (1926) found that *O. agardhii* favoured comparatively high temperatures (15—25°C).

The temperature dependence of a reaction is often characterized with the aid of Q_{10}, the quotient of the reaction rates at two temperatures with a difference of 10°C (for a convenient calculation method, see Ahlgren 1978). The material of the present study gives a Q_{10} of 4.3 for *O. agardhii* between 14 and 19°C. In laboratory experiments, Ahlgren (1978) found a value of 3.6 between 12 and 17°C, and Foy et al. (1976) a similar value (3.4) between 10 and 20°C. The data of van Liere (1979) suggest a Q_{10} of 1.4 between 20 and 28°C. Thus, on the whole there is good agreement between the results obtained in the present study, and those obtained by other authors in laboratory experiments and in the field. It should be remembered, however, that strains with different physiological adaptation exist in *O. agardhii* (Skulberg 1978b). For example, Ahlgren (1978) reported an optimum temperature of 23—25°C for her strain of *O. agardhii*, isolated from L. Norrviken in Sweden, while van Liere (1979) reported a temperature optimum of 32°C for his strain, isolated from L.

Veluwemeer in the Netherlands.

The effect of the hydrological regime of the bay on the growth of *O. agardhii* is shown in Table 6. Low dilution rates mean long residence times of the water in the bay, which may influence the temperature and the nutrient concentrations of the water. In shallow eutrophic lakes release of tot. P from the sediment has often been reported (Ahlgren 1975, Ojanen 1979); in the present case, there is direct contact between the sediments and the trophogenic layer. Thus, the effect of the freshwater discharge rate on phytoplankton growth in the area may be a compound one. Stream discharge also influenced the salinity of the water in the bay. In the Baltic, *O. agardhii* is considered a eutrophic brackish-water species (Niemi 1979), which fits well with the picture revealed by Tables 4 and 5.

Oscillatoria agardhii is regarded as oligophotic (Berger 1975, van Liere 1979), but its light energy requirements may be influenced by the temperature (Foy et al. 1976). The extremely low Secchi disk transparencies recorded in the study area indicate a favourable environment for oligophotic species.

2. Nutrients and growth

As discussed by Persson (1979), *O. agardhii* has generally been associated with high concentrations of nutrients, especially nitrogen. However, van Liere (1979) writes that the concentration of nutrients in the water is "by no means an indication of their availability for algal growth, as fluxes and/or cell contents are neglected". This view is also expressed by Ahlgren (1977, 1979). Zevenboom & Mur (1978) observed that the nitrogen uptake of the natural *O. agardhii* population in L. Wolderwijd varied greatly during a growing season, depending on the kind of growth limitation prevailing. The uptake of nutrients is a function of the physiological state of the algae, and also of the form in which the nutrients are present (Kokyrtsa 1975). In the present study, only a crude estimate of the total nutrient concentrations was available, and the nutrient uptake kinetics was not studied. Nevertheless the data show that the total nutrient concentrations influenced phytoplankton growth and succession in the study area.

N/P ratios are often quoted in discussions on the nutrients limiting algal growth. The N/P quotient of the algal cells seems to be at least as relevant as the N/P quotient of the external supply (van Liere 1979). In nitrogen-limited *O. agardhii*, van Liere (1979) found N/P quotients of 5—9, depending on irradiance and the growth rate. Ahlgren (1980) considered that *O. agardhii* required a N/P ratio of 12—13 in a full medium where either nitrogen or phosphorus was limiting. Furthermore, she found growth limitation by both N and P at low dilution rates, when the N/P ratio of the supply corresponded to the needs of *O. agardhii*. Since Kaupunginselkä Bay represents a situation in which nutrients are supplied in excess of requirements, some limited comparisons may be made. Melin & Lindahl (1973) found stimulation of *O. agardhii* by nitrogen alone in waters with $N/P < 10$. This and the observations mentioned above indicate that the criteria of Forsberg & Ryding (1980) may be applicable in the present study area: at $N/P < 10$ nitrogen would be limiting, at $N/P = 10—17$ N or P or both may be limiting, and at $N/P > 17$ P would be limiting. Thus, most of the time nitrogen may have been the nutrient limiting algal growth in the study area. However, the limiting nutrient may change during the growing season (e.g. Zevenboom & Mur 1978). The results presented in Table 5 may reflect changing nutrient limitation, or the combined effect of tot. N and tot. P. No nutrient limitation of *O. agardhii* occurred during the exponential phase of growth, but it may have operated later in the summer. This view is supported by Table 5 and the fact that in spite of favourable temperature conditions other species of blue-green algae tended to predominate in the late-summer algal blooms.

The correlations between the biomasses of the phytoplankton and *O. agardhii* and the environmental parameters (Table 5) are rather weak, and have low coefficients of determination (r^2). Thus, it is not possible to single out a key factor regulating the phytoplankton biomass in the area. The results indicate that throughout the summer several environmental factors interact, resulting in changing competitive advantages for different species of algae. However, the detailed analysis presented in Table 6 suggests

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that in early summer, when the nutrient requirements of *O. agardhii* are presumably fully met, the temperature and the hydrological regime of the bay are the master factors explaining the growth and development of this alga.

3. Other factors

Although van Liere (1979) did not believe that organic matter plays a role in the occurrence of blue-green algae, this factor cannot be totally disregarded. *Oscillatoria agardhii* is generally found in waters polluted by sewage (Häyrén 1921, Välikangas 1926, Cornelius & Bandt 1933, Ahlgren 1970, Berger 1975, Alasaarela 1979, Niemi 1979), and some strains have been demonstrated to be potentially heterotrophic (Saunders 1972, Guest & Fay 1976). Organic matter may also provide chelators for trace elements and thus promote growth indirectly (Reynolds & Walsby 1975). This view is partly supported by the observations of Lindahl & Melin (1973) and Melin & Lindahl (1973) on *O. agardhii*.

Grazing by zooplankton may probably be discounted as a major ecological factor affecting the abundance of *O. agardhii* in the study area, as large filamentous blue-green algae are generally considered a poor source of food for the small species of zooplankton predominating in eutrophic waters (Brooks 1969).

Muddy odour was found in fish caught in the study area during or slightly after the biomass maximum of *O. agardhii* (Persson 1977, 1978, 1980, 1981). This may indicate that production of muddy odour metabolites, in this case geosmin (Persson 1979), is enhanced during adverse environmental conditions. The present results suggest that occurrence of muddy odour could perhaps be forecasted by monitoring the temperature and hydrological conditions in the bay.

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