Effects of cooling water discharge on the structure and dynamics of epilithic algal communities in the northern Baltic

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Abstract

The Forsmark Biotest Basin is a shallow coastal ecosystem that receives brackish cooling-water discharge from a nuclear power plant. The effects of the discharge on epilithic algal communities were investigated by analysing samples taken every third week throughout one year at 11 sites differentially affected by temperature and/or flow rate enhancement. Community variation was summarized in a canonical correspondence analysis (CCA) of species abundances as a function of site and date. The temperature increase favoured blue-green algae at the expense of red and brown algae. Blue-green algae were however abundant in summer in stagnant water, whether heated or not, and some red and brown algae became abundant in winter in heated sites with flowing water. Green algae and diatoms increased in biomass in the heated sites, but not in relative cover-abundance. The absence of ice and snow cover at sites with heated and/or flowing water caused autumn species to persist into winter, because of the higher light intensity (compared with natural conditions) and the absence of the mechanical abrasion by ice. The thermal discharge lowered species diversity (Shannon-Weaver index) both in summer and winter at sites with flowing water, but not at sites with quiescent or stagnant water. CCA showed alternate periods of stability and rapid change within the seasonal cycle. Individual species were placed according to their optimum; red and brown algae in winter/spring, green algae in spring/summer, blue-green algae in summer, and diatoms at various times. Exceptions to this pattern were species endo- or epiphytic on species of a different group. Analysis of the effects of temperature, flow rate and ice cover on the seasonal pattern of particular species showed that different species respond in individualistic ways to different combinations of these environmental variables.

Introduction

Power stations that use cooling water to discharge waste thermal energy modify the aquatic environment in their discharge area by increasing water temperature and flow rate. The faster flow can also increase nutrient supply, and the combination of increased temperature and flow rate can prevent an ice cover from forming in areas where this would normally occur. The elimination of ice and snow cover makes more light available during winter, and removes the usual mechanical abrading effect of the ice. Each of these environmental changes has the potential to affect the composition, structure and dynamics of aquatic ecosystems.



Fig. 1. Location map.

The Forsmark nuclear power plant (Fig. 1) discharges cooling water into the Baltic via the Forsmark Biotest Basin, an artificial basin used for environmental impact studies (e.g. radioecology, Notter (1986); heavy metals, Gustavsson (1982); nutrients, Nitchals (1985) and Snoeijs (1985); phytoplankton, Willén (1985); benthic fauna, Mo (1984), Snoeijs & Mo (1987) and Snoeijs (in press); fish ecology, Karås (1987)). The aim of this study is to show how the various environmental changes caused by the thermal discharge seperately and together affect communities of benthic algae in the hydrolittoral zone, i.e. the zone that extends ca. 0.5 m above the annual minimum water level up to the mean summertime level (Du Rietz, 1930, 1950; Wærn, 1952). Being attached, benthic algae react to changes in their immediate environment, and those characteristic of the hydrolittoral are mostly opportunistic and react quickly (Littler & Littler, 1980, 1981; Wallentinus, in press). In contrast to the sublittoral zone, the hydrolittoral has a pronounced seasonal cycle and is colonized anew each year. Normally ice abrades the previous year's growth in winter, and the remaining basal parts are killed by desiccation during low water in spring (Wærn, 1952; Hällfors et al., 1975). Many of the characteristic species of the hydrolittoral (e.g. diatoms and unbranched, uniseriate green algae) are therefore small, fast-colonizing algae, that are relatively insensitive to water-level fluctuations but quick to react to changes in other environmental factors. The epilithic macroalgae are slower colonizers but mainly annual, and therefore rapid indicators of environmental change.

Many studies on the effects of cooling water discharge on algal assemblages have been based on artificial substrates. Our study deals only with natural communities. We describe natural communities in and around the Biotest Basin in terms of their species composition and community structure throughout one seasonal cycle. The design of the Biotest Basin allowed us to choose sites affected to different degrees by the increase of temperature, flow rate, or both. We consider all algae found on rocky substrates, including diatoms in so far as they formed macroscopic colonies. Species were identified with the help of the following works: blue-green algae: Geitler (1932), Lindstedt (1943), Hällfors (1984); diatoms: Hustedt (1930, 1959), Krammer & Lange-Bertalot (1986); *Enteromorpha* spp.: Bliding (1963), Koeman (1985); other algae: Wærn (1952), Wallentinus (1979). The systematics mainly follow Christensen (1980) and Christensen *et al.* (1985); see Snoeijs (1987) for taxonomic notes.

Area description

The Biotest Basin

Forsmark is located on the east coast of Sweden at the southern end of the Gulf of Bothnia (Fig. 1). The power plant consists of three boiling water reactors. Unit 1 became operational in 1980, unit 2 in 1981 and unit 3 in 1985. The samples were taken before unit 3 started. The combined electrical output of units 1 and 2 is 1800 MW, but their total thermal output is 5400 MW (Forsmarks Kraftgrupp AB & Statens Naturvårdsverk, 1985). The excess heat is removed by brackish cooling water (salinity 5-6%) taken from an inlet of the Baltic (Fig. 2). A 2350 m tunnel under the sea-bed carries the heated water back to the Baltic via the Biotest Basin, which is something between a river and a lake, with more features of one or the other at different sites. It has a surface-area of 0.9 km^2 , a mean depth of 2.5 m, and a maximum depth of 5 m; its total volume is 2.3×10^6 m³ (Grimås, 1979). The bottom consists of solid rock, sand and stones.

The water is heated 8–10 °C as it passes through the reactor. Most of the basin is 8–10 °C warmer than the water outside, but the backwaters are cooler than the rest. Vertical temperature variation is generally <0.5 °C, seldom >1 °C (Andersson, 1983). The water flux at full operation is 86 m³ s⁻¹. The flow rate is 0.1-0.3 m s⁻¹ through the main part of the basin and ca. 2 m s⁻¹ through the outlet channel (Andersson, 1983). Most of the water (70–90%) is transported between the intake channel of the



Fig. 2. The Forsmark nuclear power plant and the Biotest Basin, showing the sampling sites. (Unit 3 was not yet operational during the sampling period).

power plant and the outflow channel from the Biotest Basin within 3–6 hours. The lagoon, an area partly separated from the rest of the basin by a ca. 400 m long pier, has a longer retention time (up to a few days) and quiescent water. There is also a stand-by outlet where part of the cooling water can be released directly from the tunnel into the sea; if this is open then only ca. 25% of the cooling water flows through the basin (Notter *et al.*, 1987).

No chemicals are used to diminish fouling organisms in the water tunnels. Instead they are

mechanically cleaned with small rubber balls. Overhaul of the power plant takes place in summer, during which each unit in succession is turned off for a few weeks.

In this part of the Baltic winter ice cover normally forms in December and lasts 100–130 days. The ice becomes covered with snow and light intensities beneath the ice become very low. The combination of raised temperature and flow rate in the Biotest Basin prevents the formation of an ice cover.

Table 1. The sampling sites

Site	Situation	Flow factor	Mean temperature anomaly (°C)	Ice cover in winter
F	inlet	6	9.3	no
С	inside basin	4	8.2	no
E	outlet	6	7.8	no
Α	stand-by outlet	3 or 6	5.9	no
G	intake channel	5	0.0	no
K	lagoon	2	6.4	no
В	outside basin	3	2.1	yes
D	channel unit 3	2	1.7	no
Н	outside basin	2	0.6	yes
I	inside basin (backwater)	1	4.3	no
J	outside basin	1	1.3	yes

Flow factor: 1: stagnant, 2: quiescent, 3: quiescent-natural waves, 4: slowly flowing, 5: flowing, 6: rapidly flowing. Mean temperature anomaly: yearly mean temperature minus the yearly mean temperature at site G for the period March 1984–March 1985.

Sampling sites

Eleven sites were chosen in and around the Biotest Basin (Table 1, Fig. 2). A 'site' here refers to an area of 10 m along the water line.

Five sites have flowing water. Site G, in the intake channel, has fast flow but natural temperature. Sites F, C and E are in the main flow path through the basin, with fast flow and raised temperature. Site A is anomalous: it receives fast-flowing heated water when the stand-by outlet is open (Snoeijs, 1985) and is otherwise quiescent, but heated by leakage through the doors of the stand-by outlet.

Four sites have quiescent water. Site K is inside the basin, and therefore has heated water, but is isolated from the main flow. Sites B, D and H are outside the basin but B and D are slightly heated by leakage (Andersson & Hillgren, 1986); this sufficient to prevent an ice cover from forming in winter at site D, but not at site B.

Finally, sites I and J have shallow, stagnant water. Site I is inside the basin and heated; J is outside the basin and cold.

Methods

Sampling and laboratory techniques

Samples were taken every third week from March 1984 to March 1985, 18 times altogether. On each occasion eight flat stones (diameter 7-12 cm) were sampled randomly from a depth of 20-50 cm. Generally four samples were taken per site/date but on some occasions three or five, depending on the size of the stones. No samples could be taken at sites B, H and J during winter because of the ice cover. The total area of each sample was 200-400 cm². The same type of stones occurred at all sampling sites because of the use of dynamite in the construction work. Water temperatures were measured at each site, and water samples for nutrient measurements were taken at sites G and E. Nitrate, orthophosphate and silicon were analysed at the SNV laboratory in Uppsala, using methods described in Ahlgren & Ahlgren (1975) and Nitchals (1985). Light intensity at the water surface and at 1 m depth, and water level inside and outside the basin, were extracted for each sampling date from data supplied by SMHI (the Swedish Meteorological and Hydrological Institute).

The bulk of the algae was separated from the stones in the laboratory, and fixed with 70% ethanol. The stones were then dried and investigated for crust-forming algae. In total 690 samples were studied for algal species composition at $10 \times$ to $50 \times$ magnification, and between three and six microscopic preparations per

Table 2. Cover-abundance scale

Score	Cover	Abundance	Mean cover					
9	76-100%		87.5%					
8	51-75%		62.5%					
7	26-50%		37.5%					
6	11-25%		17.5%					
5	6-10%		7.5%					
4	1-5%		2.5%					
3	<1%	> 10 individuals	~0.5%					
2	<1%	5-10 individuals	~0.5%					
1	<1%	1-5 individuals	~0.5%					





Fig. 3. Water temperatures measured during sampling. Site C (not shown) had water temperatures similar to site E. Closed symbols apply to sites receiving cooling water discharge; open symbols apply to sites not receiving cooling water discharge, although possibly getting some leakage of heated water from the basin. Sites B, H an J were ice-covered in winter.

sample were studied at $100 \times$ to $400 \times$ magnification. Cover-abundance was estimated on the 1-9 scale of van der Maarel (1979), with a slight change in the definition of classes 1-4 (Table 2). The scale provides a way to combine information from algae of different sizes and growth forms. Colonies of unicellular algae were considered as individuals; diatoms were only recorded if they formed macroscopic structures in colonies of their own, or attached to the macroalgae. The resulting three to five species lists per site/date were combined into one list to reduce the effect of patchiness and to make sample sizes comparable between site/dates. The final data set thus consisted of 181 species lists with cover-abundance values, each list corresponding to a particular site and date.

Data analysis

Overall changes in community structure were analysed by aggregating the species lists for all sampling dates in summer/autumn (May-November) and winter/spring (December-April), then comparing taxonomical composition and total community diversity between sites for each of these two seasons. This aggregation was made for practical reasons; in December-April no samples were taken at the three ice-covered sites, which would influence e.g. diversity if yearly averages are compared between sites. Diversity can be measured in several ways (Whittaker, 1965; Hill, 1973; May, 1975; Whittaker, 1977; Patil & Taillie, 1979; Peet, 1984; Alatalo, 1981; van der Maarel, in press). We computed four indices based on the abundance data: (1) the Shannon-Weaver index, an index of heterogeneity; (2) Simpson's index, an index of the concentration of *dominance*; (3) the evenness measure of Pielou, a measure of equitability in the distribution of species (Peet, 1974); and (4) the Gini coefficient, which measures inequality in the distribution of species as twice the area between the Lorenz curve and the 'line of equality' (Alker, 1970; Taillie, 1979). These measures were compared with one another and with simple species richness.

The multivariate effects of seasonal and between-site environmental changes on community composition at the species level were summarized by constrained ordination (ter Braak & Prentice, 1988). We used canonical correspondence analysis (ter Braak, 1986, 1987a; Jongman et al., 1987) to summarize the part of the variation in species composition that is related to site and date, which were treated as two sets of (11 and 18) dummy 'environmental' variables, the values of which are either 0 or 1. This analysis gives sample and species scores, and centroids for each site and date, on successive ordination axes. It was implemented with the program CANOCO (ter Braak, 1987b). Reference water temperature, temperature anomaly, flow rate, water level and light intensity were then added as passive variables, in order to show the direction of variation of each of these variables with respect to the space-time pattern of variation in species composition.

Results

Environmental variation within and between sites

Water temperature at the sites directly receiving thermal discharge (C, E, F, I, and K) was consistently higher than at those receiving none (G,



Fig. 4. Average light intensity (flux density of photosynthetically active radiation) measured in the week before the sampling day, above water surface and 1 m below water surface. Calculated from hourly measurements by SMHI.

similar inside and outside the basin, and causes a yearly water level fluctuation of ca. 60 cm (Fig. 5). The tidal amplitude is insignificant (a few cm).

Figure 6 illustrates the nutrient state of natural waters in the area (site G), and of water that had passed through the power plant and the basin (site E). Nutrient concentrations are high in winter and a steep drop in spring is followed by low concentrations throughout summer and a rise again in autumn. A time shift for the drop in spring at site E towards earlier in the year is caused by the extremely high primary production inside the basin during late winter-early spring (Snoeijs, 1985). Silicon levels drop before nitrate and similar inside and outside the basin, and causes a yearly water level fluctuation of ca. 60 cm (Fig. 5). The tidal amplitude is insignificant (a few cm).

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Fig. 5. Water levels and sampling depths measured on the sampling day inside and outside the basin. Data from SMHI.



Fig. 6. Nutrient concentrations in the water at the control site G (intake channel) and the heated site E (oulet channel).

phosphate in spring, indicating that diatoms are important during the high primary-production period.

The algal flora

The observed flora consisted of euryhaline marine species, lacustrine species, and specifically brakish-water species, or species with their main distribution in brackish waters. Some of the marine and freshwater species were found reduced and/or sterile, living at the limit of their distribution. A few algal species otherwise restricted to the sublittoral (Polysiphonia nigrescens, Aglaothamnion roseum and Sphacelaria arctica) occurred in low abundances; these species had been transported to the hydrolittoral by the current, and either settled or became entangled with algae already growing. Eightyeight taxa were distinguished altogether (see Appendix). The Appendix gives annual mean cover-abundances for each site; Snoeijs (1987) gives the complete data set.

Differences in species cover-abundances between sites proved more informative than differences in mere occurrence of species. Many of the taxa occurred in a high proportion of sites, irrespective of situation (see Appendix). Twenty-five taxe occurred at all sites and together accounted for 62-80% of the total annual-average cover-abundance at each site, but the cover-abundances and the timing of occurrence of these common taxa varied considerably among sites.

Effects on the abundances of the major algal groups

The cooling water discharge causes changes in the mean cover-abundance of the taxonomic divisions (Table 3). Blue-green algae tend to be more important during the warm season, and are favoured by strong heating and/or stagnant water (Fig. 7). The *number* of blue-green algal species is also greater during the warm season, and in heated or stagnant water (see Appendix). The highest abundance and species richness of blue-green algae are in shallow, stagnant water (sites I and J), where much dead and decaying plant material accumulates.

Red and brown algae, conversely, tend to be more important during the cold season. In summer/autumn they are favoured in sites with

Elem festeri				216	5			2		1	
Flow lactor:	0	- +	70	5/0	5	4	21	17	2	1	1
Temp. anom.:	9.3	8.2	7.8	5.9	0.0	6.4	2.1	1./	0.6	4.3	1.3
Site:	F	С	E	Α	G	K	B*	D	H*	Ι	J*
										MAY-	NOVEMBER
Blue-green	15.7	21.3	21.1	20.4	13.2	15.1	9.0	11.5	13.9	43.9	26.2
Red	3.0	3.3	2.8	5.9	6.1	3.0	7.4	1.9	3.8	2.0	13.9
Brown	5.8	2.5	1.9	4.8	10.4	2.6	3.3	4.6	5.0	1.9	1.8
Diatoms	22.4	18.7	22.8	22.1	29.1	19.2	25.6	22.0	22.8	12.7	8.8
Green	52.9	53.9	51.1	47.1	40.9	59.9	54.2	60.1	54.5	39.4	48.7
										DECEM	BER-APRIL
Blue-green	7.3	18.8	8.4	9.2	9.6	15.2	**	6.3	**	40.5	**
Red	16.5	5.4	6.3	13.6	14.2	2.2	**	5.4	**	4.4	**
Brown	16.3	3.2	9.3	9.8	22.4	5.3	**	8.6	**	1.5	**
Diatoms	28.9	28.1	33.2	36.9	26.7	27.5	**	38.9	**	10.3	**
Green	30.9	44.6	42.9	30.4	27.0	49.8	**	40.8	**	43.1	**

Table 3. Mean cover-abundances (%)

* = ice-covered in winter

** = no sample taken because of ice cover



Fig. 7. Mean percentages of total cover-abundance for blue-green, red and brown algae related to flow factor and temperature anomaly, given seperately for the periods May-November and December-April. Site A has flow factor 3 or 6 and is therefore plotted at an intermediate value (4.5).



unheated water (Fig. 7). They can also reach high abundances in heated sites, but only in winter. Then their highest abundances occur in fastflowing water and are mainly due to the red alga *Ceramium tenuicorne*.

No such clear patterns could be found for green algae or diatoms. This is to some extent because relative cover-abundance, rather than absolute biomass, was used to measure abundance. Green algae and diatoms are the dominant groups in terms of biomass (Snoeijs, unpublished). The lowest mean cover-abundances of green algae were at sites with fast-flowing water, despite the fact that the highest biomass of *Cladophora* glomerata was generally found at site E, and of *Enteromorpha* spp. at site F (Snoeijs, unpublished). All of the diatoms have much higher biomass inside the basin than outside throughout the year, and especially so in winter and early spring (Snoeijs, 1985).

Figure 8 shows the cover-abundance of each

taxonomic division as a function of water temperature, irrespective of site and date. Red and brown algae and diatoms decreased in percentage cover-abundance with increasing temperature. Blue-green and green algae, in contrast, tended to increase with temperature.

Effects on diversity and dominance

Between-site variation in diversity measures was assessed on the basis of the aggregated species lists for summer/autumn (n = 11) and winter/ spring (n = 8). Species number was only weakly related to the four quantitative diversity measures (r = 0.51 to 0.65), and Shannon-Weaver diversity was more closely related to variation in evenness (r = 0.98) than to species number (r = 0.65).

Shannon-Weaver diversity values were lower in the cold season (Fig. 9). Highest values in both seasons were found at the unheated site G, and



Fig. 9. Mean Shannon-Weaver index related to flow factor and temperature anomaly, given separately for the periods May-November and December-April (cf. Fig. 7)

in shallow stagnant water (whether heated or not). Among the sites with flowing water, the heated sites all had lower values than the unheated site in both seasons. Among the sites with quiescent water, the heated site K had a lower value than the slightly heated site D in the cold season, but this difference was not maintained in the warm season. Similar patterns were found in dominance-diversity and Lorenz curves (Snoeijs, 1987 and unpublished), but no such clear pattern was observed in species number.

Effects on species composition through the year

Canonical correspondence analysis of species composition data with respect to site and date yielded two major ordination axes with eigenvalues 0.26 and 0.18 (compared with 0.13 and 0.09 for the third and fourth axes). Figure 10 shows three kinds of information from this analysis: centroids for all the samples taken on a given date; centroids for all the samples taken at a given site; and vectors indicating the approximate direction and rate of change in the environmental



Fig. 10. Canonical correspondence analysis of algal communities with respect to site and date, showing the centroids for sampling sites (symbols) and dates (connected by lines). The arrows show the direction of variation in the environmental factors light intensity, reference temperature (at site G) and water level (functions of date) and mean temperature anomaly and flow factor (functions of site).

variables light intensity, reference temperature (at site G) and water level (functions of date only) and mean temperature anomaly and flow rate (functions of site only).

The date-points depict the seasonal cycle of species composition. Periods of stability (with minor fluctuations) are interrupted by periods of more rapid, directional change, corresponding to intermittent shifts in environmental structure (Allen *et al.*, 1977). The first period of stability (spring) is characterized by stable (low) temperatures, while light intensity increases; the second period of stability (summer) is characterized by both stable (high) temperatures and light intensities; the third period of stability (winter) is characterized by stable (low) light intensity while temperature is decreasing. During the first period of change both temperature and light intensity strongly increase, and during the second period of change both temperature and light intensity strongly decrease. The third period of change is more complicated as conditions are by then already similar to the first period of stability. The very beginning of the increase in light intensity seems to be crucial; directly when it starts increasing after the mid-winter minimum, the period of change is initiated, and stability is reached quickly while temperatures are still low



Fig. 11. Species ordination from the same analysis as Fig. 10. Taxa occurring less than five times altogether are omitted. For abbreviations see Appendix.

and light intensity is still rising. The gap in the seasonal cycle in Fig. 10 occurs because spring came later in 1985.

The site-points are differentiated according to the degree of heating and flow rate. Their relative positions (computed only from species composition, site and date) nevertheless reflect the environmental differences between sites. The orientation of the temperature anomaly vector towards early winter (rather than summer/autumn) reflects the fact that raised temperatures have their strongest effect in winter, by promoting the persistence of autumn species into winter.

Figure 11 shows a pattern in the distribution of different algal groups according to site and season. Blue-green algae are confined to the lefthand side of the ordination: they favour summerautumn, and sites with heated and/or stagnant water. Red and brown algae are mainly found in the right-hand side because they favour winterspring, and sites with unheated and/or flowing water. An exception is the brown alga Ectocarpus siliculosus, which is largely restricted to summer and autumn (Wallentinus, 1979). Most green algae are found in the lower half (spring/summer). Many of these are in the lower-left quadrant (summer), but the green algae typical of spring, such as Ulothrix spp., are found in the lower-right quadrant (spring). Cladophora glomerata, the most dominant macroalga, shows no apparent preference for site or season, although its highest biomass is at the heated site E and in summer (Snoeijs, unpublished). Another common green macroalga is Enteromorpha ahlneriana, which is found throughout the year at all sites, but most abundant then at heated sites with flowing water. Loose-lying green algae such as Cladophora fracta, Percursaria percursa, Oedogonium spp. and Zygnema sp., found in the lower-left quadrant, are most abundant in summer and in sites with stagnant or quiescent water.

Deviations from this general pattern can be explained by endo- or epiphytic coexistence. For example, *Chlorochytrium dermatocolax* (green alga) is an endophyte in the cell walls of *Sphacelaria arctica* (brown alga); *Porterinema fluviatile* (brown alga) is endophytic on *Cladophora* glomerata and Enteromorpha spp. (green algae); Asterocytis ornata (red alga) is an epiphyte on some filamentous green algal species.

There are diatom species for all environmental conditions. Some are epiphytes on macroalgae (e.g. Cocconeis pediculus, Synedra tabulata, Achnanthes brevipes, Rhoicosphenia abbreviata, Epithemia spp.); these taxa are found in the centre of the plot, where most of the macroalgae are found too. The diatoms that show strong seasonal or site preferences are those that form macroscopic colonies, e.g. Melosira spp. (cells in chains), Nitzschia filiformis and Amphipleura rutilans (cells in gelatin tubes), Mastogloia spp. (cells in gelatin matrix) and Gomphonema olivaceum (cells on gelatin stalks, colonies in balls of up to 1 mm; can also be epiphytic). These species do not depend on macroalgae for three-dimensional growth, and respond rapidly to environmental changes.

Interactions of temperature, flow rate and the seasonal cycle

Ordination (Figs. 10–11) summarizes the effects of site and season on overall species composition but misses more subtle effects, such as the influence of temperature, flow rate and winter ice cover on the timing of the growth period and abundance maxima of particular species. Examples of these effects are illustrated in Fig. 12, which shows the distribution of four diatom taxa by site and date.

Nitzschia filiformis responds to temperature and flow rate. It occurs in autumn/winter and only at sites with flowing, heated water. It evidently needs both high winter temperatures and flowing water, since it hardly occurs at all at the unheated sites, or at the sites with stagnant or quiescent, heated water.

Gomphonema olivaceum responds to temperature and ice cover. It is largely absent from the heated sites. It occurs in winter at sites with unheated water but no ice cover (G and D), and at the stand-by outlet (A), but forms part of the spring and autumn blooms at the unheated sites with ice cover (B, H, and J).



Fig. 12. The distribution of four diatom taxa by site and date. Sites are first arranged according to flow factor and then by temperature anomaly. Sites B, H and J were ice-covered in winter.

Melosira spp. and Amphipleura rutilans respond primarily to ice cover. They occur during a longer period and with higher abundances at heated sites, or at unheated sites with no ice cover in winter, than at unheated sites with ice cover, where they are more restricted to the spring and autumn diatom blooms. These species are not temperature-limited in winter, as they grow well at $0 \,^{\circ}C$; so it is the ice cover that is crucual. Winter light intensities are just adequate to allow these species to grow if ice cover is suppressed. They do change in abundance with temperature but their responses are opposite. *Melosira* spp. have slightly higher abundance at the heated sites than at the unheated sites; for Amphipleura rutilans it is the other way around.

Discussion

Blue-green algae

An increase in abundance of blue-green algae is a well-known effect of rising water temperature (Cairns, 1956; Hawkes, 1969; Patrick, 1969; Patrick et al., 1969; Cairns et al., 1972; Patrick, 1974; Tison et al., 1981. Wilde & Tilly, 1981). Diatoms are reported to grow best at 15-25 °C, green algae at 25-35 °C and blue-green algae at 30-40 °C (Hawkes, 1969). Patrick (1969) collected mixed communities on artificial substrates in the field and exposed them to different temperatures in the laboratory: a diatom flora established at 20-28 °C, a green algal flora at 30-35 °C and a blue-green algal flora at 35-40 °C. The water in the Forsmark Biotest Basin had a maximum summer temperature of ca. 25 °C during the study period, so it did not reach the physiological temperature optimum for blue-green algae, and they never became dominant in terms of biomass and total cover. But species number and abundance of blue-greens were highest in summer, and increased with heating. Some persist through winter in heated sites. Calothrix scopulorum, which is common in the upper hydrolittoral during late summer and autumn, is an example of an autumn species that persists through winter

because of the absence of an ice cover; it decreases in abundance because of the low temperatures but it is still found throughout winter at the heated sites, and disappears only with low water levels in spring.

Red and brown algae

The disappearance of red and brown algae is another well-documented effect of raised temperature (Roessler, 1971; Rex, 1978; Devinny, 1980; von Braun, 1980; Wilde & Tilly, 1981; Boberg et al., 1986). We have shown this effect too, again as a response both to seasonal changes in temperature and to artificial heating. But in the cold season individual red or brown algal species can profit from the temperature enhancement. For example the brown alga Pilayella littoralis prefers winter/spring, while the macroscopically similar Ectocarpus siliculosus prefers summer/ autums (Wallentinus, 1979); Ectocarpus siliculosus is favoured and Pilayella littoralis is inhibited by artificial heating (this contrast was also shown at Olkiluoto, Finland (Fig. 1) by Keskitalo & Heitto (1987) and Keskitalo & Ilus (1987)). Inside the basin Ectocarpus siliculosus profits from the extension of the growing season, and is thus an example of an autumn species that persists into winter in the heated environment, whereas Pilavella littoralis is inhibited through competition with fast-growing diatom species in winter and spring. The red alga Ceramium tenuicorne occurs in the heated water (mainly in flowing water and in the cold season), but with lower abundances than at unheated sites; in summer it loses heavily in competition with Cladophora glomerata.

Diatoms

Cairns *et al.* (1970) found that thermal pollution caused no change in the diatom flora of the Potomac River (West Virginia, USA), but this result was based on presence-absence data. Our results show that quantitative community composition is more sensitive; changes in species abundances can be substantial even if the species list hardly changes.

Diatoms are the group quantitatively most favoured in the Biotest Basin, with high biomass throughout the year, especially in winter, and enormous spring blooms at water temperatures of 6-10 °C (Snoeijs, 1985), much lower than the reported physiological temperature optimum for diatoms of 15-25 °C (Hawkes, 1969). However, there is no clear temperature optimum for diatoms as a group; some species have tolerances as broad as 0-35 °C (Patrick, 1971), others narrower temperature tolerances distributed throughout this range (Patrick, 1969). Also, because of their fast growth rates, opportunistic diatom species can quickly form large blooms and temporarily outcompete other algal species with slower growth rates.

The largest part of the diatom biomass during the spring and autumn blooms at Forsmark is made up of Amphipleura rutilans, Nitzschia filiformis and species of the genus Melosira. Melosira spp. have the highest epilithic biomass inside the Biotest Basin, but they also form large floating masses all over the basin, especially in late winter and spring. Large winter Melosira blooms have been observed at other Swedish and Finnish nuclear power stations that discharge cooling water into the sea (Rex, 1978; Hobro, 1979; Kuylenstierna, 1982; Keskitalo & Heitto, 1987). Nitzschia filiformis was only found at heated sites, and most abundantly at sites with fastflowing water; it has been reported before to grow best in warm water (31-35°C: Schwabe, 1936; 22-26 °C: Wallace, 1955; 26-28 °C: Patrick, 1974). In Forsmark it was mainly found at temperatures of 11-17 °C. Amphipleura rutilans is one of the species that normally form blooms in this part of the Baltic (Snoeijs & Kautsky, manuscript), but in the heated water in the Forsmark Biotest Basin it has to compete with Melosira spp. and Nitzschia filiformis, which reduces its relative cover-abundance at the heated sites. Of the taxa illustrated in Fig. 12, Amphipleura rutilans and Gomphonema olivaceum are the best adapted to the lowest temperatures (ca.

0 °C); Melosira spp. and Nitzschia filiformis are most abundant at higher temperatures (6–10 °C and 11–17 °C respectively). Nitzschia filiformis possibly has higher nutrient requirements, as it prefers flowing water. As temperature rises, Amphipleura rutilans and Gomphonema olivaceum presumably lose in competition with taxa that have higher temperature optima.

Green algae

Green macroalgae such as Cladophora glomerata require a longer time for establishment than unbranched, uniseriate taxa such as Ulothrix, Oedogonium and Rhizoclonium. Rosemarin (1982) reported that Cladophora glomerata has a competitive advantage because its thallus may be in different stages of growth and development, providing a variety of reproductive alternatives simultaneously. Cladophora glomerata largely disappears from the Biotest Basin in winter as macro-structures because of low temperature and low light intensity, but with no ice cover, small (0.5-2 cm high) tufts can remain through winter; the plants start growing again from last year's old basal parts. Under natural conditions the overwintering of Cladophora glomerata in the Baltic depends on the severity of the winter: after a mild winter rocks and stones are less scraped off by ice, leaving more overwintering akinetes attached to the substrate. Thus the persistence of *Cladophora* glomerata through winter at the heated sites allows it to become more abundant in spring. Keskitalo & Heitto (1987), similarly, reported that a welldeveloped Cladophora glomerata-belt formed 2-3 months earlier in heated sites than in unheated control areas. Whitton (1970) reported that Cladophora glomerata can tolerate temperatures up to 25 °C; so the temperature in the Biotest Basin never becomes lethal for it.

Enteromorpha spp. have also been reported to increase near cooling water discharges (Markowski, 1960; von Braun, 1980; Ilus & Keskitalo, 1980; Keskitalo & Ilus, 1987). At Forsmark, an increased growth of Enteromorpha ahlneriana occurred in heated sites with flowing water. In mid-summer it was partly replaced by the macroscopically similar *Enteromorpha flexuosa*. *Enteromorpha intestinalis* and *Enteromorpha compressa*, with broader thalli, were found most abundantly at sites with standing or quiescent water.

Spirogyra spp. formed large floating masses in the backwaters of the Biotest Basin; such luxurious growth was not seen outside the basin. Increased abundance of Spirogyra has also been reported in Lake Wabamun, Alberta, Canada (Hickman & Klarer, 1974). However, Spirogyra spp. were no more abundant in the benthic system (where they occur solitary, loose-and-entangled among other algae) inside the basin than outside. In the free water column they probably have less competition pressure. In the benthic system other unbranched, uniseriate algae as Oedogonium spp. and Rhizoclonium spp. are favoured in the Biotest Basin, especially at sites with standing or quiescent water.

Diversity

Hein & Koppen (1979) compared the Shannon-Weaver diversity of diatom communities on artificial substrates in the intake and discharge channels of the Oyster Creek nuclear power plant (New Jersey, USA), another site where brackish water is used for cooling. They concluded that the heating reduced diversity. We showed a similar effect for natural algal communities in sites with flowing water, but not for sites with stagnant or quiescent water in summer, where the heating increases the species number and abundances of blue-green and filamentous green algae.

The effects of no ice cover

The effects of the thermal discharge are most pronounced in winter and early spring, when the absence of an ice cover is crucial. Through the winter, nutrient concentrations are high (and nutrient availability is increased by high flow rates), light intensity is low (though higher than it would be with an ice and snow cover), and water temperatures are 6-10 °C. The algae that take advantage of these circumstances form lowdiversity communities with opportunistic, fast and three-dimensionally growing diatom species with low light-intensity requirements as dominants. Such species are otherwise found during the spring and autumn diatom blooms. Then, however, they have to compete for nutrients and space with other algae as light intensity and water temperature increase very quickly, allowing more and more species into the battle.

Conclusions

- Cooling water discharge from the power plant raises water temperatures by up to ca. 10 °C, and generates a strong water flow. Increased temperature and flow rate prevent the formation of an ice cover and thereby increase light availability in winter, and eliminate the mechanical abrading effect of the ice.
- (2) The Biotest Basin provides a range of environments affected to different degrees by temperature and flow rate enhancement, and can be used to investigate the effects of these factors on the coastal ecosystem.
- (3) Benthic algal communities on natural substrates in the hydrolittoral zone are a sensitive indicator of changes in their immediate environment.
- (4) Differences in temperature and flow rate caused major changes in the quantitative composition of the communities throughout the seasonal cycle. Species abundances were more sensitive to these differences than simple species lists.
- (5) Blue-green algae are more important during the warm season, and the artificial heating increased their abundance. Red and brown algae are more important during the cold season; the heating generally reduced their abundance. These responses are consistent with the physiological temperature optima of the groups.
- (6) Effects of flow rate cut across the temperature effects. Blue-green algae were always

Appendix: Species list with yearly mean relative cover-abundance scores per site (in $\%$)
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Taxon	Code		Site										
			F	С	Е	A	G	K	В	D	н	I	J
СУАНОРНУТА													
Anabaena variabilis Kützing	ANAB	VAR	-		-	0.4	0.2	0.1	-	~	-	0.7	-
Calothrix scopulorum (Weber et Mohr) C. A. Agardh	CALO	SCO	1.8	4.9	4.2	1.6	1.9	3.2	1.5	2.1	2.2	5.1	3.5
Calothrix sp.	CALO	SP	-	-	-	-	-	-	-		0.3	0.2	0.3
Chamaesiphonales sp.1	CHAM	SP1	0.1	-	-	-	-	-	-	-	-	-	-
Chamaesiphonales sp.2	CHAM	SP2	-	-	-	-	-	-	-	~	-	0.2	-
Chroococcus dimidiatus (Kützing) Nägeli var. submarinus Hansgirg	CHRO	DIM	-	0.1	0.2	-	0.1	0.2	-	-	0.2	1.0	0.4
Gloeocapsa crepidinum Thuret	GLOE	CRE	1.8	4.1	3.2	0.9	1.4	2.0	0.4	1.1	1.4	4.0	3.7
Gomphosphaeria aponina Kützing	GOMP	APO	-	-	-	-	-	-	-	~	-	0.2	-
Gomphosphaeria lacustris Chodat	GOMP	LAC	-	0.1	-	-	_	-	-		_	0.2	-
Lyngbya aestuarii (Mertens) Liebman	LYNG	AES	0.2	0.4	0.4	0.4	1.2	1.5		1.0	0.3	8.1	1.3
Lyngbya majuscula (Dillwyn) Harvey	LYNG	MAJ	0.3	-	0.1	0.3	0.5	0.1	-	~	0.2	1.5	0.1
Lyngbya kützingii Schmidle	LYNG	KÜT	1.1	1.3	1.6	2.6	1.0	1.8	2.5	1.6	2.0	0.9	4.5
Lyngbya semiplena J.G. Agardh	LYNG	SEM	_	_	_		_	-	_		0.1	-	_
Merismopedia punctata Meyen f. minor Lagerheim	MERI	PUN	_	_	-	-	-	_	_		_	0.2	0.1
Microcoleus chthonoplastes (Mertens) Thuret	MICR	CHT	-	-	_	0.3	_	0.1	_		0.2	1.4	_
Microcystis reinboldii (Richter) Forti	MICR	REI	_	_	_	0.1	0.1	_		~	_	0.9	0.6
Nodularia spumigena Mertens	NODU	SPU	_	0.1	-	0.1	0.5	_	0.1		_	0.1	_
Oscillatoria sp.1	OSCI	SP1	_	_	_	_	_	_	_		_	0.1	
Oscillatoria sp.2	OSCI	SP2	_	_	_	-	_	0.1	_		_	_	_
Oscillatoria sp.3	OSCI	SP3	-	_	_	-	-	-	-		_	_	0.2
Phormidium ambiguum Gomont	PHOR	AMB	0.2	0.3	0.1	0.6	_	0.3	0.5	0.9	0.7	4.5	0.6
Phormidium autumnale (C.A. Agardh) Gomont	PHOR	AUT	1.5	1.0	0.9	1.0	0.2	0.1	-	0.1	0.5	1.7	0.2
Phormidium corium (C.A. agardh) Gomont	PHOR	COR	0.9	1.0	0.6	1.4	0.1	0.3	0.2	0.2	0.7	1.8	0.1
Phormidium fragile Gomont	PHOR	FRA	1.5	3.9	2.9	0.9	1.8	3.2	0.4	0.9	1.5	3.9	3.3
Phormidium tenue (Meneghini) Gomont	PHOR	TEN	2.0	0.7	0.9	0.9	0.1	0.2	0.7	0.4	0.5	0.9	0.3
Pseudanabaena sp.	PSEU	SP	-	_	0.1	_	-	_	-		_	_	_
Rivularia atra Roth	RIVU	ATR	0.7	2.0	0.8	4.1	2.2	1.3	2.5	1.2	2.1	3.7	5.5
Schizothrix vaginata (Nägeli) Gomont	SCHI	VAG	-	0.3	_	0.1	-	-	-		_	0.5	0.6
Tolypothrix distorta Kützing	TOLY	DIS	0.4	0.1	0.2	0.1	0.5	0.4	0.1	0.1	0.3	1.2	0.9
RHODOPHYTA													
Aglaothamnion roseum (Roth) Feldman	AGLA	ROS	0.1	_	-	_	_	_	-	~	_	_	_
Asterocytis ornata (C.A. Agardh) Hamel	ASTE	ORN	0.1	0.7	0.6	0.1	0.1	1.2	0.8	0.1	0.8	0.7	2.5
Ceramium tenuicorne (Kützing) Waern	CERA	TEN	4.9	2.6	3.3	6.4	6.1	1.4	7.3	2.3	3.9	1.3	5.1
Hildenbrandia rubra (Sommerfeldt) Meneghini	HILD	RUB	-	-	-	0.2	-	_	-		_	0.6	_
Polysiphonia nigrescens (Hudson) Greville	POLY	NIG	0.2	-	-	-	-	_	-		-		1.3
Polysiphonia violacea (Roth) Sprenger	POLY	VIO	1.8	0.6	0.3	2.0	3.0	_	1.0	0.7	0.5	0.2	5.0
Rhodochorton purpureum (Lightfoot) Rosenvinge CHROMOPHYTA – CHRYSOPHYCEAE	RHOD	PUR	1.1	0.3	-	0.1	-	-	-	0.1	-	0.2	-
Chrysowaernella hieroglyphica (Wearn) Gaural et Lappilleur	CHRY	HIE	-	-	-	-	-	-	-	-	-	-	0.2
Charde film (Linnaue) Steelthouse	CHOR	EII					1.1				0.5		
Estessarius siliculosus (Dillugue) Lunchus	ECTO	FIL	10	-	-	-	1.1	-	-	-	0.5	-	-
Lithe dense subcategory Wester	ECIO	SIL	1.8	-	-	1.0	-	1.3	1.2	-	1.8	0.2	-
Dil 1 littania (Lina and Kiallar		SUB	2.3	0.4	1.8	1.2	1.6	0.3	-	-		-	-
Phayella littoralis (Linnaeus) Kjeliman	PILA		3.2	1.2	2.6	2.9	10.3	1.6	0.9	4.9	2.1	0.9	0.8
Forterinema nuviatile (Porter) waern	FURI	FLU	0.2	0.5	-	0.2	0.3	0.5	1.2	0.9	1.1	0.5	
Sphacelaria arctica Harvey	SPHA	AKC	0.5	0.3	-	0.4	0.3	-	_	-	-	-	-
Sphacelaria radicans (Dillwyn) U.A. Agardin	STHA	KAD	2.0	0.4	0.3	0.8	1.4	-	0.3	0.3	0.2	0.1	0.5
Stechlonomo olioconorum Statist	SHU		-	-	-	0.2	0.1	-	-	-	-	-	0.2
streoionema ongosporum stromieiut	SIKE	ULI	-	-	-	-	-	-	-	-	-	-	0.3

Appendix: (continued)

Taxon	Code	-	Site										
			F	С	Ε	Α	G	к	В	D	Н	I	J
CHROMOPHYTA – DIATOMOPHYCEAE													
Achnanthes brevipes C.A. Agardh	ACHN	BRE	0.6	0.5	0.2	0.5	0.2	1.3	0.4	0.4	-	0.9	0.6
Amphipleura rutilans (Trentepohl) Cleve	AMPH	RUT	3.0	3.5	3.0	5.5	7.9	1.8	1.8	7.3	3.1	16	0.6
Bacillaria paxillifer (O. F. Müller) Hendey	BACI	PAX	0.4	_	0.2	_	2.3	_	_	0.6	0.3	0.5	_
Brebissonia lanceolata (C. A. Agardh) Mahoney et Reimer	BREB	LAN	0.2	1.0	0.9	0.6	0.2	1.1	1.2	3.5	1.4	_	_
Cocconeis pediculus Ehrenberg	COCC	PED	1.0	1.2	1.0	1.5	1.0	1.6	3.8	1.2	2.3	0.7	0.9
Cymbella caespitosa (Kützing) Brun	CYMB	CAE	_	-	_	0.1	_	_	_	0.2	0.3	_	-
Cymbella lacustris (C. A. Agardh) Cleve	СҮМВ	LAC	-	_	_	_	_	_	-	3.3	_	-	_
Diatoma spp.	DIAT	SPP	0.8	_	2.1	1.4	1.9	0.9	0.6	_	0.4	0.4	1.1
Epithemia spp.	EPIT	SPP	0.8	-	_	0.9	0.4	0.4	_	_	_	1.8	_
Gomphonema olivaceum (Hornemann) Brébisson	GOMP	OLI	0.7	_	0.3	3.1	2.7	0.6	6.8	1.5	5.9	0.2	1.9
Licmophora debilis (Kützing) Grunow	LICM	DEB	0.1	_	_	_	_	-	0.5	_	_	_	_
Mastogloia spp.	MAST	SPP	-	_		0.2	0.4	0.8	1.4	_	0.5	0.6	0.5
Melosira spp.	MELO	SPP	7.4	6.1	8.8	4.0	7.3	9.1	0.9	5.2	1.1	3.4	_
Navicula lanceolata (C. A. Agardh) Ehrenberg	NAVI	LAN	-	0.6	0.5	_	_	_	0.7	_	_	_	_
Nitzschia filiformis (W. Smith) van Heurck	NITZ	FIL	2.8	5.1	3.6	3.0	0.4	0.2	_	0.3	_	0.3	_
Rhoicosphenia abbreviata (C. A. Agardh) Lange-Bertalot	RHOI	ABB	2.0	1.3	1.2	2.3	1.2	2.0	4.8	2.4	5.2	0.7	1.3
Synedra tabulata (C. A. Agardh) Kützing	SYNE	TAB	5.3	3.2	5.0	4.8	2.4	2.6	3.8	2.7	3.0	0.7	1.9
CHLOROPHYTA													
Aphanochaete sp.	APHA	SP	_	0.6	_	0.3	_		_	_	_	0.3	_
Bulbochaete sp.	BULB	SP	_	_	_	0.1	_	0.3	-	_	_	_	0.2
Capsosiphon fulvescens (C.A. Agardh) Setchell et Gardner	CAPS	FUL	0.4	0.1	-	0.3	0.4	2.0	2.3	2.9	4.5	1.4	4.4
Chaetomorpha bottnica Nom. provis. Waern 1952	CHAE	BOT	-	-	_	-	_	-	_	_	_	_	0.1
Chlorochytrium dermatocolax Reinke	CHLO	DER	0.2	0.1	-	0.2	0.1	_	_	_	_	_	_
Cladophora aegagropila (Linnaeus) Rabenhorst	CLAD	AEG	-	_	-	0.1	-	-	_	_	0.2	_	0.1
Cladophora fracta (O.F. Müller) Kützing	CLAD	FRA	1.0	1.7	2.1	1.2	-	2.3	1.0	-	0.2	3.5	4.5
Cladophora glomerata (Linnaeus) Kützing	CLAD	GLO	14.8	15.1	19.0	15.4	7.5	16.9	19.2	15.7	12.7	9.0	7.4
Cladophora rupestris (Linnaeus) Kützing	CLAD	RUP	0.7	-	_	_	-	_	_	_	_	_	_
Enteromorpha ahlneriana Bliding	ENTE	AHL	12.3	12.0	9.4	8.0	3.9	9.3	7.4	7.5	12.7	2.4	4.2
Enteromorpha clathrata (Roth) Greville	ENTE	CLA	-	_	_	_	_	_	-	_	2.9	_	-
Enteromorpha compressa (Linnaeus) Greville and	ENTE	C+I	2.6	7.3	1.7	6.9	5.6	5.0	5.9	8.4	8.2	2.3	11.9
Enteromorpha intestinalis (Linnaeus) Link													
Enteromorpha flexuosa (Wulfen) J. G. Agardh	ENTE	FLE	3.6	3.5	1.8	1.1	2.2	3.8	4.7	6.6	1.6	1.7	3.1
Enteromorpha prolifera (O.F. Müller) J. G. Agardh	ENTE	PRO	0.2	_	-	-	_	_	-	1.7	_	1.2	0.8
Mougeotia sp.	MOUG	SP	-	_	_	-	0.3	_	_	-	_	0.1	_
Oedogonium spp.	OEDO	SPP	0.1	1.2	1.0	0.3	0.7	2.9	0.3	0.9	0.8	2.4	1.3
Percursaria percursa (C.A. Agardh) Bory	PERC	PER	-	_	0.1	-	0.2	_	_	0.1	0.2	0.2	0.5
Rhizoclonium riparium (Roth) Harvey and Rhizoclonium implexum (Dillwyn) Kützing	RHIZ	R + I	1.8	3.9	6.1	1.4	1.6	7.4	1.9	4.1	1.8	10.5	4.6
Spirogyra spp.	SPIR	SPP	1.4	0.7	1.4	0.9	1.8	0.7	0.3	0.6	1.4	1.5	1.9
Stigeoclonium cf. tenue (C.A. Agardh) Kützing	STIG	TEN	1.1	_	_	_	0.1	_	-	_	_	_	_
Ulothrix pseudoflacca Wille	ULOT	PSE	0.8	0.7	0.2	0.7	1.3	0.7	0.8	0.7	0.5	0.6	0.3
Ulothrix subflaccida Wille	ULOT	SUB	1.7	2.9	4.1	2.7	7.0	3.8	2.7	2.6	2.6	3.2	1.9
Ulothrix zonata (Weber et Mohr) Kützing	ULOT	ZON	1.6	0.5	0.5	0.9	2.9	0.7	5.4	0.7	2.2	0.6	0.7
Urospora penicilliformis (Roth) Areschoug	UROS	PEN	_	_	0.4	-	_	_	_	_	_	_	_
Zygnema sp.	ZYGN	SP	-	-	-	-	-	-	-	-	0.1	0.1	0.8

abundant in stagnant water. *Ceramium tenuicorne* (red) was abundant in fast-flowing water in winter.

(7) Measures of community diversity based on the distribution of abundances among taxa were more sensitive to environmental differferences than simple species richness. Variation in Shannon-Weaver diversity values among sites and seasons was related to variation in evenness rather than species number.

(8) The heating lowered diversity in both

seasons at sites with flowing water. However diverse assemblages of blue-green and uniseriate green algae occurred in stagnant water, whether heated or not.

- (9) Individual species tended to follow the seasonal pattern of their taxonomic group, and to respond to environmental differences in a similar way. Some deviations can be explained by species being endo- or epiphytic on species of a different group. Diatoms, however, show a wide variety of seasonal and environmental responses.
- (10) Canonical correspondence analysis (constrained ordination) is an effective way to summarize seasonal and environmental effects on community composition, but gives only limited information on the response of individual species.
- (11) Different species respond to different combinations of temperature, flow rate and ice cover. With no ice cover some species (e.g. the green alga *Cladophora glomerata*) can persist through winter and thereby become more abundant during the rest of the year. Others (e.g. the diatom *Gomphonema olivaceum*) may shift their time of maximum abundance from spring or autumn to winter. The absence of ice cover especially favours fast-growing, three-dimensional diatom taxa such as *Melosira* spp. This explains the very large *Melosira* blooms observed in heated water at Forsmark and other comparable sites.

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