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Influences of bag dimensions on the development of enclosed plankton communities during POSER

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ABSTRACT: During POSER (Plankton Observations with Simultaneous Enclosures in Rosfjorden) natural plankton communities were enclosed by large plastic bags anchored in situ. Enclosures of different dimensions, ranging in depth from 3 to 40 m and containing 1.5 to 30 m^3 of water, facilitated the study of dimension effects of the enclosure on the development of the plankton inside. When comparing mean values in small bags with those of the total mixed layer of large bags, phytoplankton development was very similar in large and small enclosures. Although large and small enclosures had been filled simultaneously, bacterial numbers increased faster in small than in large enclosures, probably because of closer contact with the substrate. Copepod populations suffered high mortalities, in particular in small bags. Their mortality may have been influenced by the extremely cold weather prevailing during the experiment. It appeared that fluctuations in environmental factors (temperature, light, nutrients, etc.) were much more important for plankton development than the dimensions of the enclosure. The suitability of enclosures for studying natural plankton ecosystem is discussed. It is concluded that optimum dimensions depend on the aim of the experiment, number of trophic levels enclosed, population density at these levels and on the species present at these levels. For ecotoxicological experiments with marine phyto- and zooplankton communities in eutrophic waters, enclosures of 1 to 2 m^3 are sufficiently large, and for practical reasons should be preferred over larger ones. In more oligotrophic waters, enclosures with a volume of ca. 10 m^3 are to be preferred, so that larger zooplankton samples can be taken.

INTRODUCTION

In the marine environment, natural plankton communities enclosed by large, flexible, translucent plastic bags have frequently been used as models for natural ecosystems (for reviews see Kinne, 1976; Reeve et al., 1976; Menzel and Steele, 1978; Davies and Gamble, 1979; Kuiper, 1982). Important aspects of these experiments are the replicability of experimental units in an experiment and the extent to which the model is representative for the real system.

Unfortunately, replicability and representativity seem to be inversely correlated properties of experimental design (Gamble and Davies, 1982). A monospecies algal culture in the laboratory is not representative for most mechanisms acting in nature (e.g. competition, grazing, etc.), but the possibilities for replication are very large. On the other hand, the ocean is the only representative for itself, though it is not replicable.

Two factors are of prime significance for an experimental design: duration of the experiment and dimensions of the enclosure, both factors being related via the generation time of enclosed organisms and the rate of fouling on the walls. Optimal duration of (ecotoxicological) experiments was discussed by Grice et al. (1980), Kuiper (1982), and others. Concerning the size, and excluding very short-term experiments (1 to 2 d), enclosures of widely different dimensions have been used (0.3 to 16 000 m^3) to study natural plankton. In applied research, such as ecotoxicology, enclosures as small as possible are preferred for convenience of experimental handling, possibilities of replication, and cost reduction (Davies and Gamble, 1979).

Experiments with marine plankton communities in large (Takahashi et al., 1975: 68 m^3) and relatively

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small enclosures (Brockman et al., 1977: 3 to 4 m^3; Kuiper, 1977a: 1.5 m^3) showed that the development of bacteria, phytoplankton and zooplankton replicated sufficiently for periods of up to 4 to 8 wk; hence pollutant effects can be detected by comparison with non-polluted controls. However, possibilities for replication decrease with increasing enclosure size (Gamble and Davies, 1982). It is not clear which aspects of representativity are lost with decreasing enclosure size.

One of the aims of POSER was to compare the development of planktonic ecosystems in enclosures of different dimensions. The depth of the enclosures used varied from 3 to 40 m, thus they included only a part of, or more than, the euphotic zone. The contents of the enclosures varied from 1.5 to 30 m^3.

MATERIALS AND METHODS

In 2 experiments relatively small (depth 3 m, volume 1.5 m^3) and large bags (depth 40 m, volume 30 m^3) were filled simultaneously. On 6 March 1979 the first experiment was started (POSER 1). Six small bags were simultaneously filled with a Vanton Flex-i-liner pump (Kuiper, 1981), the inflow hose of the pump being displaced from a depth of 20 m to 0.5 m during pumping so as to correct for zooplankton patchiness. On the same day, 4 large bags were filled according to Brockmann et al. (1983) so that in these bags the vertical stratification was nearly the same as in the fjord. Both in bags and fjord the development of phytoplankton, zooplankton and bacteria was monitored, as well as physico-chemical parameters potentially influencing the biota (nutrients, pH, temperature, salinity, incident light). Sampling methods and analytical methods were described by Brockmann and Hentzschel (1983) and Kuiper et al. (1983). A detailed account of physical, chemical and biological variations in the fjord was given by Brockmann et al. (1981).

During the first week of the experiment bad weather prevailed and on 12 to 13 March strong currents were present in the fjord. These currents caused a total exchange of water masses in the Børøy Bight (Brockmann et al., 1981). As a result, direct comparisons between plankton development in bags and in the fjord were difficult; hence the experiment was terminated.

A second experiment was started on 16 March (POSER 2). This time 7 small bags (1.5 m^3) and 2 large bags (length 20 m, volume 15 m^3) were filled. Some bags received additional nutrients; 2 small systems and 1 one large one were monitored without any additions (cf. Kuiper et al., 1983). The same parameters were measured as during the first experiment. During POSER, a total of 34 enclosures were launched. Results of some of them are used here for comparison with results obtained from the experiments described. Details on enclosure experiments are summarized in Table 1.

Table 1. Starting days, dimensions and duration of various enclosure experiments during POSER

Experiment	Bag code	Dimensions		Starting day	Duration (d)
		depth (m)	contents (m^3)		
POSER 1	11	3	1.5	6 March	8
	12	3	1.5	6 March	8
	18	40	30	6 March	8
	19	40	30	6 March	8
POSER 2	21	3	1.5	16 March	20
	22	3	1.5	16 March	20
	24*	3	1.5	16 March	20
	25*	3	1.5	16 March	20
	28	20	15	16 March	10
Norwegian control	C	15	11	6 March	29
German controls	U	40	30	3 March	12
	V	40	30	4 March	9
	BB	40	30	19 March	18
	CC	40	30	21 March	16
	DD	40	30	22 March	10

* All enclosures refer to natural plankton populations as harvested during the experimental period. Additional nutrients were added to Bags 24 and 25

RESULTS

Phytoplankton and nutrients

During POSER 1 phytoplankton concentrations in all bags decreased in the same way as in the fjord. This

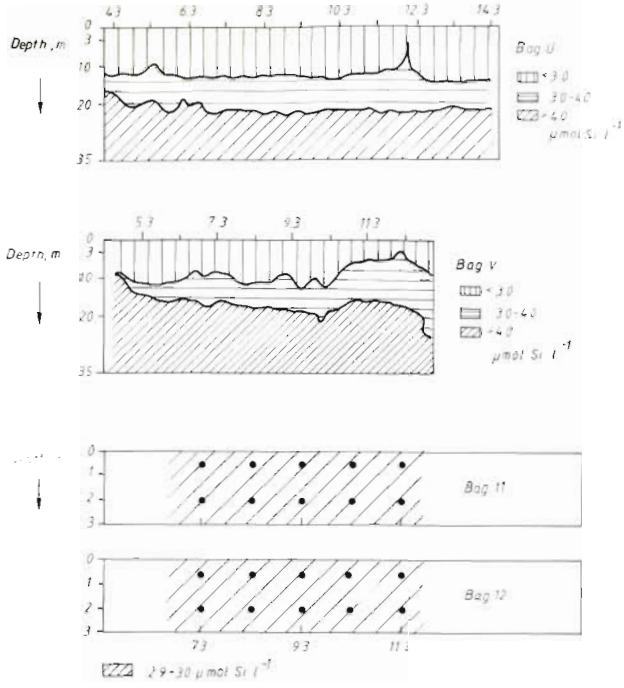

Fig. 1. Development of concentrations of reactive silicate in 2 large and 2 small enclosures during POSER 1

was probably due to the settling of cells. Concentrations of reactive silicate, in 2 small and 2 large bags (U and V) are shown in Fig. 1. These concentrations remained constant during this period. In the large enclosures, the stratification remained undisturbed; the small bags were not stratified. In the different bags

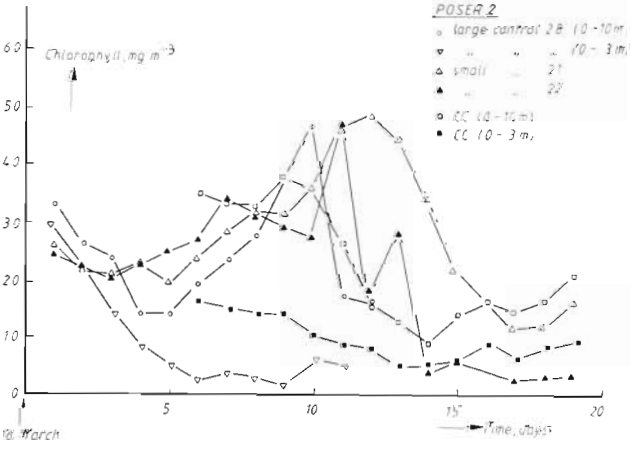

Fig. 2. Development of chlorophyll concentrations in enclosures during POSER 2

the other nutrients showed the same pattern with time. The phytoplankton growth was probably reduced and no important differences could be detected between the different enclosures.

The development of average chlorophyll concentrations during POSER 2 in 2 small enclosures (No. 21 and 22) and in 1 large enclosure (No. 28) is shown in Fig. 2. For the large bag the average concentration is presented in the upper 10 m. In this layer the bulk of primary production occurred (Jahnke, pers. comm.). After the bags had been filled, chlorophyll concentrations decreased, owing to the settling of phytoplankton cells. After the third day in the small and after the fourth day in the large bag, chlorophyll concentrations increased, due to growth of diatoms, of which *Thalassiosira nordenskiöldii* was dominant. *Chaetoceros debilis* and *C. borealis* also increased in numbers during this period. In all bags maxima were reached around Days 10 to 11 (27 March), after which chlorophyll concentrations decreased again. The average concentrations in all bags were about the same.

In Fig. 2 the average chlorophyll concentration in Bag CC is also indicated. Bag CC was filled some days later than the others. For this enclosure mean values of the upper depths corresponding to the small bags are also presented; this facilitates comparison of the development at different depths. In the large bags the chlorophyll concentrations near the surface showed a development differing very much from that in the small bags or from the average of the upper 10 m of the large bags. In Bag BB a maximum could also be found on Day 10. This maximum was generated by the same diatoms as in the other enclosures.

Two small bags, also filled on 16 March, were spiked with nutrients (No. 24 and 25, 8 µg at NO_3 l^{-1}, 1,5 µg at PO_2 l^{-1} and 5 µg at Si l^{-1}; see Kuiper et al., 1983 for details). Fig. 3 shows the development of chlorophyll

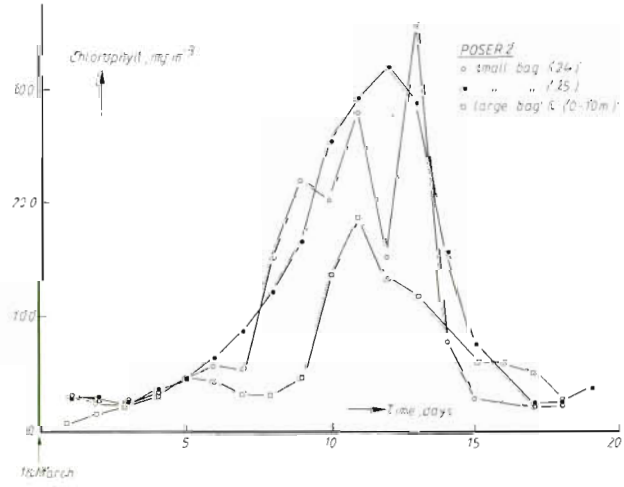

Fig. 3. Chlorophyll concentrations in 2 nutrient-spiked small bags and 1 nutrient-rich large enclosure during POSER 2

concentrations in these bags and in 1 large bag (C), filled with nutrient-rich water on 6 March. In the nutrient-spiked bags a bloom of the same diatom species as in the other bags occurred, with a maximum in both bags around Day 12. Remarkably, a bloom of the same

species was found in Bag C, although it was filled much earlier with different water.

Fig. 4 shows the development of silicate and phosphate concentrations in 2 small (No. 21 and 22) and 2

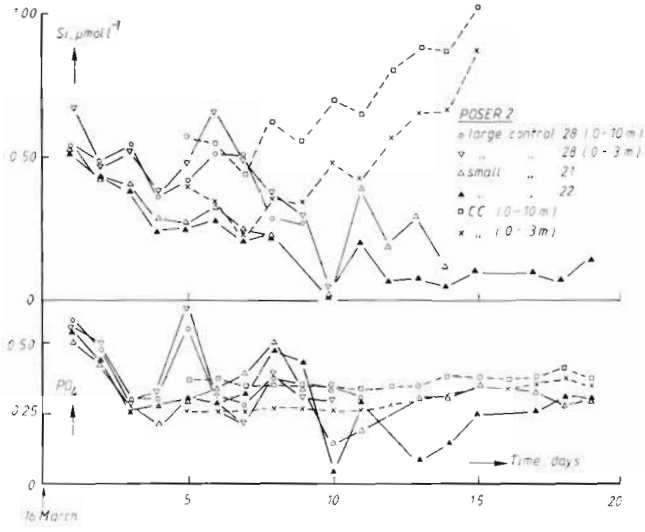

Fig. 4. Reactive silicate and phosphate concentrations in 2 small and 2 large enclosures during POSER 2

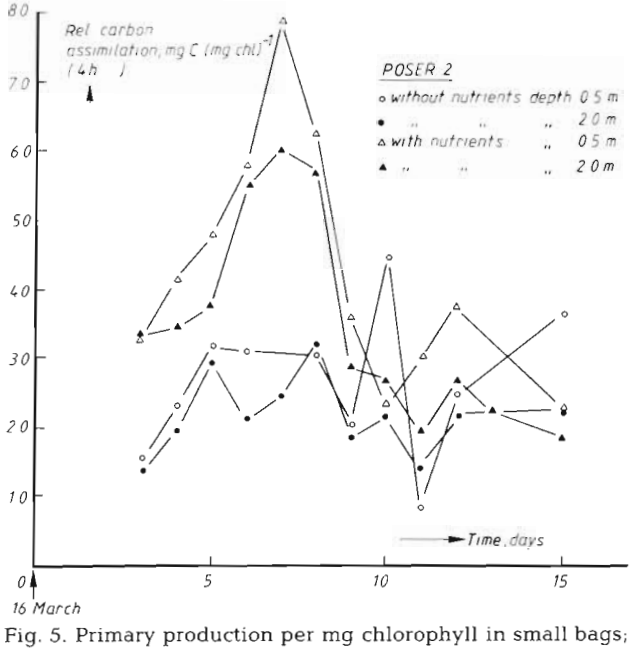

Fig. 5. Primary production per mg chlorophyll in small bags; averages of 2 bags with and without nutrients added during POSER 2

large bags (No. 28 and CC). The growth of diatoms caused a decrease of silicate concentrations. This decrease was faster in the small bags than in the large bags, but it was never observed in Bag CC either at its surface or within the upper 10 m. The phosphate concentrations in Bag CC, with which the experiment had been started later, were lower at the surface and increased during the experiment. In particular in the small bags, phosphate concentrations showed stronger fluctuations than within Bag CC.

Fig. 5 illustrates primary production mg^{-1} chlorophyll in the small bags at different depths during POSER 2. Inhibition of primary productivity by high light intensities near the surface, which could be a disadvantage of small bags, was not found. Rates of primary production in Bags 21 and 22 are clearly limited by low nutrient concentrations.

Zooplankton

In POSER 1 initial conditions prevailing in small and large bags were very similar, calanoid copepods being the most important. Numbers of copepods seemed to remain constant, but the experiment was too short to allow conclusions on possible differences between the bags.

At the start of the second experiment the zooplankton community resembled that of the preceding period. Nauplii of *Calanus finmarchicus* were most numerous. *Acartia clausi, Centropages hamatus, Pseudocalanus elongatus, Oithona similis* and an unidentified harpacticoid copepod were also found. Nauplii were most abundant. Fig. 6 shows the total number of copepods in

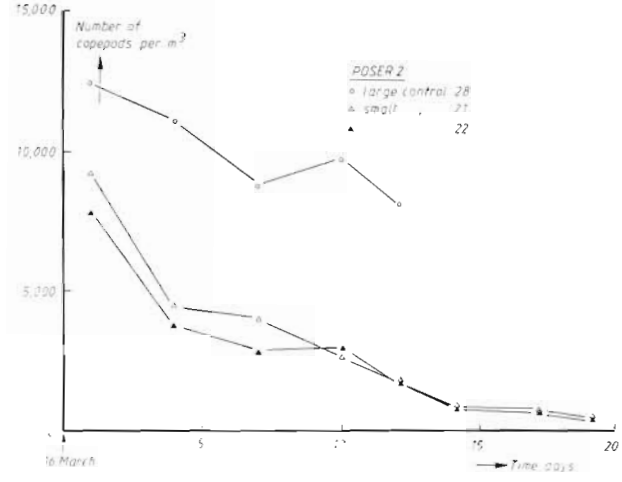

Fig. 6. Total number of copepods (all stages) in 2 small and 1 large enclosure during POSER 2

2 small (21 and 22) and 1 large (28) bag during the experiment. Table 2 lists the species composition and number of organisms in the same bags on selected days during the experiment. In all bags the numbers of copepods decreased; in the large bag total numbers decreased at ca. 20 % wk^{-1}; mortality in the small bags was even larger (> 50 % wk^{-1}). Table 2 shows that in the large enclosures declining numbers were primarily caused by mortality of nauplii of *Calanus finmarchicus*. In the small bags all species suffered high

Table 2. Numbers of copepods m^{-3} in large and small bags on selected days during POSER 2. Bags were filled on 16 March, 1979. n nauplii, c copepodites, a adults

Bag		Large (28)		Small (21 and 22)		
Day		1	12	1	12	19
Species						
T. longicornis	n	400	250	663/612	153/255	–/–
	c	10	50	102/51	–/102	–/–
	a	30	10	–/–	–/–	–/–
A. clausi	n	1050	800	816/510	561/459	153/153
	c	50	–	204/153	–/–	–/–
	a	10	–	–/–	–/–	–/–
C. hamatus	n	650	400	1224/1122	204/255	153/51
	c	110	240	204/51	51/102	–/51
	a	–	–	–/–	–/–	–/–
C. finmarchicus	n	9700	5450	5714/4847	612/357	102/51
	c	140	790	–/51	51/–	–/–
	a	–	–	–/–	–/–	–/–
O. similis	n	150	–	–/51	–/51	–/–
	c	100	50	51/102	–/–	51/–
	a	–	10	–/–	–/–	–/–
Others		10	40	205/205	51/–	–/51
Total		12410	8130	9233/7805	1683/1683	765/357

mortalities, although the numbers of *Oithona similis* were too low to allow conclusions.

In the fjord, numbers remained more or less constant. Development of the copepod nauplii into larger stages could not be detected because the water masses exchanged during the experimental period. In the large enclosure No. 28 numbers of (small) copepodites of *Calanus finmarchicus* increased gradually from 140 to 790 m^{-3} during 12 d. Apparently, the larger nauplii developed very slowly into small copepodites.

Bacteria

During POSER 1 total numbers of bacteria (epifluorescence counts) increased in the small bags from 2.5 to 5 × 10^5 ml^{-1} in 6 d (Kuiper et al., 1983). Too few samples are available from the simultaneously filled large bags to allow any conclusions. In Bag U, however, numbers of colony forming units (CFU) increased from 600 to 2000 ml^{-1} during the first week; later, numbers decreaed again. A similar increase in the number of CFU was observed in Bag V, filled in the same period (Hentzschel, pers. comm.). In Bag C, CFU numbers increased by a factor of 10 during the first 10 d, the increase in total numbers (estimated by epifluorescence technique) being somewhat smaller. It seems that during the first period of POSER bacteria developed rather similarly in the different enclosures.

Fig. 7 shows the number of bacteria in small and large enclosures (No. 21, 22, 28) during POSER 2. In the small bags the number of bacteria increased, but in

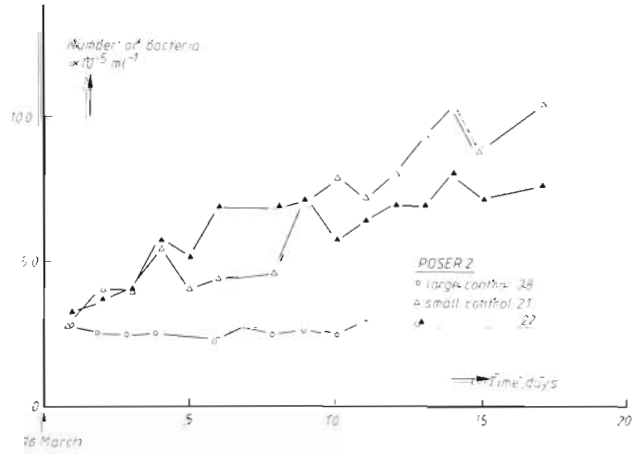

Fig. 7. Number of bacteria in 2 small bags and 1 large enclosure during POSER 2

the large bag, numbers were more or less constant. In other large bags available for comparison (BB and CC), CFU numbers showed a slight increase with time, 2 clear maxima occurring around 24 and 31 March in both enclosures (Hentzschel, pers. comm.). Comparison with the epifluorescence counts is difficult, however, because a changing proportion of the total number found may be colony forming.

DISCUSSION AND CONCLUSIONS

Menzel and Steele (1978) argued that the optimum size of an enclosure depends on the number of trophic

levels. They stated that 'the most likely acceptable volume to avoid adverse complications (like fouling) is 30 m^3'. The choice of this volume was not supported by measurements or further arguments. If carnivorous zooplankton is included it was assumed that a minimum of 100 m^3 is necessary. Case (1978) indicated that the objective of the experiment is also an important factor in dimensioning an enclosure. We shall now discuss the development of the plankton community at the various trophic levels in relation to enclosure size.

Phytoplankton

In the experiments reported here no principal differences were found between the development of the phytoplankton in large and small bags when comparing the mean values of small bags and those of the total mixed layer of the large bags. This similarity was probably caused by remineralization in the small bags where the biomass could not leave the region near the surface, and by diffusion and remineralization from the lower depths in the large enclosures. The differences of phytoplankton development in the corresponding depths (Fig. 2) are caused by sedimentation of elements bound to particles out of the surface region in the deep enclosures (Fig. 4). This interpretation is supported by nutrient measurements (see below).

During POSER 2 an increase in diatoms occurred in all bags, and the species composition of these blooms was very similar. In the fjord and in the bags to which nutrients had been added, the same dominant species were found. The species composition was expected to be one of the first parameters which would be influenced by a stress exerted by containment in a bag.

Another indication for the absence of a dominant bag influence was that the diatom bloom around 27 March occurred in nearly all bags filled with natural plankton, irrespective of the day of filling. Even in Bag C, filled on 6 March, a diatom bloom of *Thalassiosira nordenskiöldii, Chaetoceros borealis* and *C. debilis* could be observed around 27 March (3 wk after filling). These findings indicate that environmental factors such as light, nutrients and temperature regulate the development of the enclosed phytoplankton. The development in bags ranging from 1.5 to 30 m^3 appears to be quite natural. The factors initiating the bloom probably can be found in the increasing water temperature and the increasing light conditions (Jahnke et al., 1983; Kattner et al., 1983).

Surface inhibition of primary production was not found. Primary productivity at depths 0, 0.5, 2 and 3 m was very similar. Jahnke et al. (1983) measured primary production in the fjord at 0, 3, 10 and 20 m. They observed slightly lower values at the surface only a few days, and report an average relative carbon assimilation of 2.37 mg C (mg chl)$^{-1}$ (6 h)$^{-1}$ ($N = 32$, s. d. = 1.33) at 0 and 3 m. Surface inhibition could limit the application of enclosures with low depths, although in these cases a perspex cover, absorbing most of the light < 300 nm, would largely prevent such inhibition (Brockmann et al., 1974).

Throughout the first part of POSER the phytoplankton was probably inactive, and nutrient concentrations remained constant in small and large bags. During POSER 2, nutrient concentrations in large bags increased or at least decreased more slowly than in the small bags (Fig. 4). Presumably, this can be attributed to (1) lower rates of nutrient consumption by phytoplankton, owing to the limitation of primary production at greater depths in large bags by lack of light; (2) nutrient diffusion coming up to the mixed layer from the nutrient-rich layer below 10 m depth. This latter assumption is supported by the strong increase of silicate compared to phosphate in Enclosure CC caused by the late phase dominating dinoflagellates (Jahnke et al., 1983) utilizing phosphate but no silicate. In experiments with the explicit aim of studying light dependence of several processes, deep enclosures are necessary, but for ecotoxicological experiments differences in the rate of nutrient consumption do not seem to be relevant. The effect of such differences on the phytoplankton could be that maxima of blooms are reached earlier in small enclosures than in the large ones.

Zooplankton

Calanoid copepods formed the most important part of the zooplankton during POSER. *Calanus finmarchicus* dominated the community, a phenomenon which is very usual in the northern North Sea and the waters of the Norwegian current (Furnes, 1976; Matthews et al. 1978). Nauplii were most abundant; this shows that the spring increase had started, since *C. finmarchicus* hibernates in the copepodite Stage V in these waters (Matthews et al., 1978).

During POSER the numbers of nauplii did not increase; if at all, nauplii developed very slowly into larger stages. Apparently, the extraordinary low temperatures (Kolstedt, 1973) limited further development of copepods, although appropriate food was available. Colebrook (1979) found a similar situation during a normal phytoplankton spring bloom and a delayed development of copepods in the very cold waters off Greenland and the Grand Banks region in the northern Atlantic Ocean.

During the short POSER 1 experiment, the numbers of copepods seemed to remain constant in the bags during the first 6 d. In bags and fjord the same species

and stages were found. During the second experiment, the numbers of copepods declined in all bags. In the large bag the rate of decrease (20 % wk^{-1}) seems to be too high for natural conditions, since predators were not observed. Mortality in the small bags was related to enclosure size.

In the small bags, all species decreased in numbers. This is remarkable, since in experiments with enclosed plankton from Dutch coastal waters (Kuiper, 1977a, b, 1981) or from Helgoland (Brockmann et al., 1977), partly the same species were present as in the Børøy Bight, and in the Dutch experiments they developed at a rate comparable to that in the open North Sea (Kuiper, 1977b). This indicates that the high mortality observed during POSER is not a consequence of the relatively small bag volume; rather, it appears to be due to the extreme low temperatures of the upper water layers (−1 to +2 °C). Krause (pers. comm.) found maximum densities of *Calanus finmarchicus* and *Pseudocalanus elongatus* in the Børøy Bight at 40 m. The figures of Grice et al. (1977) on the patchy distribution of zooplankton in large bags, with nearly all the nauplii near the bottom, also point to the possibility that the organisms tended to swim downwards. In the small bags such downward migration may be stimulated by the water in the upper layers being less shaded and colder than that in the deeper, large bags. In much larger bags – as used in the CEPEX programme (100 to 1300 m^3) – unexplained decreases in copepod numbers were also found (Reeve and Walter, 1976; Parsons et al., 1978; Davies and Gamble, 1979).

Another drawback of the small bags in Børøy Bight was related to the low density of the zooplankton. Removal by sampling of more than 5 % wk^{-1} of the zooplankton had to be avoided, and therefore the numbers of organisms in the samples from the small bags were low. Low numbers increase the error of the measurements, and therefore make discrimination between treatments more difficult.

Bacteria

During POSER 2, the numbers of bacteria increased more strongly in the small bags than in the larger ones. Stronger increase seemed also to prevail during the first experiment. This may have been caused by the fact that in small bags dead phytoplankton does not settle to a great depth, but remains in close contact with the upper water layer. Therefore, in the small bags the bacteria in the water may react more directly to changes in the phytoplankton than in the large bags. Such immediate reaction of bacteria in the water column may speed up the regeneration of nutrients, which then become directly available for phytoplankton growth. In experiments where most nutrients are regenerated by bacteria the rate of succession of phytoplankton may therefore be faster in small enclosures than in larger ones. In ecotoxicological experiments this does not seem a disadvantage.

Advantages and limitations of different bag sizes

In various experiments the development of enclosed marine communities was compared to that in the external environment to study the extent of representation of the experimental design (Davies et al., 1975; Takahashi et al., 1975; Gamble et al., 1977). Available information suggests that the development of an enclosed community is at least qualitatively similar to that of the free community during periods up to four weeks (Menzel and Steele, 1978). Barica et al. (1980) used enclosures of 9 and 230 m^3. They showed that in enclosures of both sizes for several months the development of the phytoplankton was similar to that in the lake. Also important differences exist between a free and an enclosed community (in the latter: less turbulence, no advection of new species, only small scale patchiness) which must have an important influence on a longer time scale. Even in the very large enclosures employed by Lund (1972, 16 000 m^3) the plankton community diverged from the free community after several months.

As regards to the phytoplankton Menzel (1977) reported that similar patterns of succession were obtained in 4 l flasks and 68 m^3 enclosures, suggesting that small scale laboratory experiments with natural phytoplankton assemblages can be used with some confidence to predict events at the phytoplankton level in much larger systems. Experiments with continuous cultures when natural assemblages of phytoplankton were used pointed in the same direction (DeNoyelles et al., 1980). An essential advantage of larger enclosures, i. e. the possibility of studying the interactions between trophic levels, disappears, however, when these much smaller enclosures are employed. It depends on the aim of the experiment which experimental set-up can be chosen.

Apart from drawbacks, such as limited possibilities for sampling sparse populations (carnivorous zooplankton), limited extent of representation for deep, stratified waters, etc., small bags (1.5 m^3) also present advantages over large enclosures. With very large enclosures it is very difficult to start with identical plankton communities (Parsons et al., 1977; Takahashi et al., 1977; Case, 1978) which is essential if the development in various bags has to be compared. Moreover, many samples must be taken from large enclosures, because the plankton distribution can be

very patchy (Takahashi et al., 1975; Grice et al., 1977; Davies und Gamble, 1979).

The most serious drawback of using bags in plankton research is the much lower turbulence and consequent lower mixing inside a bag as compared with the turbulence in natural waters (Verduin, 1969; Takahashi and Whitney, 1977; Steele et al., 1977; Menzel und Steele, 1978; Davies and Gamble, 1979). This lower turbulence influences, for instance, the sinking rates of phytoplankton and therefore influences the development of the total system (Steele and Henderson, 1976). One consequence of the low mixing rate is that in very large bags addition of nutrients is necessary to keep primary production going. Nutrients which are mineralized in the sediment of the bags do not return to upper layers, where most of the primary production occurs.

Artificial addition of nutrients is a drawback since it renders the system more unnatural and since effects of added chemicals on the mineralization process cannot be studied on the enclosed system as a whole. Sometimes the contents of a bag are artificially mixed (Strickland and Terhune, 1961; Brockmann et al., 1974; Parsons et al., 1977; Sonntag and Parsons, 1979), but the mixing of very large containers appears to be a problem (Sonntag and Parsons, 1979). In small enclosures mixing is easier and partly the result of sampling activities. Another drawback of large and deep enclosures is that they are much more vulnerable to changes in the salinity of the surrounding water (Grice et al., 1977; Case, 1978; Kremling et al., 1978; POSER results) limiting general application in many marine waters. When smaller bags are used, experimental handling and interpretations of the data is easier and costs are lower. The optimum dimensions of enclosures in plankton research are related to the aim of the experiment, the number of trophic levels, the population density at these levels and the species present at these levels. For ecotoxicological experiments with plankton communities, excluding fish and other larger carnivores, enclosures with a capacity of 1 to 2 m^3 appear to be sufficiently large in eutrophic waters like Dutch coastal waters, with their relatively high zooplankton densities. In more oligotrophic waters, like those in Børøy Bight, larger bags are preferred to allow sufficiently large zooplankton samples. Enclosures containing about 10 m^3 seem to be large enough in these cases.

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