

Plankton succession and responses to manipulations in a marine basin for larval fish rearing

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ABSTRACT: A marine basin was constructed in order to provide fish larvae a natural environment for growth and survival. In nature, similar enclosed systems are limited by stagnant water and anoxic conditions. Consequently, 3 types of manipulations were performed: (1) turbulence with a propeller; (2) artificial fertilization; (3) pumping water into the basin. Positive correlations were found between chlorophyll content *a*, diatom concentration and oxygen saturation. Turbulence induced by the propeller, together with supply of nitrate and silicate, promoted diatom growth and resulted in increased oxygen concentrations. In general, the manipulations resulted in improved water quality by favoring diatoms, increased oxygen concentrations, and at the end of the investigation, increased production of calanoid nauplii. Detrended correspondence analysis of species composition indicated that phytoplankton was most affected by turbulence, while ciliates were most affected by fertilization. No effects on composition of the larger zooplankton were identified. The production capacity was estimated and discussed in relation to closed vs advective systems.

INTRODUCTION

Enclosures have been extensively used in studies of marine planktonic food webs during the last 2 decades (Grice et al. 1980, Øiestad & Moksness 1981, Grice & Reeve 1982, Nixon et al. 1984, Beyer et al. 1985, Gamble & Hay 1989). Parallel to mesocosm ecosystem experiments, several attempts have been made to use enclosures as production units for marine fish larvae (Blaxter et al. 1983, Huse et al. 1984, Paulsen et al. 1985, Van der Meeren 1991). In comparative studies many features of the enclosure technique have proven to be superior to larval rearing on monocultures of prey organisms (Witt et al. 1984, Van der Meeren 1991), even if prey concentrations in the enclosures are exceptionally low (Gamble & Houde 1984).

The usefulness of large basins (lagoons) for mass-rearing of marine fish fry was confirmed in 1983 when 75 000 cod *Gadus morhua* L. fry were successfully reared beyond metamorphosis in Hyltrollen, a 60 000 m³ seawater lagoon at the Austevoll Aquaculture Research Station in Norway (Kvenseth & Øiestad 1984). The method was based on natural production of plankton in an ecosystem where natural predators (i.e.

fish, medusae, chaetognata) were replaced by fish larvae. In 1984, the former freshwater lake Svartatjønn was filled with seawater, and during spring 1984, 30 000 cod fry were reared to harvestable size there (Øiestad et al. 1984).

This method is based on the establishment of an environment which offers natural food particles during the first critical feeding period of the fish larvae; furthermore, the fish larvae should be the top predators in the environment. Thus, the method's success depends on the possibility of creating a natural environment where appropriate food for fish larvae is abundant, but where predators of the fish larvae are absent. Two different approaches may be used to achieve this goal. In one, the water is continually renewed at a high rate. An example is a tidal pond where inflowing water is filtered for predators, but where food particles are allowed to pass. The outflowing water is also filtered in order to retain the fish larvae within the production basin. Such systems may be termed advective, as the environment depends on external rather than internal processes. In contrast to such systems are closed or semi-enclosed systems, in which the environment is dominated by internal rather than external processes.

For aquacultural purposes the corresponding terms 'intensive' and 'extensive' systems have been defined in Naas (1990). The present system, Svartatjønn, was managed as a semi-enclosed extensive system.

The water columns of natural semi-enclosed systems on the western coast of Norway (termed polls) are often devoid of oxygen, due to vertical water-density stratification followed by low or no exchange of bottom water. Since anoxic conditions are lethal to fish larvae as well as to their prey, manipulations must be performed in order to avoid anoxia. In the present study, 3 kinds of manipulation were carried out in the experimental basin: generation of turbulence by a propeller, artificial fertilization, and supply of outside seawater. We report on changes in physical, chemical and biological variables in a semi-enclosed system, before and after the manipulations. Species composition, succession, and abundances are compared to those in natural systems. Finally, we estimate the production capacity and comment on the function of closed vs advective systems.

MATERIALS AND METHODS

Basin system, hydrographical samples, and manipulations. The experimental basin (Fig. 1) was located near Austevoll Aquaculture Research Station in Nor-

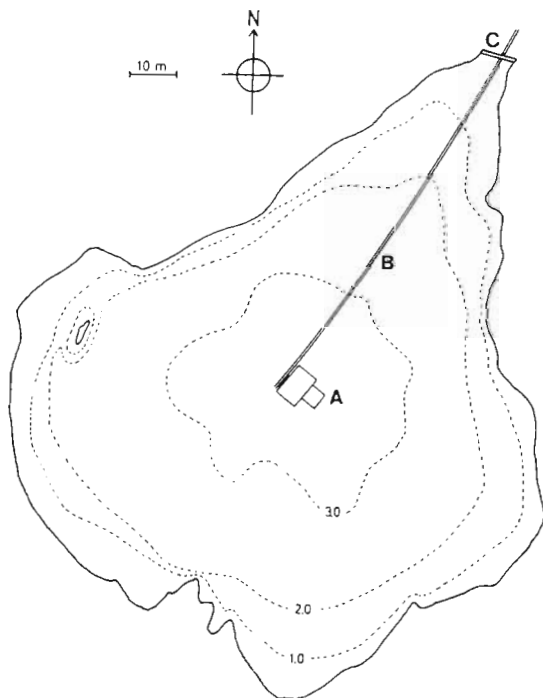


Fig. 1. The investigated basin, Svartatjønn, near Austevoll Aquaculture Research Station in Norway. (A) Sampling float; (B) pipe from outside pump; (C) concrete dam with overflow outlet

way. As stated above, the basin had been converted into a saltwater lake by pumping in seawater. Maximum pump capacity was $9000 \text{ m}^3 \text{ d}^{-1}$. Completely filled, the lake contained $20\,000 \text{ m}^3$, with a maximum depth of 3.5 m. The basin outlet was closed by a concrete dam with an overflow. A 30 m^2 sieve ($300 \times 900 \mu\text{m}$ mesh size) was placed inside the basin in front of the dam. The basin was filled with surface seawater during the first 3 days of July 1984, and during September small amounts of zooplankton were harvested from the basin and fed to larvae of turbot *Scophthalmus maximus* L. reared in plastic enclosures (Van der Meeren 1991).

Daily temperature and oxygen measurements were carried out at 0, 0.5, 1, 2, and 3 m depth with a YSI oximeter Model 57. Water samples for salinity and nutrient analysis were collected at weekly intervals. Salinity was determined by an Inductive Salinometer, Model 83, IME Pty Ltd, Australia. Nutrient samples were analyzed for nitrate (including nitrite), orthophosphate and silicate using standard procedures (Parsons et al. 1984) adapted for a Chemlab autoanalyzer. Particulate organic material (POM) and particulate inorganic material (PIM) were determined from 0.25 to 0.5 l water samples filtered through Whatman GF/C $0.45 \mu\text{m}$ filters. The filters were precombusted at 500°C for 24 h. Secchi disc readings were taken daily.

A propeller, moored to the sampling float in the center of the basin at 3 m depth, rotated from 2 August until the end of the experiment (28 September). Seawater was supplied in varying amounts in late July and August (see Fig. 2A). In late August different commercial fertilizers were added (Table 1). All manipulations were performed in order to raise the low oxygen concentrations.

Phytoplankton, chlorophyll *a*, and zooplankton. Samples for phytoplankton were preserved in both 2 ml formaldehyde neutralized with NaHCO_3 and 2 ml saturated Lugol's solution per 100 ml sample water. As recommended by Thronsdon (1978), diatoms and coccolithophorids were examined in formaldehyde-preserved samples, whereas dinoflagellates and flagellates were examined in Lugol-preserved samples. Sub-samples of 10 ml were examined with an inverted microscope using the sedimentation method (Hasle 1978) at $640\times$ or $160\times$ magnification, depending on cell size and abundance. Diatoms were identified in accordance with Hustedt (1959) and Drebes (1974), dinoflagellates as in Dodge (1982) and Drebes (1974), and coccolithophorids as in Heimdal & Gaarder (1980, 1981).

Samples for chlorophyll *a* (chl *a*) were prefiltered through a $100 \mu\text{m}$ net to avoid contamination by larger zooplankton. Sample water in volumes of 50 to 500 ml was filtered through Sartorius membrane filters (0.45

Table 1 Schedule of fertilizer addition to the experimental basin

Date (1984)	Fertilizer ^a	Amount (kg)	Composition ^b (% of weight)		
			N	P	Si
22 Aug	Urea	15.0	46.0	–	–
23 Aug	Urea	15.0			
24 Aug	Ammonium-nitrate	25.0	34.5	–	–
25 Aug	NPK complex (Cl-free)	14.0	12.6	5.5	– ^c
26 Aug	NPK complex (Cl-free)	9.0			
27 Aug	NPK complex (Cl-free)	20.0			
28 Aug	NPK complex (Cl-free)	7.0			
	Ammonium-nitrate	10.0			
29 Aug	NPK complex (Cl-free)	4.5			
	Ammonium-nitrate	5.0			
30 Aug	NPK complex (Cl-free)	6.5			
31 Aug	NPK complex (Cl-free)	6.5			
1 Sep	NPK complex (Cl-free)	4.5			
2 Sep	NPK complex (Cl-free)	6.5			
4 Sep	NPK complex (Cl-free)	6.5			

^a Manufactured by Norsk Hydro A/S, Porsgrund, Norway
^b From the manufacturer's handbook
^c SiO₂ is added to the fertilizer in the granulating process during production

µm) and analyzed fluorometrically according to Holm-Hansen et al. (1965).

Small zooplankton was sampled by pumping water (36 l min⁻¹) through a net (40 µm mesh size). Samples were taken both from 0, 0.5, 1, and 2 m depth, and from 0.5 and 0.2 m above the bottom. Larger zooplankton were collected in a 2-chambered net (350 µm mesh size) as described by Kvenseth & Øiestad (1984); these samples were collected by means of horizontal hauls across the basin at 0, 0.5, 1.0, 2.0, and 2.5 m depth. Of the samples obtained in parallel (pump and net hauls), those with the highest number of a given taxon were chosen to represent that taxon. All zooplankton samples were preserved in 4 % formaldehyde neutralized with hexamethylene-tetramine. Subsamples for identification and enumeration were obtained using a modified Folsom splitter. Ciliates were counted in the Lugol-preserved phytoplankton samples and identified in accordance with Leegard (1915).

For some of the zooplankton species, minimum mortality estimates (M) were calculated from observed population decreases as $M = (\ln N_{t_2} - \ln N_{t_1}) / (t_2 - t_1)$, where N is the number at time t . This estimate may be close to the true mortality for those species which had no, or low numbers of, juveniles (indicating low recruitment). For *Paracalanus* sp., mortality was estimated using the stage-frequency equations given by Manly (1977) (see also Aksnes & Høisæter 1987). It was assumed that the generation time for this species was 17 d, and that development through the copepodite stages took approximately 1 wk (Aksnes & Magnesen 1988).

Detrended correspondence analysis (Gauch 1982) was run on counts of phytoplankton, ciliates and larger zooplankton. This technique is a multivariate analysis of sample composition. The samples are plotted in 2 dimensions and separated corresponding to the first or second principal component in the analysis.

RESULTS

Hydrography, nutrients, and particulate material

No temperature or salinity gradients were observed within the water column, except in late September when salinity was 28.0 and 30.6 ppt at the surface and 3 m depth respectively. The 1 m depth was therefore chosen as hydrologically representative for the basin. Salinity was quite stable throughout the investigation, while temperature initially was 17.5 °C and decreased to 12.6 °C at the beginning of September, after a maximum of 18.1 °C in early August (Fig. 2A, B). Factors affecting salinity and basin temperature – i.e. water pumped into the basin, air temperature, total solar radiation, water-column mixing, and precipitation – are shown in Fig. 2.

In late July, oxygen deficiencies developed in the bottom layers (Fig. 2C). The starting of the propeller in early August caused the water to become uniformly oxygen-saturated during August and the first part of September. Two periods of critical oxygen deficiencies (below 75 % saturation) were measured at all depths in August, with a temporary improvement during the

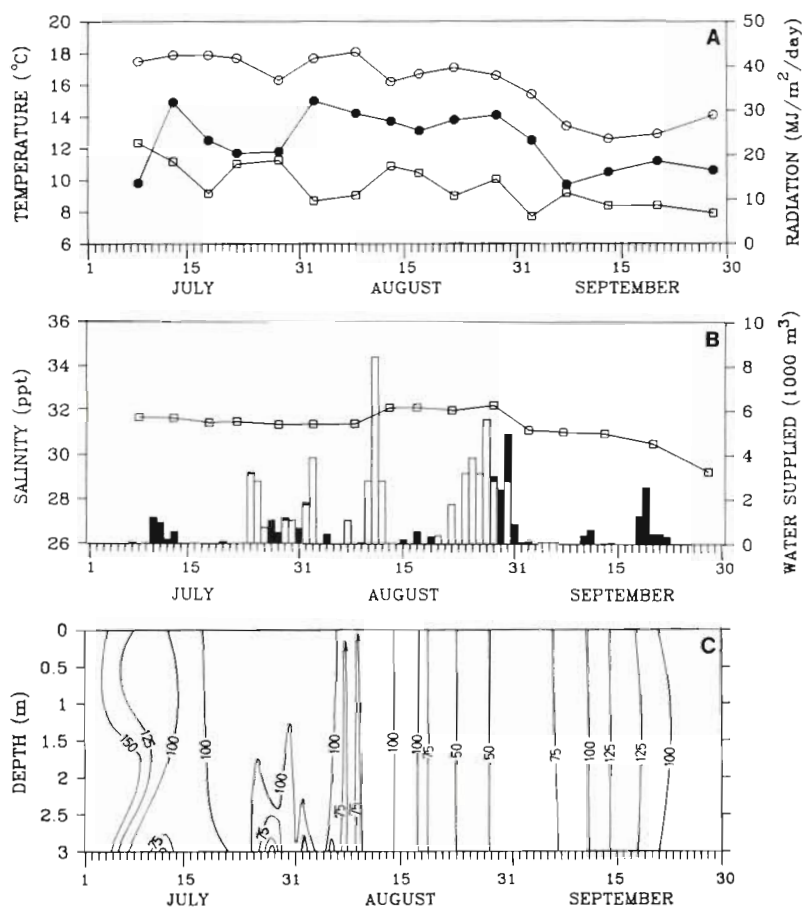


Fig. 2. Hydrography of the basin. (A) Water temperature at 1 m (\circ — \circ), total global radiation (\square — \square), and air temperature (\bullet — \bullet). (B) Salinity at 1 m (— \square); solid bars: freshwater supplied to the catchment area due to precipitation; open bars: supplied saltwater (C) Isolines of oxygen saturation (values represent percentage of oxygen saturation)

intervening period. In September, oxygen saturation increased to more than 125 %.

During July and the first part of August, the nitrogen nutrients (NO_3^- and NO_2^-) were almost exhausted (Fig. 3A). After fertilization in late August, NO_3^- increased to non-limiting concentrations ($>5 \mu\text{M}$). Of the measured nutrient compounds, silicate was the first to diminish after fertilization. Orthophosphate fluctuated within the range of 0.5 to 2.0 μM during the experiment.

The Secchi disc readings were generally low, indicating high concentrations of particulate material (Fig. 3B). The clearest water with readings exceeding 3 m was observed in the beginning of September. POM and PIM varied between 1.6 and 9.0 mg l^{-1} , with pronounced peaks on 28 August of 23.3 and 76.3 mg l^{-1} respectively (Fig. 3B).

Phytoplankton abundances

The phytoplankton community of Svartatjønn was numerically dominated by small-sized coccolithophorids, monads and flagellates during the investigation (Fig. 4). In July and August, coccolithophorids accounted for a great part of the standing stock. On 22

July, *Emiliania huxley* occurred at >12 million cells l^{-1} . An increasing population of a small unidentified coccolithophorid species (probably belonging to *Gephyrocapsa*) was also recorded in late July, with a maximum of 177 million cells l^{-1} on 2 August. Later, the coccolithophorids declined rapidly, and they were absent at the end of August. The group 'monads and flagellates' also increased in abundance throughout July. A maximum was recorded on 2 August, with cell densities exceeding 150 million cells l^{-1} in the smallest size fraction ($<5 \mu\text{m}$) and 9 million cells l^{-1} in the 5 to 10 μm fraction. On the same date, a total maximum phytoplankton concentration of 359 million cells l^{-1} was recorded. Monads and flagellates declined throughout August, with minimum densities on 2 September. During the first half of September a new population of monads and flagellates arose, and their concentrations remained high for the rest of the month (50 million cells l^{-1}).

The succession of diatoms can be divided into 2 major periods, each with a distinct abundance peak in mid-August and mid-September. In July and August *Leptocylindricus minimus* was the dominant species, with maximum numbers on 17 August (19 million cells l^{-1}). At the same time, *Nitzschia longissima* occurred

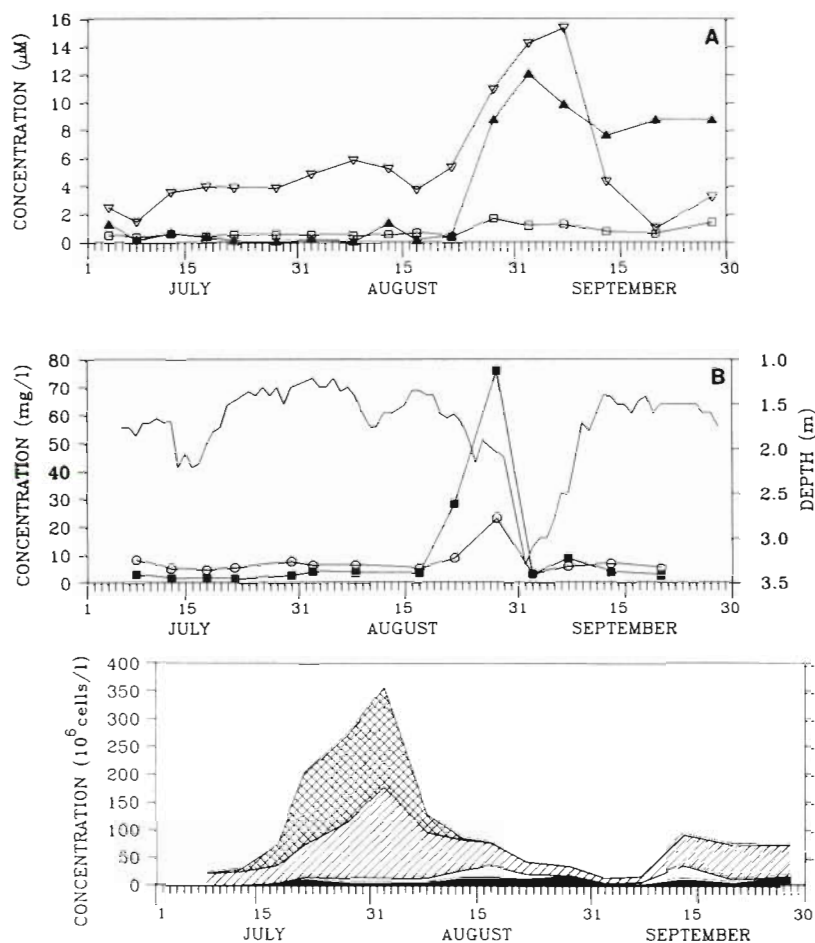


Fig. 3. Nutrients and particulate material in the basin. (A) Nitrate (▲—▲), silicate (▽—▽) and phosphate (□—□) at 1 m. (B) Particulate inorganic material (■—■), particulate organic material (○—○), and Secchi disc readings (—)

Fig. 4. Concentration of phytoplankton in the basin at 1 m

with more than 1 million cells l^{-1} . At the end of the month, diatom abundances were dramatically reduced, with almost no diatoms left on 28 August. During September, a *Skeletonema costatum* bloom developed and reached a maximum on 13 September of 15 million cells l^{-1} . In the same period *Chaetoceros simplex*, *Rhizosolenia delicatula*, *Thalassiosira anguste lineata*, and a small unidentified *Thalassiosira* species occurred with cell numbers exceeding 1 million cells l^{-1} . A scarce but rather diverse dinoflagellate population was observed during the entire sampling period. Relatively small species dominated, and dinoflagellates did not represent any important fraction of the phytoplankton.

Chlorophyll a

Two distinct chl *a* peaks were observed, one in mid-August and the other in mid-September. Both peaks coincided with the observed diatom blooms (Fig. 5A). Over the whole experimental period a significant correlation between chl *a* and diatom cell numbers was

found (Table 2). No associated increase in chl *a* concentration was seen as a result of the coccolithophorid and 'monad and flagellate' bloom in early August. Oxygen saturation and chl *a* (Fig. 5B) were significantly correlated, both before and during mixing of the water column by the propeller (Table 2).

Ciliate abundances

At the beginning of July relatively few ciliates were recorded, but between 13 and 22 July rapid growth of *Tintinnopsis* sp. and *Lohmaniella* sp. was observed (Fig. 6). Six days later this population had vanished and was replaced by a population of the small and autotrophic *Mesodinium rubrum* on 2 August (40 000 cells l^{-1}). In mid-August *Lohmaniella* sp. were again dominant, but by the end of the month a smaller *Lohmaniella* sp., accompanied by *Balanion* sp., had taken over. On 7 September a maximum number of ciliates (150 000 cells l^{-1}) was recorded, mainly consisting of *Lohmaniella* sp., *Balanion* sp. and *Strombidium* sp. By 13

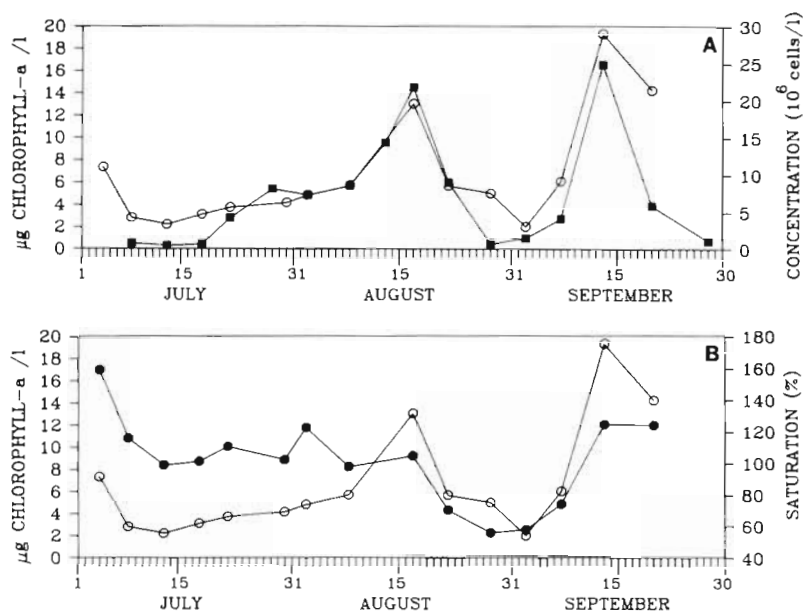


Fig. 5. (A) Chlorophyll a (○—○) and diatom concentrations (■—■) in the basin at 1 m. (B) Chlorophyll a (○—○) and oxygen saturation (●—●) at 1 m

September the *Balanion* sp. population had disappeared and a new *Strombidium* sp. occurred in high numbers ($100\,000\text{ cells l}^{-1}$).

Zooplankton

On 13 July 32 rotifers l^{-1} were observed. Five days later, however, only 0.3 l^{-1} remained (Fig. 7), reflecting a daily mortality higher than $60\% \text{ d}^{-1}$. Along with the decline in rotifers we observed a rapid increase in *Podon* sp., *Evadne* sp., and copepod nauplii. The highest abundances of *Podon* sp. and *Evadne* sp. were observed on 22 July and were close to 6 ind. l^{-1} . The subsequent numerical decrease amounted to a mortality higher than $34\% \text{ d}^{-1}$ for *Podon* sp. and higher than 14% for *Evadne* sp. Among the calanoid copepods, abundances of *Pseudocalanus/Paracalanus* spp. and *Acartia longiremis* increased most at the start of the investigation. The highest adult abundances (5.8 and 4.5 ind. l^{-1}) were observed on 8 and 17 August respec-

tively (Fig. 8). *Temora longicornis* reached maximum adult abundances (3.8 ind. l^{-1}) on 20 August. Average mortality for *Pseudocalanus/Paracalanus* spp. was estimated at $11\% \text{ d}^{-1}$, while the decreases observed for *A. longiremis* and *T. longicornis* amounted to a mortality of 7 and $10\% \text{ d}^{-1}$ respectively. Adult abundances of *Centropages hamatus* increased during the investigation, apart from the decrease observed between 20 and 28 August. At the same time a decrease in adult *A. longiremis* and *T. longicornis* was observed. The highest numbers of both juvenile and adult *C. hamatus* were recorded on the last sampling day (20 September). Early in the investigation adult *C. hamatus* increased in number before juveniles, indicating that the early adults of this species were not recruited in the basin, but instead were supplied via the intake water. Of the less-abundant zooplankton, *Calanus finmarchicus* increased from the start of the experiment until 17 August, when it reached a maximum of 0.01 ind. l^{-1} . This population consisted exclusively of older copepodite stages and, as with the early *Centropages hamatus*

Table 2. Regressions of chlorophyll a (chl a) vs diatom cell numbers (DiatNo), and of oxygen saturation (O_2sat) vs chl a. r: regression coefficient

Regression	r	p
Chl a vs diatom cell numbers: Chl a = $0.57\text{ DiatNo} + 2.83$	0.8438	<0.0001
Oxygen saturation vs chl a before mixing ^a : $\text{O}_2\text{sat} = 11.11\text{ Chl a} + 70.69$	0.8991	<0.01
Oxygen saturation vs chl a after mixing ^a : $\text{O}_2\text{sat} = 4.24\text{ Chl a} + 50.98$	0.8999	<0.005

^a Mixing of water column in basin by propeller started on 2 August

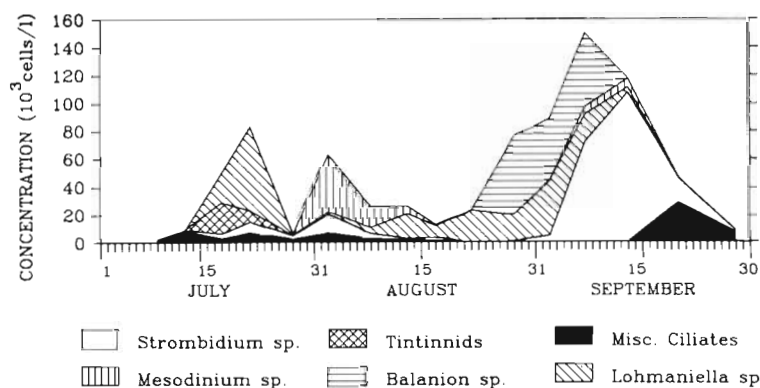


Fig. 6. Concentration of ciliates in the basin at 1 m. Misc.: miscellaneous

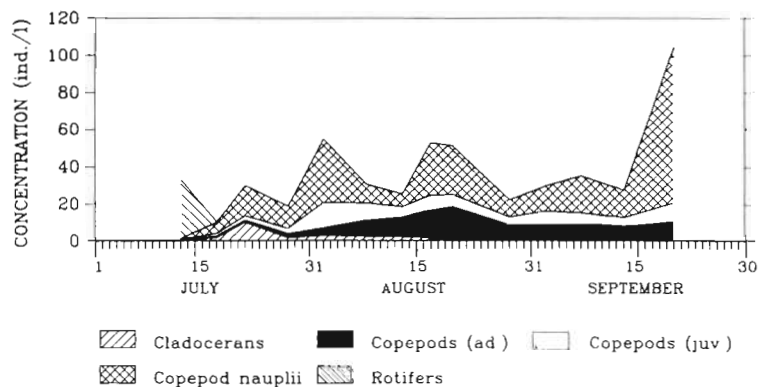


Fig. 7 Concentration of zooplankton in the basin (values integrated over the water column). ad.: adults; juv.: juveniles

population, obviously displayed no self-recruitment. The decrease in *Calanus finmarchicus* after 17 August amounted to a daily mortality of $13\% \text{ d}^{-1}$. Medusae were not abundant, and *Sarsia tubulosa* and the ephyra of *Aurelia aurita* were observed at densities of ca 1 ind. m^{-3} .

Apart from 13 July, when the rotifers were numerically dominant, copepod nauplii constituted the most abundant group. The highest abundance (82 ind. l^{-1}) was observed at the end of the investigation. The peaks in abundance of copepod nauplii (Fig. 7) corresponded to those of juvenile copepodids of *Pseudocalanus/Paracalanus* spp. and *Acartia longiremis*.

DISCUSSION

The experiment was divided into 2 periods, the first characterized by development of an oxygen deficiency in the bottom water layers, the second including fertilization, use of a propeller, supply of deep-water and associated recovery from oxygen deficiency.

Development of oxygen deficiency

Immediately after the basin was filled, oxygen saturation was high at all depths. After 1 wk, low oxygen concentrations were measured at the bottom, decreas-

ing to $<25\%$ saturation by the end of July. Oxygen measurements indicated a stable water column in late July, although no stratification was suggested by the temperature and salinity profiles.

Diatoms were almost absent on the first 3 sampling dates (Fig. 4). Compared to similar enclosure studies, a diatom bloom could have been expected as a response to the filling of the basin (Davis 1982). However, concentration of nutrients in the inoculate water was relatively low. One day after the basin was filled (4 July) silicate content was only $2.5 \mu\text{M}$. Paasche (1980) proposed that concentrations twice the half-saturation constant (K_s) for silicate uptake are limiting. Although diatom half-saturation constants for silicate uptake range from <1 to >7 (Paasche 1980), one can assume that silicate limited diatom growth during the first part of the study. As stated by several authors (Parsons et al. 1978, Maestrini & Bonin 1981, Takahashi et al. 1982) low nitrate concentrations favor algae with low K_s values for nitrate (i.e. small flagellates). As early as 8 July nitrate concentration was $<0.5 \mu\text{M}$ hence favoring small flagellates. During July a combined population of coccolithophorids and small unidentified flagellates increased to very high concentrations, reaching >350 million cells l^{-1} by the end of July.

During the entire study ciliates were abundant. In mid-July, *Tintinnopsis* sp. and *Lohmaniella* sp. dominated. Both are heterotrophic and were probably able to graze on the growing population of small phyto-

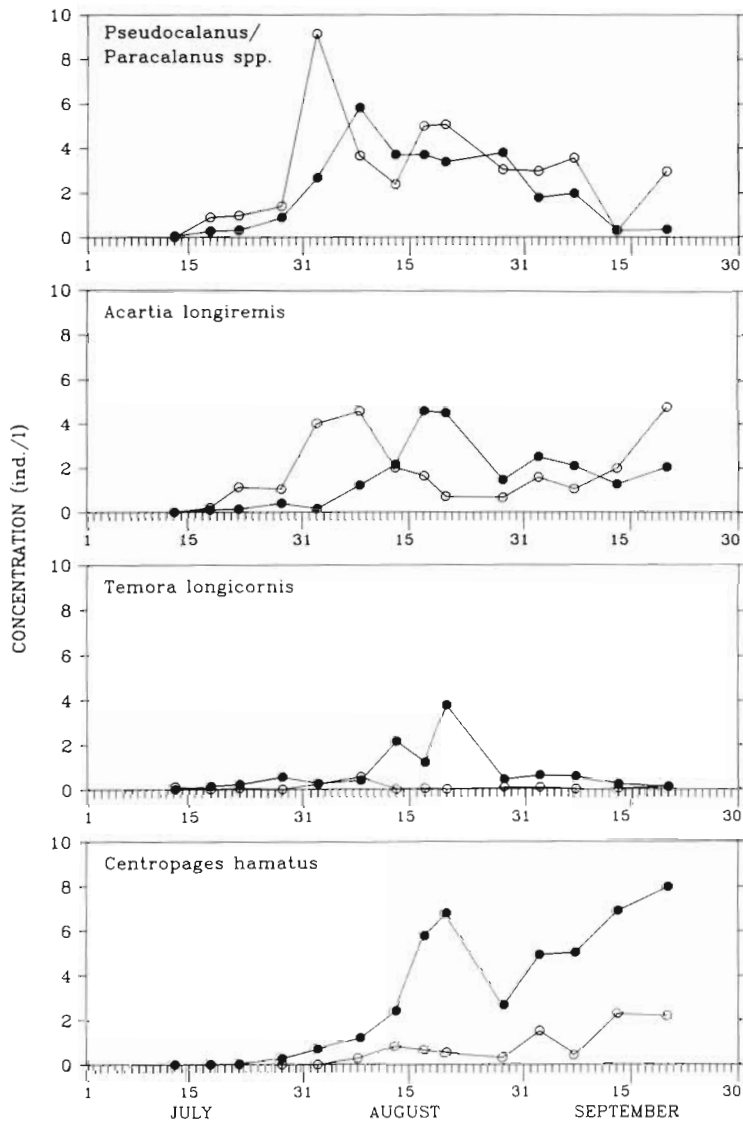


Fig. 8. Concentrations of dominant calanoid copepods in the basin: (○) juveniles and (●) adults (values integrated over the water column)

plankters. By the end of July, *Mesodinium rubrum* was abundant (>40 cells ml^{-1}). This species is autotrophic (Lindholm 1985) and is frequently reported as a 'red tide' species discoloring the water (Dale & Dahl 1987, Dugdale et al. 1987, Jimenez & Intriago 1987). The ability of *M. rubrum* to vertically migrate down to oxygen-poor and nutrient-rich water has been reported from a stratified Baltic Sea inlet (Lindholm & Mörk 1990). With respect to stability and oxygen deficiency below a certain depth, the Baltic Sea inlet corresponds in many ways to Svartatjønn, and a similar migration pattern could explain the *M. rubrum* bloom. However, Dale (1988) was not able to increase numbers of *M. rubrum* (= *Myrionecta rubra*, T Dale pers. comm.) by addition of nutrients, and it is possible that the *M. rubrum* bloom in Svartatjønn was sustained by partial heterotrophy, as reported by Smith & Barber (1979).

Immediately after the filling of Svartatjønn, high abundances of rotifers were recorded. Five days later this population had vanished and was gradually replaced by cladocerans and nauplii of calanoid copepods. By the end of July the cladocerans had almost disappeared, and the zooplankton community was dominated by all developmental stages of the calanoid copepods *Pseudocalanus/Paracalanus* spp. and *Acartia longiremis*. Rapid growth and disappearance of rotifers have been observed frequently in similar enclosure experiments (K. Naas & L. Berg unpubl.). The cladocerans, by reproducing asexually, are also able to compete well in early stages of succession.

Both high phytoplankton values (350 million cells l^{-1}) and high numbers of *Mesodinium rubrum* contributed to the relatively high concentrations of POM by the end of July. No in situ light measurements were taken, but the Secchi disc readings indicated a compensation

depth of approximately 3.5 m. Considering the stable water column, it is clear that no or very low net oxygen production occurred near the bottom of the basin, resulting in the low oxygen concentrations in late July. The bottom substrate in Svartatjønn was composed mainly of detrital organic matter precipitated during the limnic history of the basin. No perennial forms of attached algae or benthic fauna could have established themselves in Svartatjønn during the few months of marine conditions. In addition, the sediment of Svartatjønn was very soft and muddy and did not provide substrate for attached algae. The absence of a distinct bottom probably discouraged establishment of any meio- or macrobenthos. Hence, the oxygen values next to the bottom were probably less affected by benthic algae or fauna. However, decomposition of organic matter at the bottom probably contributed to the oxygen deficiencies.

Effects of manipulations

In general, the manipulations resulted in improved water quality by favoring diatoms, increased oxygen concentrations, and at the end of the investigation, increased production of calanoid nauplii. Similar results have been achieved in freshwater ponds, where addition of nitrogen nutrients has changed phytoplankton species composition from Cyanophyceae-dominated to Chlorophyceae-dominated, thereby increasing oxygen concentrations (Barica et al. 1980). In addition, seawater-mesocosm studies, involving either controlled addition of nutrients or artificial upwelling of nutrient-rich deep-water, have clearly demonstrated increased phytoplankton biomass and primary production (Neve et al. 1976, Parsons et al. 1977a, Takahashi et al. 1982, Aksnes et al. 1985).

The deep-water introduced close to the bottom was more saline and colder than the basin water and did not induce any major mixing of the water. It also did not improve oxygen content near the bottom, and so the propeller was used. The propeller mixed the water masses thoroughly, thereby ensuring a homogeneous and turbulent water column. In a series of experiments it has been shown that turbulence affects phytoplankton composition by favoring species with no self-motility (i.e. diatoms) (Eppley et al. 1978, Margalef 1978, Walsby & Reynolds 1980, Bröckel 1982). Ten days after the propeller was started, a diatom peak was observed, probably as a result of the increased turbulence and supply of nutrient-rich water from the bottom layers. The diatom population consisting mainly of *Leptocylindricus minimus*, vanished by the end of August, probably because of nutrient depletion. An increasing *Skeletonema costatum* population, however, occurred

in the first part of September. This second diatom peak coincided with the increased nutrient concentrations after fertilization.

The input of both turbulent energy and nutrients seemed to favor diatom growth and to increase chl *a* concentrations in the basin water. Also, oxygen saturation temporarily improved by the first diatom peak, and the increasing *Skeletonema costatum* population at the beginning of September was followed by increased oxygen saturation from <50 % to >100 % at all depths. The diatoms consisted of larger species than did the other phytoplankton, and consequently cell numbers did not adequately reflect diatom biomass relative to the other classes. Thomas et al. (1978) also demonstrated higher productivity values for diatoms than for other algae in natural seawater, and the production/consumption ratio for oxygen was generally higher for diatoms than for other phytoplankton groups. Thus, considering biomass and productivity, diatoms probably played the dominant role in net oxygen production in Svartatjønn. This was supported by the positive correlations found between chl *a*, diatom concentration and oxygen saturation (Table 2).

Detrended correspondence analysis of the phytoplankton data yielded 2 groups of samples along the first axis, one before 2 August and the other after 13 August (Fig. 9). This separation coincides with the start of the propeller and the associated mixing of the water column. Two sampling dates, 13 July and 8 August, fall between the groups. On both these dates, the water column was partly stagnant, and it is possible that the analysis reflects a transition community between stagnant and turbulent regimes.

The addition of inorganic fertilizers in late August was accompanied by high concentrations of particulate material. The PIM/POM ratio exceeded 1, and a large fraction of the particles probably consisted of undissolved fertilizer material. The peak concentration in particulate material was followed by increased Secchi disc values. This phenomenon has been observed in other enclosure experiments (K. Naas unpubl.) and may be the result of precipitation of humic particles caused by increased concentration of nutrient salts and inorganic particles. However, in the same period, the first diatom bloom collapsed, and chl *a* concentration was reduced from 13 to 2 $\mu\text{g l}^{-1}$, which may also have contributed to the clarity of the water.

In the period between the 2 diatom blooms a population of *Balanion* sp. dominated the ciliates. Stoecker et al. (1986) found that *Balanion* sp. selected small dinoflagellates. However, the only phytoplankton present in Svartatjønn at that time were small prasinophyceans and cryptophyceans. Along with the increasing *Skeletonema costatum* population in the first part of September, *Balanion* sp. disappeared and was

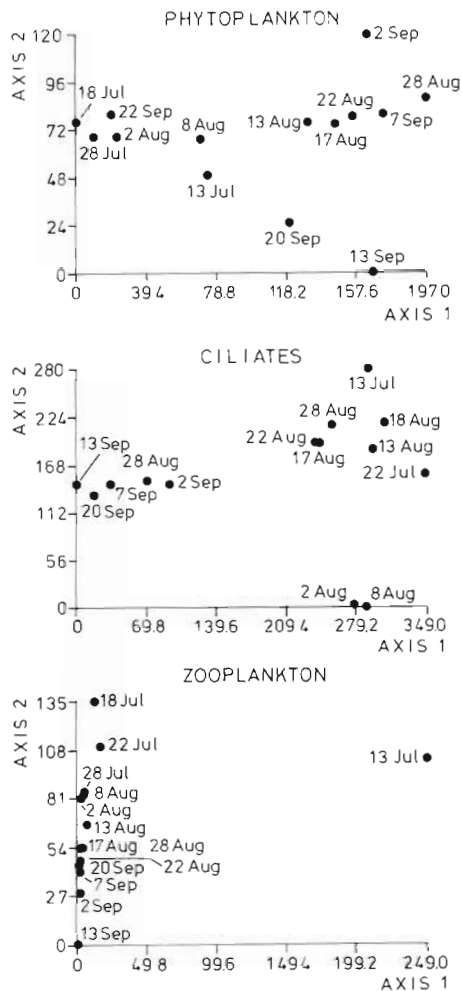


Fig. 9. Plot of detrended correspondence analysis of phytoplankton, ciliates and zooplankton. See 'Discussion – Effects of manipulations' for explanation

replaced by heterotrophic specimens of *Strombidium* sp. The most pronounced grouping of samples was revealed by detrended correspondence analysis of the ciliates (Fig. 9). The time of separation of samples coincides with the time of fertilization. As also indicated by species composition, this shift may reflect a trophic change from a mainly bacterivorous ciliate population to a heterotrophic population, in response to the increased phytoplankton biomass after fertilization.

The most critical oxygen deficiencies were recorded between 23 and 27 August. During the same period a reduction in abundances of nauplii and adult stages of most calanoid copepods occurred (Fig. 8). The decreasing concentration of nauplii may have reflected that the nauplii grew into juveniles, and that no recruitment occurred. Of the adult copepods, *Acartia longiremis*, *Centropages hamatus* and *Temora longicornis* were reduced by ca 50 % between 22 and 28 August, which may partly have been due to the deteriorating oxygen

conditions. Adults of the combined *Pseudocalanus/Paracalanus* spp., however, did not decrease likewise. The most intense renewal of water was also carried out in the same period but probably did not affect the larger zooplankton, due to the filtration of the outlet water.

At the beginning of September, the *Acartia longiremis* and *Centropages hamatus* populations were obviously reproducing, and by the end of the investigation an increasing population of calanoid nauplii was recorded (Fig. 7). By that time the basin ecosystem had recovered, with high oxygen levels and sufficient food supply, due to the *Skeletonema costatum* bloom. Næss (in press) has subsequently documented the impact of diapause eggs on zooplankton composition in Svartatjønn. However, before the present study the sediments in Svartatjønn were totally limnic. Furthermore, diapause eggs produced during summer were, according to Næss (in press), difficult to hatch without an intermediate drop in temperature. Thus, the increase in nauplii was probably a result of reproduction rather than hatching of diapause eggs.

No apparent grouping of zooplankton samples was revealed by detrended correspondence analysis (Fig. 9), apart from those of the first sampling date, when rotifers were entirely dominant (Fig. 7). In contrast to phytoplankton and ciliates, larger zooplankton display a relatively long generation time, and hence a longer response time to possible environmental alterations.

Production capacity of closed vs advective systems

The present basin system was designed to provide an environment in which natural food particles were available to fish larvae during the first feeding period. In this context the zooplankton, in particular the copepods, are of interest. *Paracalanus/Pseudocalanus* spp., *Centropages hamatus*, *Acartia longiremis* and *Temora longicornis* dominated, with individual copepodite and adult abundances ranging from 1 to 10 ind. l^{-1} (Fig. 8). Total nauplii abundances ranged between 10 and 40 ind. l^{-1} , but approached 80 ind. l^{-1} on the last sampling date (Fig. 7). In the natural enclosed fjord Lindåspollene, Lie et al. (1983) and Aksnes & Magnesen (1988) found maximum abundances (during June) of <1, 1, 6, 7 and 20 ind. l^{-1} for *A. longiremis*, *T. longicornis*, *Paracalanus parvus*, *Pseudocalanus elongatus*, and copepod nauplii respectively. Thus, concentrations of the dominant copepod species and nauplii in Svartatjønn did not differ considerably from those found in nearby natural waters during summer. Mortality estimates of the Lindåspollene populations ranged between 7 and 23 % d^{-1} and the present minimum

estimates for the Svartatjønn populations are within this range. Aksnes & Magnesen (1988) estimated an average production of 2 to 3 mg dry wt d⁻¹ m⁻³ for the 4 most dominant copepods. Assuming the same values in Svartatjønn, we arrive at a copepod production level of 40 to 60 g dry wt d⁻¹ for the entire basin.

Nitrogen input through fertilization corresponded to about 3 kg d⁻¹ from 22 August to 4 September (Table 1). Assuming a dry wt:nitrogen ratio of 15 (Parsons et al. 1977b), this corresponds to a potential production of 45 kg dry wt d⁻¹. Due to this high nutrient load and the rather high phytoplankton abundances during the investigation (Fig. 4), it may be concluded that the secondary producers were not limited from below. Low initial numbers, combined with temporary oxygen deprivation, were a more probably limitation for the copepods. Consequently, copepod production would probably not have increased had the nutrient load increased. However, the supplied nutrients did improve oxygen concentrations and initiate a diatom bloom. These 2 factors probably both contributed to the reproduction of calanoid copepods in September, and hence the secondary production of Svartatjønn was increased through the manipulations.

According to Otterå & Lie (1990), 19 mm cod fry experienced about 50 % survival during weaning to formulated feeds. In a consumption model proposed by Blom et al. (in press), a 2 cm cod fry (10 mg dry wt) would consume about 3 mg copepod dry wt d⁻¹. Assuming the above copepod production of 60 g dry wt d⁻¹, Svartatjønn would have a production capacity of 20 000 cod fry, i.e. 1 larva m⁻³. In comparison, during spring 1984, 30 000 cod fry, 4 cm in size, were collected from the basin. However, these fry were fed dry pellets after metamorphosis in addition in the zooplankton diet (Øiestad et al. 1984).

A volume of 56 000 m³ seawater was supplied during the 12 wk investigation period. This corresponds to an average renewal rate of 3 % d⁻¹; such a low rate indicates that production of phytoplankton and herbivores, on the time scale of the study, was dominated by local rather than advective processes, i.e. reflected an extensive system (Naas 1990). Generally, closed and semi-enclosed production systems exhibit much lower production capacity for local predators (fish larvae) than do advective systems. Predators in an advective system are able to consume at a rate equal to the renewal rate of prey (Aksnes et al. 1989). As long as the prey is planktonic, this rate is likely to equal the water-exchange rate. Thus, greater water renewal means higher production capacity. In contrast to advective systems, however, are closed systems, in which future prey production depends on the size of the current prey stock. This means that potential future production will decrease if the prey abundance of the system is low-

ered by predation. Therefore, in the closed system predation must be balanced by local prey production in order to avoid prey deprivation and a corresponding decline in future production. This is the main limitation of closed culturing systems. However, in recent years, several copepod species which produce diapause eggs in Svartatjønn have been identified (Næss in press). In November 1989, as many as 2 million copepod nauplii m⁻², or 2000 nauplii l⁻¹ basin water, were hatched from the sediment. By manipulations, such as supplying warm, oxygen-rich deep-water, it is possible to manage the time of hatching in order to increase current prey stock. Hence, the main restriction to production in such closed culturing systems can to a certain extent be overcome by proper management.

CONCLUSIONS

The present study has shown that fertilization and mixing by propeller seem to be suitable manipulations for preventing anoxia in the water column. Production capacity at the copepod level was estimated at 2 to 3 mg m⁻³ d⁻¹ during the investigation. Theoretically this production may satisfy the food requirements of 2 cm cod fry at an abundance of 1 ind. m⁻³. Through prevention of anoxia and increasing the initial standing stock of zooplankton, production could have been increased.

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