NUTRIENT ENRICHMENT EXPERIMENTS IN PLASTIC CYLINDERS AND THE IMPLICATIONS OF ENHANCED PRIMARY PRODUCTION IN LINDÅSPOLLENE, WESTERN NORWAY

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Water from 34 m depth was introduced in a continuous flow rate of 0.8 and 0.4 litre/min to the surface layer of two plastic cylinders being 1 m in diameter and 18 m deep. The nitrate content of the deep water ranged from 4.0 to 9.0 μM (probably underestimated nitrogen content), phosphate from 1.1 to 2.5 μM, and silicate from 8.7 to 21.9 μM during the course of the experiment. From 10 to 12 July the primary production in the cylinders increased with a factor of 5 to about 300 mg C/m^2 per hour and the highest primary production, 340 mg C/m^2 per hour or 3.23 g C/m^2 per day, was reached on 23 July. Inside the cylinders the highest chlorophyll content (127.1 and 127.7 mg Chl *a*/m^2) was measured on 18 July in cylinder 1 (C1) and on 14 July in cylinder 2 (C2). Later there was a distinct decrease in the chlorophyll content, reaching about 70 mg Chl *a*/m^2 in both cylinders on 23 July and coinciding with a drastic increase in phaeopigments. From 8 to 23 July the mean number of cells per litre increased by a factor of about 5, reaching about 0.9×10^6 cells outside, and 9.3×10^6 and 8.0×10^6 cells per litre in the two cylinders, with the highest number in the cylinder with the highest flow-rate. The phytoplankton community inside the cylinders was dominated by *Leptocylindrus danicus*, *Skeletonema costatum*, and *Chaetoceros* spp., whereas *Nitzschia delicatissima* and *Emiliania huxleyi* dominated outside. The expected ecological consequences of nutrient enrichment to the natural system in Lindåspollene is discussed.

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INTRODUCTION

Fjords, and particularly the land-locked fjords (polls), are characterized by distinct stratification of the water-masses, especially during summer. As a result of the stratification, LÄNNERGREN (1975) found that the upper layers of the water masses in Lindåspollene were practically devoid of nutrients during summer, and, as a consequence, the primary production was correspondingly low, averaging about 0.5 g C/m^2 per day. (LÄNNERGREN 1976, 1978). The vertical turbulent activity in Lindåspollene is low (AURE 1972), and the primary production during summer is therefore primarily based on nutrients regenerated in the water column or, to a lesser extent, derived from fresh-water runoff (LÄNNERGREN 1976).

The phytoplankton community during summer is characterized by the dominance of microflagellates and monads (LÄNNERGREN 1976), and the zooplankton community generally has a low biomass and is dominated by small species (HAUG 1972; ELLINGSEN 1973; MAGNESEN 1982; LIE & al. 1983; SKJOLDAL & al. 1983). LIE & al. (1978) argued that the slow growth of the local herring stock in Lindåspollene was a consequence of the small zooplankton biomass and, particularly, of the size composition of the zooplankton community.

The particle-size composition and the dynamics of the pelagic ecosystem in Lindåspollene seem to be determined by the physical and chemical properties of the surface layer. The stratification and the low turbulence lead to nutrient deficiencies during summer, which favour small species of both phytoplankton and herbivores. This, in turn, seems to favour medusae and ctenophores (STRAND 1983; RIISØEN 1983) at the expense of pelagic fishes.

Small, enclosed coastal ecosystems, such as Lindåspollene, located in areas with virtually no industrial or domestic pollution, are particularly amenable to management and cultivation of biological resources. However, rational utilization of the biological resources requires nutrient enrichment during the summer when light conditions and temperatures favour growth of plants. Increased primary production would enhance the growth potential for filtering bivalves, such as oysters or mussels. If the enrichment with nutrients in addition would lead to a change in the composition of the phytoplankton community towards large diatoms, it is conceivable that there would be a corresponding change in the zooplankton community and an enhanced growth of plankton-feeding fishes. Thus, enrichment of the upper layers could have a significant influence on the level of exploitation of biological resources in enclosed coastal systems.

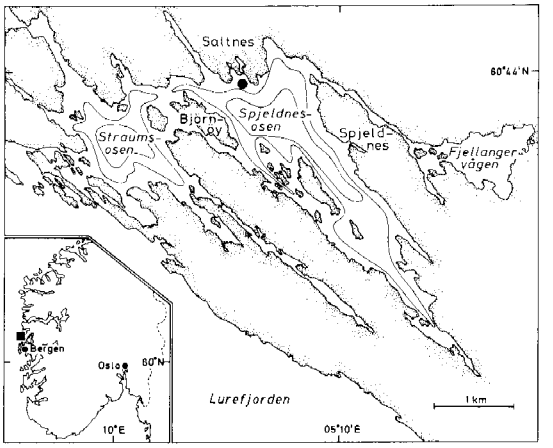

Fig. 1. Lindåspollene. Large filled circle shows location of laboratory barge.

Deep water is an obvious source of nutrients for enrichment of surface waters and there are a number of examples of enrichment experiments with deep water (e.g. BROWN & PARSONS 1972; NEVÉ & al. 1976; PLATT & al. 1977; DODSON & THOMAS 1977; PAUL & al. 1979; TERRY & CAPERON 1982a, b). There are a number of particularly interesting papers published during the last decade (e.g. OTHMER & ROELS 1973, ROELS & al. 1975; ROELS & al. 1979; ROELS 1980, 1983) on the effect and the economic potential of artificial upwelling in a basin at St. Croix, US Virgin Islands.

These experiments are all characterized by being carried out in artificial structures such as plastic bags or tanks or in small basins, whereas there have been few attempts at enrichment of larger natural systems. West-Norwegian polls are especially suitable for such experiments because of their relatively small size, high concentration of nutrients in the deeper water masses (LÄNNERGREN 1975), and limited exchange of water with outside systems. However, the total ecosystem effects of nutrient enrichment are not readily predictable. For example, it is not known whether enrichment would affect the particle size distribution in the ecosystem, or if produced organic matter would be transported from the system rather than regenerated within it. Furthermore, the increased primary production may result in an increased stress on the oxygen content of the deeper water, and the increased turbulence and the reduced stability may have a negative effect on the production process.

Clearly, the cost of large-scale experiments with entire ecosystems and the uncertainty of the outcome call for detailed pilot studies on some of the effects of enrichment. The present paper reports on the results obtained in enrichment experiments with 1-m diameter plastic cylinders of 18 m depth. The purpose of the experiment was to see if the phytoplankton community could utilize the nutrients resulting from a 10–15 % daily exchange of the upper 10 m surface layer with deep water, and if the enrichment would lead to a distinct change in the species composition and the size spectrum of the phytoplankton community. Furthermore, the present paper discusses the possible ecological consequences of a similar experiment applied to the natural system in Lindåspollene.

MATERIAL AND METHODS

The site of the experiment was in the northern part of Spjeldnesosen (Fig. 1), where a number of plastic-bag experiments have been performed previously (SKJOLDAL & al. 1983). The water depth was about 40 m, and a 50 m^2 moored barge served as laboratory.

Two open-ended plastic cylinders made of flexible plastic (BROCKMAN & al. 1974) were attached to the south-west side of the barge. The cylinders, which separated a 0.8 m^2 water column from the surrounding water down to a depth of about 18 m were filled by lowering them slowly from the surface.

Nutrient-rich water from about 34 m depth was pumped into a 900 liter basin on the barge. The basin was filled every six hours, and a continuous flow from the basin supplied the cylinders with nutrient-rich water. The flow during the first five days (4 July to 9 July) was about 2.5 litre/min in one cylinder (C1) and about 0.9 litre/min into the other (C2). In the evening of 9 July these flow rates were reduced to 0.8 litre/min and 0.4 litre/min for C1 and C2, respectively.

Addition of high-density deep water to the surface water in the cylinders resulted in a constriction of the upper part of the cylinders. Both cylinders (C1 on 4 July and C2 on 9 July) were therefore perforated by two small holes (about 1 cm^2) 30 cm below the surface, and surface water was thereby allowed to mix in with the nutrient-rich water. As a result, the cylinders remained fully extended throughout their lengths, and the continuous mixing of deep water with surface water simulated more closely the mixing processes expected in a future large-scale experiment outside the cylinders.

Salinity and temperature were measured by a Kent EIL salinotherm at 0.5, 2, 5, 7, 10, 12, and 15 m depth both outside and inside the cylinders. Water samples were obtained from the same depths with 1.8 and 5 liter Ruthner samplers.

Static stability (POND & PICKARD 1978) was estimated as the rate of change of density with depth:

$$E_i = -\frac{1}{\varrho_i} \times \frac{\delta \varrho_i}{\delta z_i}$$

where ϱ_i is the density at depth z_i and $\delta\varrho_i/\delta z_i$ is the derivative at z_i of the 2. degree Lagrangian interpolation polynomial relevant to the three successive points (HILDEBRAND 1959):

$$(z_{i-1}, \varrho_{i-1}), (z_i, \varrho_i) \text{ and } (z_{i+1}, \varrho_{i+1}).$$

Table 1. Geometric mean regression equations for the relationship between chlorophyll *a* (CHL, mg/m^3) and fluorescence (F), with correlation coefficients (r) outside (OS) and inside the two plastic cylinders (C1 and C2). Each regression is based on 7 sets of observations.

	12 July Equations	r	18 July Equations	r
OS	CHL = 2.83F − 0.63	0.83	CHL = 1.29F	0.65
C1	CHL = 3.48F − 1.47	0.96	CHL = 1.93F + 1.78	0.85
C2	CHL = 3.62F − 1.27	0.98	CHL = 1.89F + 1.10	0.91

With varying frequency, measurements of nutrients, fluorescence, chlorophyll *a*, phaeopigments, and primary production, and samples for estimating phytoplankton and zooplankton abundance were obtained from the water samples. In addition, nutrient measurements were made on the inflowing water sampled from the deck basin.

The concentrations of nitrate, phosphate, and silicate were measured by a Chemlab Autoanalyser. On 12 and 18 July chlorophyll *a* was measured directly, but for the remaining sampling dates the chlorophyll content was estimated from measurements of fluorescence on the basis of the geometric mean regression equations (RICKER 1973) in Table 1. The fluorescence measurements were made *in vitro* by a Turner fluorometer. Samples for measurements of chlorophyll *a* and phaeopigments were filtered through 0.45 μm Sartorius membrane filters. The filters were frozen, and later analysed by acetone extraction in accordance with HOLM-HANSEN & al. (1965). From 12 to 18 July there was a distinct change in the slopes of the regression equations. In the conversion of fluorescence data to chlorophyll *a* the regression equation for 12 July was used for the dates before and including 12 July, for 18 and 23 July the regression equation for 18 July was used, whereas the fluorescence observations from 14 and 16 July were converted by weighted interpolation of the chlorophyll *a*/fluorescence measurements from 12 and 18 July.

Primary production was estimated by the ^{14}C-method in 4-hour (1000 h to 1400 h) *in situ* incubation of 125-ml bottles at the same depths as those where the water samples were taken. The contents of the bottles were filtered on 0.45 μm Sartorius membrane filters which were frozen immediately and later measured for radioactivity with a Packard Tri-Carb scintillation counter. Because of insufficient time and manpower during the field experiment only two sets of primary production bottles could be exposed simultaneously. Daily primary production in the cylinders was estimated on the basis of Steele's production equation (STEELE 1962) on the assumption that production was not limited by nutrients. The mean of the highest measured photosynthetic rates in the cylinders was used as maximum photosynthetic rate, and the optimum light (10 Langleys/hour) was estimated to obtain the best fit to the observed primary production in the 4-hour incubation experiments.

Data for incident radiation were obtained from the published measurements of hourly radiation at the Geophysical Institute, University of Bergen (ANON 1984). SKJOLDAL & al. (1983) demonstrated good agreement between radiation measurements from Lindåspollene and published data from the Geophysical Institute (correlation coefficients from 0.90 to 0.94).

Composite samples of phytoplankton were obtained by adding 10 ml of the water sample from each depth, and of zooplankton by filtering (mesh-size 60 μm) 4.8 litre from each of the sampling depths.

RESULTS

Hydrography

The surface temperature outside the plastic cylinders, which was 13.8° C when the cylinders were filled (4 July), increased to a maximum of 19.5° C on 9 July and decreased to 14.7° C on 18 July (Fig. 2). The temperatures at all depths below 5 m varied by less than 1° C during the experimental period. The steepest vertical temperature gradient was greater than 1.2° C/m, located between 10 and 12 m. The minimum and maximun values observed in 15 m were 6.4 and 6.8° C respectively.

The temperature variations observed inside the cylinders were similar to the variations outside, but the absolute values differed slightly. The temperature was on the average 0.5° C lower inside the cylinders than outside at 0.5 and 2 m, while it was about 0.15° C higher inside than outside at depths greater than 2 m.

The salinity distribution inside and outside the cylinders in the upper 15 m are shown in Fig. 2. The surface salinity values outside the cylinders were in the range 25.4–27.4 ‰ during the experiment. An increase in salinity was observed in the upper 7 m, while it remained rather constant below. As with the temperature, the steepest salinity gradient was observed between 10 and 12 m (about 0.8 ‰/m). The salinity at 15 m was about 31.5 ‰. In the period from 9 to 18 July the salinity in C1 was about 29.5 ‰ at 0.5 m and 30 ‰ at 15 m, and in C2 about 28 ‰ at 0.5 m and 30 ‰ at 15 m. No steep salinity gradient was observed inside the cylinders (Fig. 2).

On the average, the salinity from 8 to 18 July in C1 was 2.9 ‰ higher than the outside value, while it was 2.0 ‰ higher in C2. However, the average salinity in C2 on 7 July was considerably higher than in C1 (Fig. 3). The explanation is that the perforations near the surface in C2 were not made until 7 July, and the deep water was therefore not mixed with surface water as in C1. After the surface holes were made in C2 the average salinity rapidly fell below the C1 level and from 8 to 9 July C2 remained at a permanently lower salinity level than C1 (Fig. 3).

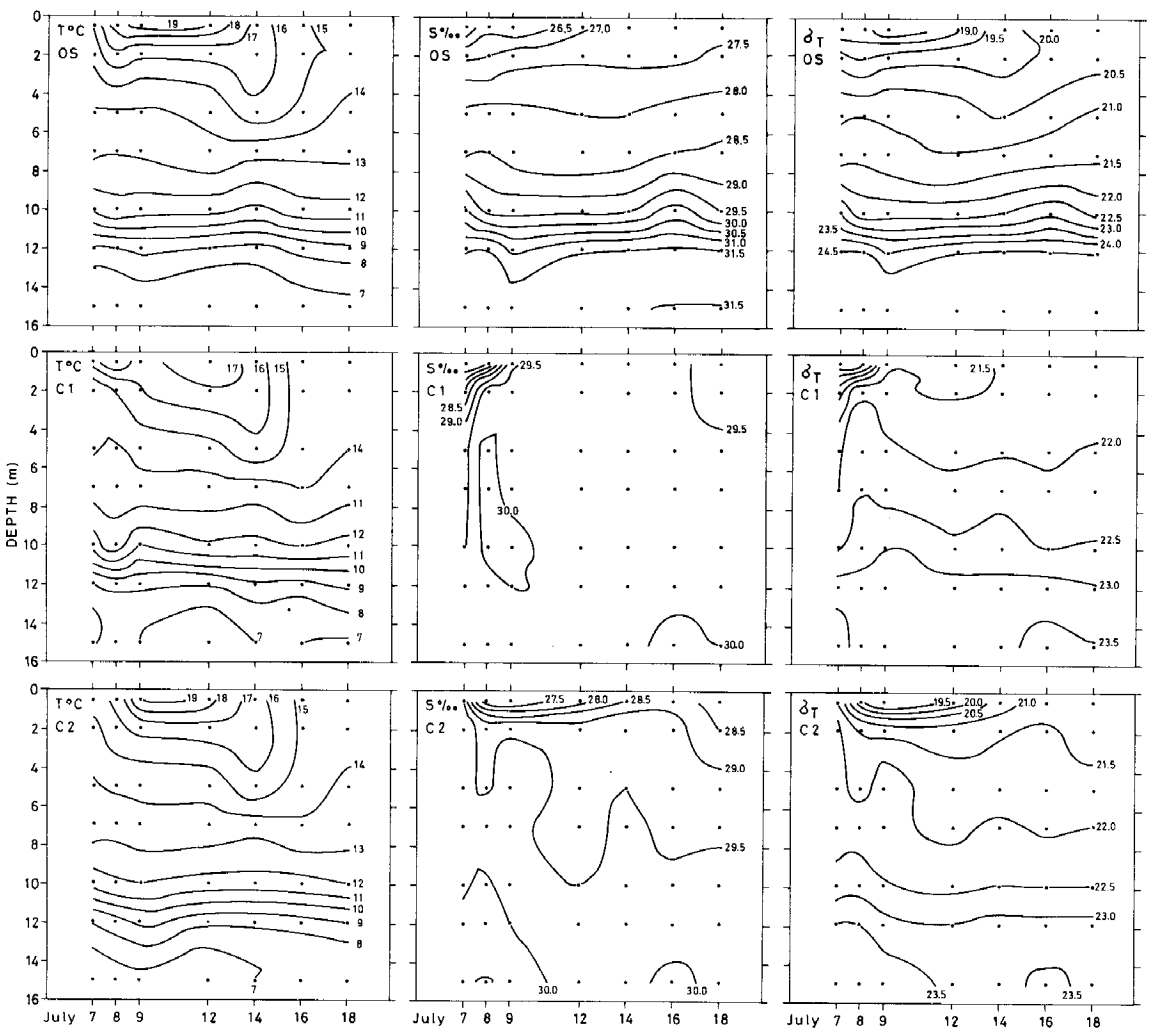

Fig. 2. Isopleths of temperature (°C), salinity (‰), and density (σ_t) outside (OS) and inside the two plastic cylinders (C1 and C2).

On 8 to 9 July the change in salinity inside the cylinders had ceased, resulting in equilibrium salinity distributions determined by the actual salinity of the introduced deep water and that of the surface water entering through the perforations. The salinity contents at the equilibrium indicate that the deep water was mixed with 37 % and 44 % surface water in C1 and C2 respectively. The supply of mixed surface and deep water into the cylinders was therefore calculated as 1.3 litre/min for C1 and 0.75 litre/min for C2, which corresponds to a flow-rate of water through the cylinders of about 0.1 and 0.057 m/hour for C1 and C2 respectively.

Table 2. Mean static stability (E × 10^6) outside (OS) and inside the two plastic cylinders (C1 and C2).

Depth (m)	OS	C1	C2	OS/C1	OS/C2
2	342	80	504	4.3	0.7
5	230	112	127	2.1	1.8
7	290	132	128	2.2	2.3
10	724	209	251	3.5	2.9
12	591	187	236	3.2	2.5

Because of the homogeneous salinity distributions inside the cylinders, the density stratification was reduced compared to the outside water column (Fig. 2). In the period from 8 July to 18 July the difference in σ_t between 2 and 15 m varied in the range 1.3–2.0 in C1, 2.0–2.5 in C2, and 4.3–5.2 outside.

The steepest density gradient outside the cylinders was found between 10 and 12 m (Fig. 2). Inside the cylinders the gradient was reduced, and the static

stability (Table 2) at 10 and 12 m depth was reduced by a factor of 3.2–3.5 and 2.5–2.9 in C1 and C2, respectively. From the empirical relationship between vertical turbulent diffusion (Kz) and static stability (E): $Kz = aN^{-2}$ (DENMAN & GARGETT 1983) where N = gE (the Brunt-Väisälä frequency) it may be deduced that the reduction in stability inside the cylinders had caused a significant increase in the vertical turbulent diffusion.

Nutrients

Nitrate

The nitrate concentration in the water pumped in from 34 m depth varied from 4.0 to 9.0 μM (Table 3). Outside the cylinders the concentration remained low during the period of investigation, not exceeding 0.5 μM (Table 3), and no trend with time or depth could be detected.

The total nitrate content in C1 was very low on 7 July, but remained above 8.2 mmol/m^2 during the rest of the period. In C2 there was a distinct reduction in the total nitrate content towards the end of the experiment.

Phosphate

The phosphate values measured in the deep water were low on 7 July (Table 3), but for the rest of the sampling dates the values ranged from 2.11 to 2.50 μM. Except for one measurement (18 July, 0.5 m) the phosphate values in the water column outside the cylinders did not exceed 1.0 μM, and the figures were variable without clear trends with depth or time (Table 3).

On six occasions the phosphate concentration in C1 exceeded that of the deep water, and from 9 July the total phosphate content in C1 was consistently higher than in C2. In C1 the total phosphate content in the 15 m column ranged between 4.53 and 32.00 mmol/m^2, and in C2 between 5.40 and 17.46 mmol/m^2 (Table 3). There was no distinct trend with time and depth in the phosphate concentration inside the cylinders, but the concentration was at

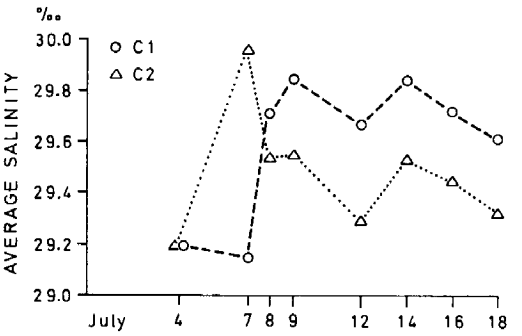

Fig. 3. Average salinity (‰) inside the plastic cylinders (C1 and C2) during the sampling period.

Table 3. Nitrate, phosphate, and silicate (μM) outside (OS) and inside the two cylinders (C1 and C2) during the experiment. The column total represents mmol per m^2 in the water column 0–15 m, and inflow represents concentrations in the inflowing water. Missing data are marked with –.

	7 July 1500 h			9 July 1000 h			12 July 1700 h			14 July 0900 h			18 July 1600 h			23 July 1200 h		
Depth (m)	OS	C1	C2	OS	C1	C2	OS	C1	C2	OS	C1	C2	OS	C1	C2	OS	C1	C2
Nitrate																		
0.5	0.0	0.0	0.2	0.0	1.3	-	0.1	0.5	0.7	0.2	2.3	0.9	0.5	0.9	0.1	0.4	1.6	0.6
2.	0.0	0.0	0.0	0.1	1.7	-	0.2	0.2	0.2	0.1	2.4	0.8	0.1	1.4	0.7	0.0	1.6	0.1
5.	0.1	0.0	0.0	0.1	0.0	-	0.2	0.1	0.1	0.1	1.5	0.3	0.1	0.9	0.1	0.1	0.2	0.4
7.	0.3	0.0	0.0	0.0	1.2	-	0.1	0.1	0.0	0.0	0.3	0.1	0.1	0.2	0.3	0.0	0.6	0.1
10.	0.3	0.0	0.3	0.1	1.2	-	0.2	0.9	2.3	0.0	0.3	0.0	0.0	0.1	0.1	0.0	0.0	0.0
12.	0.3	0.0	3.8	0.2	0.0	0.8	0.1	0.7	0.9	0.1	0.3	0.2	0.1	0.2	0.2	0.0	0.2	0.0
15.	0.3	0.1	1.3	0.1	0.0	0.1	0.5	4.0	3.1	0.4	1.8	1.9	0.2	0.3	0.2	0.2	0.1	0.0
Total	3.0	0.2	12.5	1.1	11.5	-	2.8	11.6	14.2	1.6	17.0	7.3	1.9	8.2	3.8	1.1	8.3	2.2
Inflow	9.0			4.0			4.4			8.9			-			8.7		
Phosphate																		
0.5	0.01	0.07	0.18	0.05	1.22	0.23	0.22	4.12	1.17	0.31	1.70	0.83	2.17	1.52	1.34	0.00	0.82	0.66
2.	0.00	0.15	0.14	0.30	1.47	1.34	0.28	1.91	1.19	0.19	1.40	1.07	0.75	1.70	0.90	0.13	1.17	1.04
5.	0.07	0.25	0.25	0.28	0.64	1.42	0.19	1.60	1.30	0.14	1.44	1.11	0.34	3.11	1.08	0.12	1.28	0.25
7.	0.04	0.45	0.21	0.25	1.31	0.67	0.12	1.61	0.47	0.16	1.58	1.15	0.25	2.16	1.07	0.17	1.21	0.65
10.	0.10	0.19	0.58	0.34	1.27	0.38	0.10	1.49	1.17	0.24	1.46	1.23	0.17	1.36	1.09	0.15	0.94	0.58
12.	0.18	0.68	0.69	0.35	0.54	0.93	0.30	1.52	1.14	0.29	1.49	1.28	0.87	1.95	1.46	0.19	0.80	0.71
15.	0.10	0.12	0.36	0.40	0.38	0.41	0.42	1.49	0.82	0.48	1.45	1.19	0.58	3.22	1.34	0.35	0.89	1.39
Total	1.14	4.53	5.40	4.39	14.80	12.42	3.31	27.23	15.57	3.61	22.38	17.15	9.34	32.00	17.46	2.39	15.57	10.72
Inflow	1.13			2.42			2.32			2.50			-			2.11		
Silicate																		
0.5	0.8	1.5	1.5	1.2	13.4	4.8	0.3	13.4	9.3	0.0	10.5	5.8	0.5	10.1	3.8	0.0	9.1	6.0
2.	0.2	7.0	4.8	0.9	14.0	16.8	0.2	13.3	10.7	0.0	11.2	7.6	0.0	10.4	4.6	0.0	10.7	7.4
5.	0.1	8.0	8.4	0.4	13.5	17.8	0.2	12.9	11.4	0.0	11.0	8.2	0.0	10.7	7.1	0.0	11.0	7.3
7.	0.1	9.5	8.1	0.2	13.1	15.7	0.2	12.7	10.4	0.0	10.7	9.8	0.0	7.4	2.5	0.0	9.9	5.0
10.	0.3	9.8	8.0	3.4	12.5	13.0	1.3	12.1	12.4	1.1	11.6	10.8	0.8	6.9	7.2	0.1	6.0	3.7
12.	1.1	9.7	8.2	1.1	10.8	12.6	1.5	12.6	12.1	1.6	16.7	11.6	1.3	7.0	7.1	0.5	3.9	5.7
15.	2.4	2.1	2.7	2.2	10.2	11.7	2.6	11.8	6.3	2.6	11.5	11.2	2.9	8.9	3.3	1.9	5.7	10.9
Total	9.1	113.3	98.5	19.6	188.3	207.6	12.7	190.1	160.9	10.7	175.4	142.2	10.2	129.4	79.8	4.4	121.0	94.8
Inflow	8.7			20.5			20.8			21.9			-			20.0		

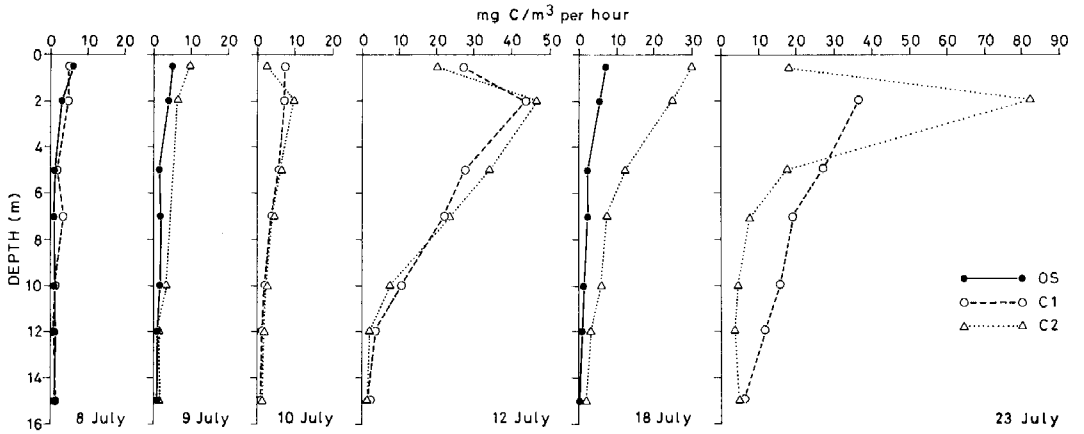

Fig. 4. Vertical distribution of primary production (mg C/m^3 per hour) outside (OS) and inside the two plastic cylinders (C1 and C2).

least one order of magnitude higher than in the outside water column and highest in C1.

Silicate

The silicate concentration, as the phosphate concentration, in the deep water was low on 7 July (Table 3), but on the other dates it ranged from 20.0 to 21.98 μM. In the 15-m column outside the cylinders the silicate concentration was always low, and usually less than 1 μM, and highest, but not exceeding 3.5 μM, in the lower part of the water column.

In both cylinders the highest concentrations of silicate were measured on 9 July (Table 3). In C2 there was a distinct reduction in the silicate concentration above 10 m depth during 9 to 14 July, and this reduction was extended to the entire 15-m water column during the last two days of sampling. In C1 the silicate concentration remained relatively high in the entire water column until 14 July, but during the last two sampling dates there was a distinct reduction in the silicate levels in the 7–15-m depth range.

Primary production

The depth-integrated primary production outside the plastic cylinders ranged from 28 to 37 mg C/m^2 per hour, in C1 from 34 to 340 mg C/m^2 per hour, and in C2 from 55 to 304 mg C/m^2 per hour (Table 4). In both cylinders the maximum was observed on 23 July.

The vertical distributions of the carbon fixation rates outside the cylinders (OS) and in C1 were practically identical on 8 July (Fig. 4), on 9 July there was a distinct difference between OS and C2, and on 10 July the rates in the two cylinders were nearly identical and distinctly higher than the rates outside on the two preceding dates. Between 10 and 12 July there was a drastic increase in the primary production in both cylinders, and the vertical distributions were almost identical.

On 18 July the primary production in C1 was considerably lower than on 12 July, and the lack of light inhibition near the surface indicates light-limited production. Outside the cylinders, however, the integrated primary production and the vertical distribution in the carbon fixation rates did not differ significantly from those observed on 8 and 9 July, indicating that production there was nutrient limited rather than light limited. On 23 July the depth-integrated primary production in the two cylinders was fairly similar (Table 4), but the vertical distributions of the carbon fixation were distinctly different

Table 4. Primary production (mg C/m^2) and statistics for vertical distribution in the 0–15-m water column outside (OS) and inside the two plastic cylinders (C1 and C2). Production per day estimated by Steele's production equation (Steele 1962).

	8 July		9 July		10 July		12 July		18 July		23 July	
	OS	C1	OS	C2	C1	C2	C1	C2	OS	C2	C1	C2
Production per hour	29	34	28	63	55	55	290	301	37	165	340	304
Production per day		323		598	522	522	2755	2860		1568	3230	2888
1 depth quartile	1.2	1.8	1.5	1.9	2.0	2.4	2.2	2.3	1.3	1.4	2.1	1.9
Median depth	3.2	4.1	3.6	4.6	4.2	4.1	4.1	4.2	3.0	3.2	4.7	2.9
3 depth quartile	7.9	7.5	8.1	7.7	7.1	6.7	6.6	6.5	6.3	6.2	8.3	4.7

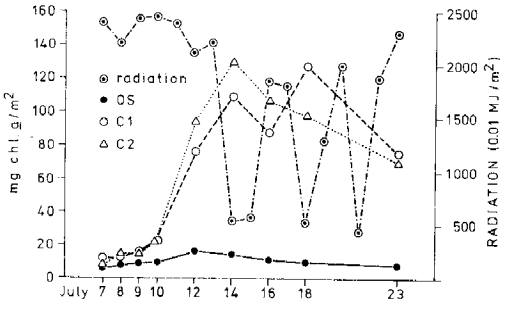

Fig. 5. Integrated chlorophyll *a* (mg Chl/m^2) in the upper 15-m-layer outside (OS) and inside the two plastic cylinders (C1 and C2), and incident radiation (MJ/m^2).

(Fig. 4). At depths between 5 and 15 m the carbon fixation rates in C1 were considerably higher than in C2, whereas at 2 m the rate was twice as high in C2 as in C1. Unfortunately, the loss of the sample from 0.5 m in C1 prevents comparison of the rates at this depth.

Chlorophyll a

The chlorophyll *a* content in the upper 15 m of the water column outside the plastic cylinders remained low throughout the period of investigation, ranging from 6.2 to 16.2 mg Chl *a*/m^2 (Fig. 5). The concentation of chlorophyll *a* did not exceed 1.6 mg Chl *a*/m^3, and in the major part of the water column the concentration ranged between 0.5 and 1.0 mg Chl *a*/m^3 (Fig. 6). There was a gradual reduction in the chlorophyll *a* concentration at all depths between 14 and 23 July.

The chlorophyll *a* content in the plastic cylinders increased approximately exponentially between 7 and 14 July (Fig. 5), from 11.0 to 110.4 mg Chl *a*/m^2 in C1 and from 6.9 to 127.7 mg Chl *a*/m^2 in C2. In both cylinders there was a significant decrease from 14 to 16 July. In C2 the chlorophyll content continued to decrease, reaching 70.0 mg Chl *a*/m^2 on 23 July, whereas in C1 the chlorophyll *a* content increased to 127.1 mg Chl *a*/m^2 on 18 July and then decreased to 74.5 mg Chl *a*/m^2 on 23 July. Until 13 July the incident radiation was very high (Fig. 5), but on 14 and 15 July the radiation was reduced to about 20 % of that of the preceding period. The resulting low primary production may explain the change in the rate of increase in the chlorophyll *a* content from 12 to 14 July, and the reduction on 16 July. The high radiation on 16 and 17 July may explain the increased chlorophyll *a* content on 18 July, although the incident radiation on that date was very low. From 19 to 23 July, with the exception of 21 July, the radiation was quite high, and the low chlorophyll *a*

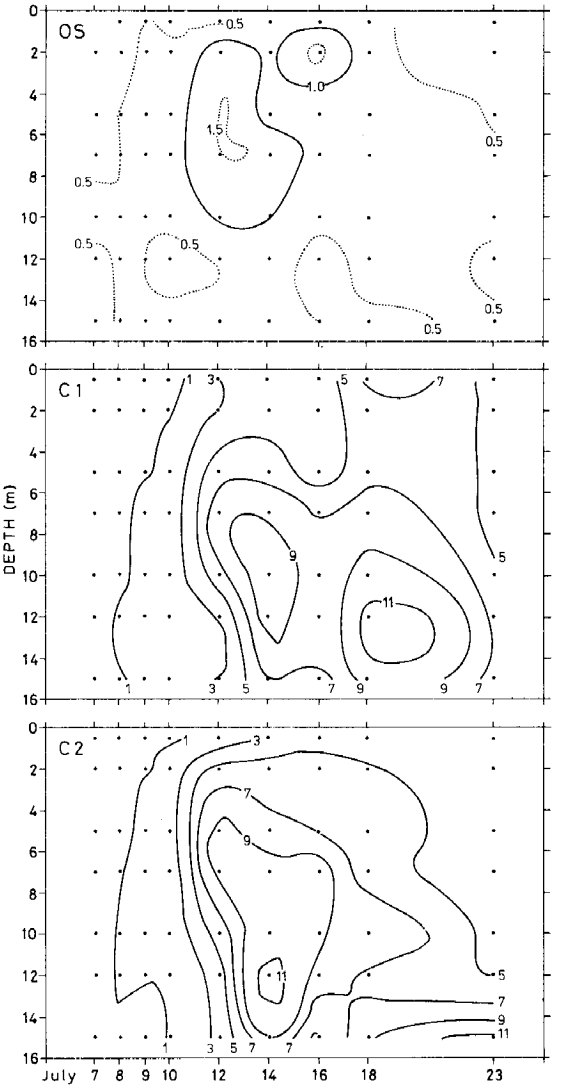

Fig. 6. Isopleths of chlorophyll *a* (mg Chl/m^3) outside (OS) and inside the two plastic cylinders (C1 and C2).

content in both cylinders cannot, therefore, be explained on the basis of radiation. However, the drastic increases in the levels of phaeopigments from 12 to 18 July (Table 5) may indicate that grazing

Table 5. Integrated phaeopigments (mg/m^2) and chlorophyll *a*/ phaeopigment ratios in the 0–15-m water column outside (OS) and inside the two plastic cylinders (C1 and C2).

	Phaeopigments			Chlorophyll *a*/ phaeopigment		
Date	OS	C1	C2	OS	C1	C2
12 July	3.42	1.33	1.05	4.73	56.86	89.43
18 July	5.87	18.35	15.76	1.15	6.93	6.23

Table 6. The relationship between photosynthetic rates (mg C/mg Chl *a* per hour) and depths (m): log(C/Chl *a*) = a + b × depth, with correlation coefficients (r) outside (OS) and inside the two plastic cylinders (C1 and C2). Number of observations (n).

	a	b	r	n
OS	1.03	−0.08	−0.89	21
C1	1.14	−0.09	−0.95	27
C2	0.98	−0.09	−0.89	33

contributed to the reduced rate of increase and even reduction in the chlorophyll *a* content in the cylinders from 14 to 23 July.

The vertical distribution of chlorophyll *a* was quite similar in the two cylinders from 7 to 12 July (Fig. 6), but from then on the development differed. In C1 there were chlorophyll *a* maxima on 14 July and 18 July, located at about 10 and 12 m, while a maximum in C2 occurred at 12 m on 14 July.

Photosynthetic rates (P/Chl a ratios) and Pmax

The depth-specific photosynthetic rates (g C/g Chl *a* per hour) both outside and inside the cylinders decreased exponentially with depth. The slopes of the regressions of mean $\log_{10}$ P/Chl *a* on depth (Table 6) were not significantly different at the 5 % level of probability when tested with the Tukey-Kramer method (Sokal & Rohlf 1981).

With three exceptions (C2 on 10 and 23 July and C1 on 12 July) the highest rates were observed at 0.5 m (Table 7), but it is not possible to determine whether the highest measured P/Chl *a* ratios represent Pmax. Furthermore, most of the chlorophyll *a* data are estimated from regressions of fluorescence measurements on chlorophyll *a* (Table 1), which may introduce some inaccuracy in the P/Chl *a* ratios. This is particularly the case for the observations outside the cylinders where the chlorophyll *a* concentration was very low. On 12 and 18 July, however, chlorophyll *a* was measured directly, and one may therefore conclude that a minimum estimate of Pmax was in the range 12–14 g C/g Chl *a* per hour.

The depth-integrated photosynthetic rates for the 15-m water column (Table 7) were considerably higher during the period 12–23 July than during the first part of the experiment. The exception is in C2 on 18 July, when the incident radiation was only about 20 % of the mean radiation for the other dates (Fig. 5).

Phytoplankton composition

The most characteristic feature in the samples from outside the cylinders was an increase in *Emiliania huxleyi* and *Nitzschia delicatissima* from 9 to 23 July (Table 8). Inside the cylinders there was a distinct increase in the abundance of the diatoms *Leptocylindrus danicus, Skeletonema costatum, Chaetoceros compressus, C. ceratosporum,* and *Nitzschia delicatissima.*

The total number of cells showed some interesting patterns when the counts of monads and flagellates were excluded (Table 8). The total counts in the two cylinders were remarkably similar at all the dates, and the counts were about 10 times higher than in the water masses outside the cylinders. The considerable difference in the number of cells at the starting date, 9 July, may be explained by the fact that the cylinders were filled already on 4 July, and the phytoplankton had thus 5 days of growth with nutrient enrichment inside the cylinders before the first sample was obtained.

Zooplankton composition

The quantitative composition of zooplankton in the composite samples from outside the cylinders and in C1 on 9 July, and from outside and in both cylinders on 23 July was determined (Table 9). On both dates there was a noticeably higher number of zooplankton organisms in the outside water masses than in the cylinders, and consequently it may be concluded that the increased primary production in the cylin-

Table 7. Photosynthetic rates (mg C/mg Chl *a* per hour) in the sample depths and integrated for the 0–15-m water column outside (OS) and inside the two plastic cylinders (C1 and C2). Missing data are marked with –.

Depth (m)	8 July		9 July		10 July		12 July		18 July		23 July	
	OS	C1	OS	C2	C1	C2	C1	C2	OS	C2	C1	C2
0.5	25.1	13.1	8.1	15.0	14.7	3.4	8.8	12.4	13.5	9.9	–	5.3
2	13.0	12.9	6.1	7.3	7.8	5.8	13.7	8.5	8.2	4.8	8.7	20.9
5	3.1	2.1	1.7	–	3.3	3.0	4.4	3.5	3.1	2.0	6.6	5.0
7	1.8	4.1	2.2	–	2.2	2.0	2.6	2.4	3.1	1.1	5.0	2.3
10	2.5	1.1	2.4	2.8	1.0	1.1	1.7	1.3	1.7	0.7	2.9	1.3
12	1.9	0.8	1.7	0.7	0.7	0.8	1.0	0.5	0.9	0.4	1.8	0.7
15	0.9	0.5	1.3	1.8	0.4	0.5	0.6	0.5	0.6	0.2	1.2	0.5
0–15	2.6	1.9	2.2	2.3	1.8	1.5	3.8	3.2	3.9	1.7	5.6	4.7

Table 8. Mean abundance (cells/ml) of phytoplankton and ciliates in the 0–15-m water column outside (OS) and inside (C1 and C2) the two plastic cylinders.

Taxon	9 July OS	9 July C1	9 July C2	12 July OS	12 July C1	12 July C2	23 July OS	23 July C1	23 July C2
Leptocylindrus danicus (CLEVE)	77	825	808	170	2530	2728	82	132	276
Skeletonema costatum (CLEVE)	0	38	0	0	22	93	143	1303	80
Chaetoceros compressus (LAUDER)	33	385	616	16	1056	489	99	4800	165
C. ceratosporum (OSTENFELD)	0	0	0	0	0	110	22	1540	77
Nitzschia delicatissima (CLEVE)	22	220	110	11	115	154	192	1083	111
Dactyliosolen sp.	11	33	27	11	33	27	22	11	16
Emiliania huxleyi (LOHMANN)	44	110	11	220	1100	550	319	440	66
Calycomonas ovalis (WULFF)	0	0	0	22	0	0	0	0	13
Total	187	1611	1572	450	4856	4151	879	9309	805
Microflagellates/monads				1100	440	132		0	16
Ciliates	6	1	3	2	1	10	31	17	

ders did not result in increased secondary production in the > 60 µm zooplankton within the 15 days experimental period.

DISCUSSION AND CONCLUSIONS

The pioneering work on fertilization of Loch Craiglin with artifical fertilizers (GROSS & al. 1944) showed, in spite of some unexpected shortcomings, the great potential of such endeavours. In an analysis of the Loch Craiglin experiment, COOPER & STEVEN (1948) pointed to some concrete improvements, including substituting the artificial fertilizers with natural nutrients from deep water outside the loch. They suggested a system of sluices allowing deep nutrient-rich water to enter the loch with the rising tides, and the impoverished surface water to leave with the falling tides. This idea was further developed by SHIELS & HOOD (1970), who suggested utilizing the tidal range to draw deep, nutrient-rich water into a shallow bay through a pipe. On the basis of the resulting flow and the difference in nutrients between the deep water and the bay water, and a consideration of the nutrient dynamics in plant production, the authors estimated the expected increase in primary production in an Alaskan bay. This concept was tested and the conclusions supported in artificial upwelling model experiments carried out in Alaska by NEVÉ & al. (1976) and PAUL & al. (1979).

Most results from experiments with enrichment of surface water with deep water indicate significant increase in the primary production. However, PLATT & al. (1977) argue that stimulation of primary production by artificial upwelling is not achieved by inorganic enrichment alone. Organic compounds were considered equally or more important, and PLATT & al. (1977) and TERRY & CAPERON (1982a, b) report on inhibitory effects on the primary production with an increasing proportion of deep water in algal cultures.

The hydrographic conditions in Lindåspollene have been investigated with varying frequency every year since 1971 (LIE & DAHL 1981). Relatively large variations in the distribution of salinity and temperature occur in the upper 25 m during the year, while small variations are found below this depth. A strong stratification evolves during spring and summer resulting in low levels of turbulent diffusion

Table 9. Zooplankton composition and abundance (organisms/40 litres) outside (OS) and inside the plastic cylinder (C1 and C2).

Taxon	9 July OS	9 July C1	23 July OS	23 July C1	23 July C2
Temora longicornis (MÜLLER)	10	0	1	1	
Acartia longiremis (LILLJEBORG)	5	2	3	0	
Centropages hamatus LILLJEBORG	1	1	1	0	
Pseudocalanus elongatus BOECK	0	2	0	2	
Paracalanus parvus (CLAUS)	0	0	0	1	
Calanus finmarchicus (GUNNERUS)	0	0	1	0	
Oithona spp.	62	39	49	29	28
Oncaea spp.	15	64	47	26	
Harpacticoida indet.	0	0	0	0	
Evadne nordmanni (LOVÉN)	6	8	23	4	
Appendicularia indet.	1	0	76	19	68
Copepoda, nauplii	102	52	110	24	1
Bivalvia, larvae	142	111	17	13	
Gastropoda, larvae	7	15	0	0	
Polychaeta, larvae	1	0	0	1	
Total	352	294	328	120	13

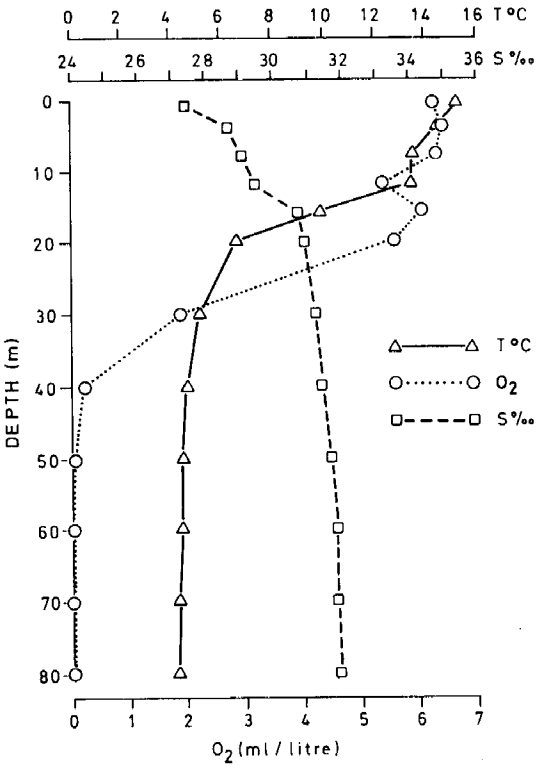

Fig. 7. Vertical distribution of temperature (°C), salinity (‰), and oxygen (O_2) in Lindåspollene, 1 August 1983.

AURE (1972) found that the average vertical turbulent diffusion of heat and salt during late spring and summer was in the range 0.06–0.19 cm^2/s in the upper 8 m and in the range 0.01–0.04 cm^2/s from 12 to 16 m. This low turbulent activity effectively hampers the turbulent diffusive transport of nutrients from the deeper water into the photosynthetic layer. Cooling of surface waters and reduced freshwater runoff during winter result in a breakdown of the stratification and increased turbulent diffusion, leading to a rise in the nutrient concentration in the upper part of the water column.

Table 10. P:N:Si ratios in the water masses in Lindåspollene.

Date	Depth (m)	PO_4–P	NO_3–N	SiO_2–Si
7 July 1983	32	1	8	8
9 July 1983	32	1	2	9
12 July 1983	32	1	2	9
14 July 1983	32	1	4	9
23 July 1983	32	1	4	10
17 July 1973	20	1	6	11
(C. Lännergren				
pers. commn)	30	1	6	13
29 April 1980	20	1	7	7
(H.R. Skjoldal				
pers. commn)	30	1	6	13

The experiments in the plastic cylinders showed that the most drastic increase in the primary production took place from 10 to 12 July, when the nutrient levels in the cylinders were high (Table 3) and the light conditions were extremely favourable (Fig. 5). The increase coincided with a doubling of the depth-integrated P/Chl *a* ratio (Table 7). On the basis of the phosphate and silicate levels in C1 and C2 there is no indication of nutrient limitation (Table 3) after 9 July. Nitrate levels, on the other hand, were low, and probably limiting the production in the cylinders. The nitrate concentration in the deep water was considerably lower than those reported at similar depths in previous studies in Lindåspollene (LÄNNERGREN 1975). It is unlikely that there has been a reduction in the nitrate concentration at this depth as a result of primary production, and the vertical turbulence is too low, as discussed above, to account for a major dilution of nitrate at 34 m depth. The distribution of oxygen in August 1983 (Fig. 7) shows, however, that there was a very steep oxygen gradient nær 30 m depth, and thus this might be an area of nitrate reduction and possible denitrification, as discussed by LÄNNERGREN (1975). This view is supported by the level of the P:N:Si ratios in the deep water, which deviated considerably from results obtained in previous investigations in Lindåspollene (Table 10) by the low NO_3 content relative to the other nutrients. Therefore, the measured nitrate levels probably underestimate the available nitrogen, which in part could be present as ammonium, and the nitrate concentrations as presented in Table 3 must be viewed with caution as minimum values. Because of the uncertainty with regard to the actual nitrogen levels in the cylinders, the conclusions on the role of nitrogen in the phytoplankton dynamics during the experiment must also be viewed with caution.

In the present study the primary production is presented as the mean carbon fixation per hour on the basis of 4-hour (1000 h to 1400 h) *in situ* light exposures. However, the high nutrient content in the inflowing water and the lack of primary production at night may have resulted in a build-up of nutrients during the night, and since the light conditions during summer at this latitude permit high production early in the morning, it is conceivable that the diel maximum in the primary production occurred before noon. If this was the case, daily production cannot be estimated with a high level of precision on the basis of the measured hourly midday production rates. However, estimates of daily production on the basis of Steele's production

equation (STEELE 1962) gave a maximum production (in C1 on 23 July) of 3.23 g C/m^2 per day (Table 4), which is close to the mean measured primary production of 3.95 g C/m^2 per day during 1966–1978 in the Peru upwelling system (WALSH 1981). BROWN & PARSONS (1972) found a primary production of 1.54 g C/m^2 per day in experiments with 100 % daily flushing of small, shallow tanks with nutrient-rich sea water, and NEVÉ & al. (1976) measured a primary production of 1.05 g C/m^2 per day in shallow ponds enriched with deep fjord water at a 95 % daily flushing rate. However, as the total depths in the latter studies were only 1–6 m, the results are not directly comparable to those of the present study.

The numerically dominating taxa of phytoplankton during the experiments (Table 8) were largely the same inside and outside the cylinders. The phytoplankton community outside the cylinders was dominated by very small species, but the expected dominance of small flagellates and monads (LÄNNERGREN 1976) could not be demonstrated. The phytoplankton samples from outside the cylinders were, however, characterized by a very high amount of detritus, particularly on 9 and 23 July, which prevented counting of the very small particles such as microflagellates and monads. On 12 July the detritus content of the sample was considerably less, and the flagellates and monads could be enumerated. On this date, the phytoplankton sample from outside the cylinders was totally dominated by those taxa.

Although the total counts of phytoplankton cells were similar in the two cylinders, there are some distinct differences in the development of the phytoplankton composition. On 9 July the quantitative composition in the cylinders was similar, and the high amount of nutrients in C1 indicates that the phytoplankton community had not yet reached its peak abundance. On 12 July when the nitrogen concentration in the upper 10 m was low in both cylinders (Table 3), C1 had much higher concentrations of *Chaetoceros compressus, Emiliania huxleyi,* and microflagellates/monads, whereas *Leptocylindrus danicus* was dominating and of about equal abundance in the two cylinders. On 23 July, when the nitrogen concentration in the upper 10 m was high in C1 and low in C2 (Table 3), there was a distinct difference in the quantitative composition of the phytoplankton in the two cylinders: *L. danicus, E. huxleyi,* and microflagellates/monads had decreased in C1 but not in C2, whereas *Skeletonema costatum, Chaetoceros* spp., and *Nitzschia delicatissima* had increased in abundance particularly in C1, but to some extent also in C2. These results are in agreement with HARRISON & DAVIS (1979) who found that centric diatoms such as *Skeletonema* and *Chaetoceros* dominated in chemostats with high flux of nitrogen, whereas flagellates and large, slow-growing diatoms (such as *Leptocylindrus*) dominated at low nitrogen fluxes. DAVIS & al (1980) showed with experiments in plastic enclosures that the centric diatoms *Chaetoceros* and *Thalassiosira* decreased in abundance at nitrogen levels below about 1 μM, whereas *Leptocylindrus* was able to sustain its high abundance under distinct nitrogen limitation. In addition, the latter species would form spores when nitrogen was added. In the present study, spores of *Leptocylindrus* were found in C1 on 23 July, but not in C2. These results suggest that in the course of the experiment nitrogen became limiting in the cylinder with the low rate of deep-water enrichment (C2), but not in the other cylinder.

The reduction in the silicate levels in the cylinders (Table 3) indicates that part of the production was performed by diatoms, as shown by the strong increase in the abundance of *Leptocylindrus danicus, Skeletonema costatum, Chaetoceros compressus, C. ceratosporum,* and *Nitzschia delicatissima* (Table 8), but the silicate level was apparently not limiting the production. The silicate level remained highest in the cylinder with the highest rate of inflow.

The standing stock of zooplankton during summer in Lindåspollene is generally low, averaging about 2–3 g ash-free dry weight/m^2 (HAUG 1972; MAGNESEN 1982; LIE & al. 1983). The zooplankton community is normally dominated by small organisms such as Cladocera, mollusc larvae, and the small copepods *Pseudocalanus elongatus, Temora longicornis, Oithona* spp., and *Oncaea* spp. (ELLINGSEN 1973; LIE & al. 1983; SKJOLDAL & al. 1983). Both the zooplankton composition and the biomass change drastically during years of bottom-water renewal (MAGNESEN 1982). Species like *Calanus finmarchicus, Sagitta elegans,* and *Aglantha digitale* become dominant, and the biomass increases by nearly a factor of two.

During the 14-day time-span of the present experiment there was no record of increased abundances in any of the identified zooplankton taxa in the cylinders (Table 9), but there was a distinct reduction in abundance of the numerically dominant taxa, such as *Oithona* spp., copepod nauplii and mollusc larvae compared to outside. The lack of increase in abundance may indicate that the duration of the experiment was not long enough for observations of possible changes in the zooplankton population dynamics, or that the dominance of large particles in the phytoplankton community was unsuited for the small zooplankton organisms present.

Although there was no increase in abundance of

the zooplankton collected with the 60-μm mesh-size plankton sieve, the increase in the levels of phaeopigments in the cylinders (Table 5) indicates increased grazing. This could be attributed to components of the microzooplankton (e.g. ciliates), which displayed a considerable incease in numbers both outside and inside the cylinders (Table 8).

The introduction of cold water with high salinity to the upper layers may affect the hydrographic structure of the water column, resulting in increased turbulence, deepening of the pycnocline, and thus increasing the pool of nutrients available for 'new production' *sensu* DUGDALE & GOERING (1967). In addition an increased production based on regenerated nutrients can be expected. Our experiment in the plastic cylinders in Lindåspollene during the summer of 1983 have demonstrated that a 10–15 % daily renewal of the upper 15-m water column with nutrient-rich deeper water resulted in a 8–10-fold increase in the primary production. Furthermore, there was a distinct change in the size composition of the phytoplankton community, from a dominance of small species to a strong dominance of large diatoms (Table 8). Assuming similar effects in an experiment carried out in a scale encompassing a major part of the central basin in Spjeldnesosen (Fig. 1), one could envisage major ecological consequences. An increase in primary production would enhance the food availability for filtering organisms both in the pelagic and in the shore zone, thus favouring the production of both zooplankton and mussels. Furthermore, assuming a similar change in the size- and species composition as observed in the plastic cylinders, the summer phytoplankton may be able to sustain a high biomass of larger planktonic herbivores, such as *Calanus finmarchicus*.

In studies of the plankton community in large plastic bags (68 m^3) PARSONS & al. (1977a) showed that primary production increased and species composition of phytoplankton changed in experiments with nutrient enrichment. However, the energetic transfer efficiency from phytoplankton to ctenophore decreased (PARSONS & al. 1977b), possibly because the dominant herbivore, *Paracalanus parvus*, was unable to utilize the large diatoms efficiently.

AKSNES & MAGNESEN (1983) showed that *Calanus finmarchicus* dominated the biomass of the zooplankton in a year of bottom-water renewal (1979), and they estimated that *C. finmarchicus* could have grazed 25 % of the total phytoplankton production in Spjeldnesosen, or 90 % of the production in the central area of Spjeldnesosen where the *C. finmarchicus* population was concentrated. It is therefore conceivable that food limitation is the reason why *C. finmarchicus* is unable to maintain a large population size in Lindåspollene, although it is regularly a numerically important species in the zooplankton during spring (ELLINGSEN 1973; ELLERTSEN 1975; MCLEAN 1979; LIE & al. 1983). Nutrient enrichment of the surface layers might therefore enhance the growth of larger zooplankton organisms, which ultimately would benefit pelagic, plankton-feeding fishes at the expense of ctenophores. However, experiments in fresh water (PARSONS & al. 1972; BARRACLOUGH & ROBINSON 1972) showed that doubling the nutrients lead to only a 30 % increase in the production of small fishes.

A 10 % daily renewal of the upper 10 m layer in the central part of Spjeldnesosen (Fig. 1) would require a flow of about 550 m^3/min of deep water to the surface. This could possibly be achieved by the use of airlift (BERGEAUD 1973) or with energy derived from utilization of the temperature range between the deep water and the surface water (ROELS & al. 1979). The dispersion of the deep water over a large area to ensure a good mixing might, however, be a major obstacle. Without such dispersion it is possible that the higher density of the deep water would lead to rapid sinking, without any major influence on the phytoplankton community. Even if the technical problems could be overcome, the possible outcome of a large scale fertilization experiment may not be only beneficial. The low oxygen concentration in the deeper water masses of Lindåspollene normally limits the distribution of marine organisms, and anoxic conditions with the presence of hydrogen sulphide occur below about 50 m depth 3 to 4 years after a major renewal of the water masses. Therefore, it is conceivable that the major increase in the primary production following a fertilization experiment might further diminish the oxygen reserves of the deeper water masses, and thus make a larger volume uninhabitable. On the other hand, mixing deep water with surface water may lead to reduced density in the deeper layers, which may increase the frequency of deep water renewal and hence of oxygenation. Mathematical models for simulation experiments to answer such questions for Lindåspollene are now being developed.

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