

PRELIMINARY STUDIES ON THE VERTICAL DISTRIBUTION OF SIZE-FRACTIONS IN THE ZOOPLANKTON COMMUNITY IN LINDÅSPOLLENE, WESTERN NORWAY

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Zooplankton collected with Clarke-Bumpus plankton samplers equipped with 180 μm mesh-size nets in 10 m depth-strata and with 2-3 hours time intervals in Lindåspollene 2-3 October 1979 and 12-13 May 1981 revealed distinct differences with regard to the vertical distribution of size-fractions in the plankton. Thus, the major part of the biomass of the $> 1000 \mu\text{m}$ size-fraction in October 1979 was concentrated in the deepest 20 m throughout the sampling period, but a smaller part of the size-fraction, composed particularly of *Sagitta elegans* and *Aglantha digitale*, performed distinct vertical migrations. In May 1981 the same size-fraction was concentrated particularly in the upper 20 m, and no diel vertical migration could be ascertained. However, the species *S. elegans* and *A. digitale* displayed diel vertical migrations similar to those observed in October 1979. The major part of the biomass of the 180-500 μm and the 500-1000 μm size-fractions was concentrated in the upper 20 m in October 1979, and a weak diel vertical migration was apparent in the upper 20 m only. In May 1981 the same size-fractions performed distinct vertical migrations in the upper 40 m of the water column. The differences in vertical distribution and in the contribution of the various size-fractions to the total biomass is discussed with reference to the change in the hydrographic conditions between the two sampling periods. A series of samples obtained with Clarke-Bumpus samplers equipped with 75 μm mesh-size nets in 5 or 10 m depth strata during 10-11 June 1981 showed that the major 20 taxa of the zooplankton differed with regard to vertical distribution, but diel vertical migrations could not be detected for any of the taxa. The biomass of the 75-250 μm size-fraction was a little higher than the biomass of the $> 250 \mu\text{m}$ size-fraction.

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INTRODUCTION

The zooplankton plays a particularly important role in the dynamics of marine ecosystems by its control of phytoplankton growth through grazing and nutrient regeneration, and by channelling energy and matter from the primary production through the pelagic food-web. Therefore, it is important to study in detail the structure and the function of the zooplankton community in order to understand the dynamics of the ecosystems.

Traditionally, the major emphasis in studies of zooplankton has been on the qualitative composition of the zooplankton community and on the quantity of biomass integrated over considerable horizontal or vertical distances. However, during the last decades there has been a growing interest in the studies of functional aspects, such as grazing, respiration, and excretion (e.g. CONOVER 1968; FROST 1974; SMITH & WHITLEDGE 1977; IKEDA & MOTODA 1978; PAFFENHÖFER & KNOWLES 1979; DEVOL 1981). Although the variability in horizontal and vertical distribution of zooplankton has been observed and

studied and the ecological consequences of vertical migration realized for a long time, there has not been the same attention to detail in the studies of distribution as in the studies of functional aspects of the zooplankton community. This is partly related to the lack of suitable sampling gear for studies of small-scale variability in the plankton. Most zooplankton studies are performed with variations of nets, which are towed horizontally, obliquely or vertically, and such samples tend to disguise the small-scale variability in the distribution pattern. Samplers for semi-continuous (the Longhurst-Hardy plankton recorder) and for discrete point sampling (plankton pumps) exist, but they have not yet found wide application in zooplankton research.

Environmental gradients in the oceans are as a rule both more pronounced and more stable in the vertical than in the horizontal plane, and DAGG (1977) argues that a food-searching zooplankton organism is therefore likely to encounter patchiness and dense concentrations of food particles during vertical migrations. Consequently, the vertical

migration of zooplankton is probably of a greater ecological significance than comparable movements in the horizontal plane. The phenomenon of vertically migrating planktonic organisms has therefore been observed and studied since the early years of plankton research (literature summarized by CUSHING 1951), and it has stimulated the formulation of numerous hypotheses searching to explain the causes, adaptive significance, and ecological consequences of vertical migration (BANSE 1964; ENRIGHT & HONEGGER 1977).

Fjords and semi-enclosed marine systems (*polls* in MATTHEWS & HEIMDAL 1980) are characterized by distinct vertical gradients in environmental factors such as salinity, temperature, nutrients, and oxygen, and sampling of biological variables is considerably less adversely influenced by currents and weather conditions than in offshore systems. Therefore, the inshore systems are particularly well suited for detailed studies of vertical migration of zooplankton, and this is abundantly reflected in the literature on the phenomenon (e.g. CLARKE 1934; HANSEN 1951; CHRISTENSEN & PACKARD 1976; HOPKINS & GULLIKSEN 1977; DEVOL 1981).

In a long-term study of the marine ecosystems in Lindåspollene, western Norway (DAHL & al. 1973) there has been considerable emphasis on hydrography (AURE 1972), nutrient chemistry (LÄNNERGREN 1975), and phytoplankton (LÄNNERGREN 1976, 1978; LÄNNERGREN & SKJOLDAL 1976; SKJOLDAL & LÄNNERGREN 1978). These studies demonstrate that there are strong gradients in temperature, salinity, density, and nutrients in the upper 15–25 m of the water column. The upper layer is characterized by strong seasonal fluctuations, whereas the deeper layer is practically invariant with regard to physical and chemical factors. The temporal and spatial distribution of oxygen differs from this general pattern. The oxygen conditions of the deeper water mass are related to sporadic and infrequent renewal of the bottom water, which seems to be triggered by meteorological conditions during January–March (LIE & DAHL 1981). High concentrations of oxygen in the deeper waters were recorded in 1970, 1977, and 1979, but in the course of a few years the oxygen content in the near-bottom water was reduced to near zero. In the upper 20 m of the water column the oxygen content showed typical seasonal variability with high values (5–7 ml O₂/l) following the phytoplankton spring bloom, and lower values (2–4 ml O₂/l) during autumn.

In an analysis of the nutrient budget in the photic zone of Lindåspollene LÄNNERGREN (1976) concluded that the relatively high primary production during summer (about 0.5 g C/m² per day) could

only be explained by regeneration of nutrients within the upper layer. It is conceivable that zooplankton excretion could be responsible for a significant part of the nitrogen regeneration (WALSH & al. 1978), but in order to estimate the quantitative significance of the excretion it is necessary to have detailed knowledge of the seasonal and diel vertical distribution of the zooplankton biomass.

Studies of zooplankton in Lindåspollene have demonstrated seasonal (HAUG 1972; ELLINGSEN 1973; MCLEAN 1979) and diel (WESTERGAARD 1975) qualitative and quantitative variability in the vertical distribution of zooplankton, but the oblique or vertical net-hauls which these studies were based on were not well suited for revealing small-scale patterns in zooplankton vertical distribution or migration. The present study is based on data sets with better resolution in time and space than in previous investigations in Lindåspollene.

One of the aims of the research programme in Lindåspollene is to study the dependence of the population dynamics and the behaviour of the local herring stock on the biotic and abiotic components of the pelagic ecosystem (DAHL & al. 1973). Mathematical simulation models were considered essential as research tools in such studies, and much of the emphasis during recent years has been on field studies and controlled field experiments (SKJOLDAL & al. 1982, 1983) which provide input to the model for the pelagic system in Lindåspollene. The zooplankton plays an important role in the model, but it is realized that the inclusion of population dynamics and ecophysiology of individual species of zooplankton would lead to models of intractable complexity (PLATT & al. 1981). However, a number of physiological rates and ecological variables are related to the size-structure in biological populations and communities (FENCHEL 1974; HALL & al. 1976; BANSE & MOSHER 1980), and this has led to suggestions for ecosystem modelling on the basis of size-structure (STEELE & FROST 1977; PLATT & DENMAN 1977, 1978; SILVERT & PLATT 1978). This approach will be tried for the modelling of zooplankton in Lindåspollene, and the present paper represents a preliminary investigation on the vertical distribution and diel vertical migration of some size-classes of zooplankton, and of the relative contribution of these size-classes to the zooplankton biomass.

MATERIAL AND METHODS

Zooplankton samples were collected in horizontal hauls with Clarke-Bumpus plankton samplers equipped with 180 µm meshsize nets from 1350 h on 2 October to 1055 h on 3 October 1979, and from 1450 h on 12 May to 1115 h on 13

May 1981. The sampling was carried out from M/B 'Knurr', a 30' motorboat with a 20 HP engine and a hydraulic winch. The sampling location was in Spjeldnesosen (Fig. 1), where the about 1000 m cruise track was marked with buoys and lights.

The intention was to sample 10-m depth strata from the surface to the bottom in oblique hauls. However, during a pilot cruise we found that it was not possible to maintain a constant and sufficiently slow hauling speed on the winch, or to compensate for the effect of wind and currents by varying the hauling speed. Furthermore, we found that attempts to compensate for the drift of the boat had different effects on the plankton samplers depending on the sampling depth. The decision was therefore made to sample in horizontal hauls in the middle of the depth strata, and to make these samples representative for the 10 m stratum.

Four Clarke-Bumpus plankton samplers were set at 5, 25, 45, and 65 m depth and towed in one direction, and on the return track the samplers were set at 15, 35, 55, and 75 m depth. This sampling scheme would allow repeating the sampling at two hours intervals. However, due to frequent malfunctioning of the gear some sampling depths had to be repeated, and a constant time interval between samples was therefore not maintained. During the 2-3 October sampling period 11 samples per stratum were obtained, and during 12-13 May 9 samples.

In connection with a project on the study of effects of oil pollution on the dynamics of the pelagic system in Lindåspollene (SKJOLDAL & al. 1982) a third 24 hours sampling series was obtained on 10-11 June 1981. As the objectives of this investigation were different, the results are not directly comparable with the results of the sampling in October 1979 and May 1981. The towing distance was the same as previously, but the sampling depths in June were 0.5, 2, 5, 10, 15, 20, 25, 35, and 45 m, and the net-mesh-size was 75 μ m.

The samples from October 1979 and May 1981 were preserved on 4 % formalin neutralized with borax. In the laboratory the samples were sieved through a set of sieves with mesh-sizes 1000 μ m, 500 μ m, and 180 μ m. This sieving technique may introduce a source of variance due to insufficient flushing, i.e. organisms may be retained by a coarser sieve than the size of the organisms should indicate. In order to reduce this source of variance all the samples were flushed for the same length of time. The major zooplankton species retained on the coarsest sieve were identified and counted, whereas only the four numerically dominant species in the contents on the other two sieves were identified and given a subjective rank of abundance. After the identification the samples were washed in distilled water and dried in an oven at 60° C until constant weight.

The samples from 10-11 June 1981 were split in two parts by the modified Folsom splitter (MORDA 1959). One part was sieved through sieves with 75 μ m and 250 μ m mesh-sizes, and the material retained by each sieve was washed in distilled water and dried in an oven at 60° C until constant weight. The other part was preserved in 4 % formalin and subsamples from 1/8 to 1/256 (usually 1/32 and 1/64) depending on the abundance of zooplankton organisms in the samples, were identified as far as possible and counted. This procedure gives a fair representation of the numerically dominating taxa, but the rarely occurring forms were lost. The most unfortunate result of this counting technique is the loss of information about some of the characteristic species in Lindåspollene, such as *Sagitta elegans* VERRILL, *Aglantha digitale* O.F. MÜLLER, and *Pleurobrachia pileus* O.F. MÜLLER.

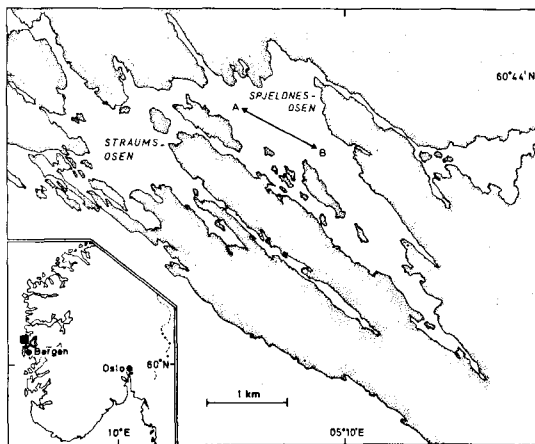


Fig. 1. Sampling location in Lindåspollene. A-B = cruise track.

RESULTS

Hydrography

The vertical distribution of temperature, salinity, and oxygen from October 1979 and May-June 1981 (Fig. 2) reflects the typical seasonal and annual variability in hydrographic factors in Lindåspollene.

During January-March 1979 there was a renewal of the bottom water in Lindåspollene (LIE & DAHL 1981), and in October there was still about 2.5 ml O₂/l near the bottom. The temperatures and salinities were nearly constant from 20 m depth to the bottom. From 20 m to 1 m depth the salinity decreased nearly linearly from 31.72 ‰ to 25.49 ‰, i.e. a gradient of 0.3 ‰/m. The temperatures in the same layer of the water column increased from 4.45° C to 10.41° C, i.e. a gradient of 0.3° C/m.

In May and June 1981 the oxygen contents of the water masses deeper than 30 m ranged from 0.6-0.0 ml O₂/l, whereas the oxygen contents of the upper 20 m layer were distinctly higher than in October 1979. The latter phenomenon was probably related to oxygenation resulting from the phytoplankton spring bloom (LIE & DAHL 1981). The temperatures below 20 m depth were about 0.5° C higher in 1981, and the temperatures of the upper 20-m layer reflect the normal seasonal development. In May the temperature increased from 4.76° C at 20 m to 10.69° C at 1 m depth, i.e. gradient of 0.3° C/m, and in June the gradient in the same layer was 0.4° C/m. The salinity gradient in May was 0.05 ‰/m and 0.1 ‰/m in June. Between 16 m and 50 m depth the salinities had decreased slightly from October 1979 to May-June 1981, whereas the salinity of the upper 16-m layer was considerably higher in 1981 than in 1979.

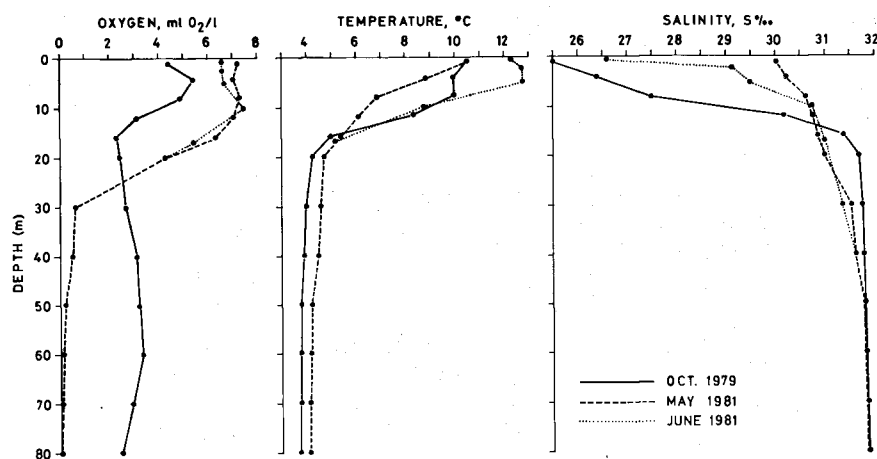


Fig. 2. Temperature, salinity, and oxygen in Lindåspollene, 2 Oct. 1979, 12 May 1981, and 10 June 1981.

Zooplankton

2-3 October 1979

1) The > 1000- μ m size-fraction

The species *Sagitta elegans*, *Aglantha digitale*, and *Calanus finmarchicus* (GUNNERUS) were numerically dominant species of this size group. *S. elegans* occurred in nearly all the samples (83 out of 87), *A. digitale* in 71 samples, and *C. finmarchicus* was particularly dominant at depths in excess of 55 m.

The total number of *S. elegans* varied from 505 individuals/m² at 1950 h to 915 individuals/m² at 0615 h, but there was no diel trend in the abundance. The mean abundance for the sampling period was 693.6 individuals/m². *S. elegans* performed a distinct vertical migration (Fig. 3), but the interquartile range of 20-30 m in the vertical distribution shows that the population was not densely concentrated. However, during the period 2030-0430 h, more than 40 % of the individuals were found in the upper 20 m and less than 20 % in the 50-80-m depth stratum.

The total abundance of *A. digitale* ranged from 579 individuals/m² to 1044 individuals/m² (mean 842.9 ± 103.3 individuals/m²). The vertical migration was similar to that of *S. elegans*, but the medians of the depth distributions were on the average about 15 m deeper than for *S. elegans* (Fig. 3). From about

20 % to 40 % of the individuals were found in the upper 20 m between 2250 h and 0430 h.

C. finmarchicus was particularly abundant in the deeper part of Lindåspollene, more than 83 % was always caught deeper than 60 m (Table 1). There was a slight tendency for an upward migration at night, but this only applies to a small part of the population.

The biomass of the > 1000- μ m size-fraction ranged from 0.82 g/m² to 1.70 g/m² (mean 1.25 g/m², comprising on the average 59.2 % of the total zooplankton biomass (Table 2).

There were distinct diel patterns in the zooplankton biomass of the > 1000- μ m size-class at all depths, except at 75 m (Fig. 4). Thus, the highest biomass at 65 m depth occurred at noon, and at 5 m depth at midnight. The time for the occurrence of maximum biomass at intermediate depths indicated a nearly constant speed during the vertical migration.

2) The 500-1000- μ m size-fraction

This group was strongly dominated by *Pseudocalanus elongatus* BOECK, which was ranked among the four numerically dominant species in all the samples, regardless of depth (Table 3). *Calanus finmarchicus*

Table 1. Depth distribution (%) of *Calanus finmarchicus* at each sampling period in Lindåspollene, 2-3 October 1979.

Depth (m)	Hours										
	1350	1530	1730	1950	2250	0030	0230	0430	0615	0815	1030
5	0	0	0.1	-	0	6.2	3.5	0	0	0	0
15	0.3	0.1	0.1	1.2	2.2	2.5	1.7	0	0	0	0
25	0	0.2	0.3	0.9	1.3	2.6	1.6	2.6	0.3	0	0
35	0	0	0.1	0.9	1.0	1.9	0.9	1.9	1.3	0	0
45	0.1	0.9	0.1	2.9	1.2	0.9	1.4	1.3	1.7	0	0
55	3.3	1.3	2.9	2.5	1.6	2.6	3.4	6.9	3.4	7.5	-
65	27.4	23.9	18.2	15.2	16.9	40.0	22.3	33.6	15.3	16.2	-
75	68.9	73.6	78.2	76.4	75.8	43.3	65.2	53.7	78.0	76.3	-

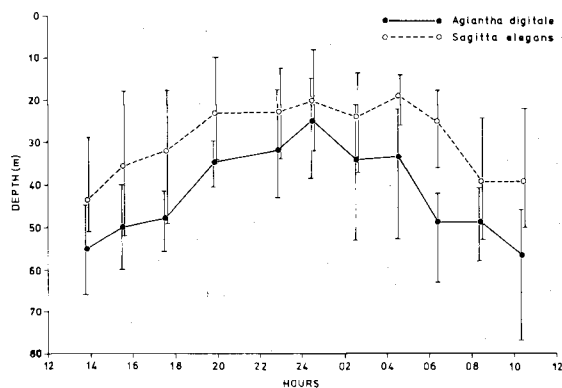


Fig. 3. Diel vertical distribution of *Sagitta elegans* and *Aglantha digitale* in Lindåspollene, 2-3 Oct. 1979. Median depths with interquartile ranges.

Table 2. Dry-weight in g/m^2 of zooplankton in Lindåspollene, 2-3 October 1979, with mean weight (\bar{X}), standard deviation (SD), and 95 % confidence intervals (C.I.) of the various size-classes.

Hours	180-500		Size-class (μm)		> 1000		Total g/m^2
	g/m^2	%	g/m^2	%	g/m^2	%	
1350	0.43	19.37	0.50	22.60	1.29	58.02	2.23
1530	0.47	30.36	0.25	16.45	0.82	53.18	1.54
1730	0.46	22.40	0.23	11.54	1.35	66.16	2.04
1950	0.45	28.01	0.22	13.57	0.93	58.42	1.59
2250	0.44	22.96	0.23	12.15	1.25	64.88	1.93
0030	0.62	34.54	0.28	15.68	0.90	49.78	1.80
0230	0.57	23.45	0.47	19.03	1.41	57.52	2.45
0430	0.64	29.10	0.37	16.76	1.19	54.14	2.20
0615	0.50	19.71	0.32	12.73	1.70	67.56	2.52
0815	0.45	16.88	0.56	20.96	1.66	62.15	2.67
1030	0.41	20.01	0.42	20.45	1.22	59.54	2.05
\bar{X}	0.50		0.35		1.25		2.09
S.D.	0.08		0.12		0.29		0.37
\pm C.I.	0.05		0.08		0.19		0.24

Table 3. Zooplankton ranked among the four numerically dominant taxa in the size-group 500-1000 μm in 87 samples in Lindåspollene, 2-3 October 1979.

Taxa	Rank	Number of samples				Total
		1	2	3	4	
<i>Pseudocalanus elongatus</i>	64	10	10	3		87
<i>Bradyidius similis</i>	9	14	18	7		48
<i>Calanus finmarchicus</i>	14	8	5	15		42
<i>Aglantha digitale</i>	2	4	9	10		25
<i>Acartia</i> spp.	3	5	2	1		11
<i>Sagitta elegans</i>	1	3	3	5		12
<i>Centropages hamatus</i>	2	-	3	-		5
<i>Temora longicornis</i>	-	1	1	1		3
<i>Evadne nordmanni</i>	-	-	1	-		1

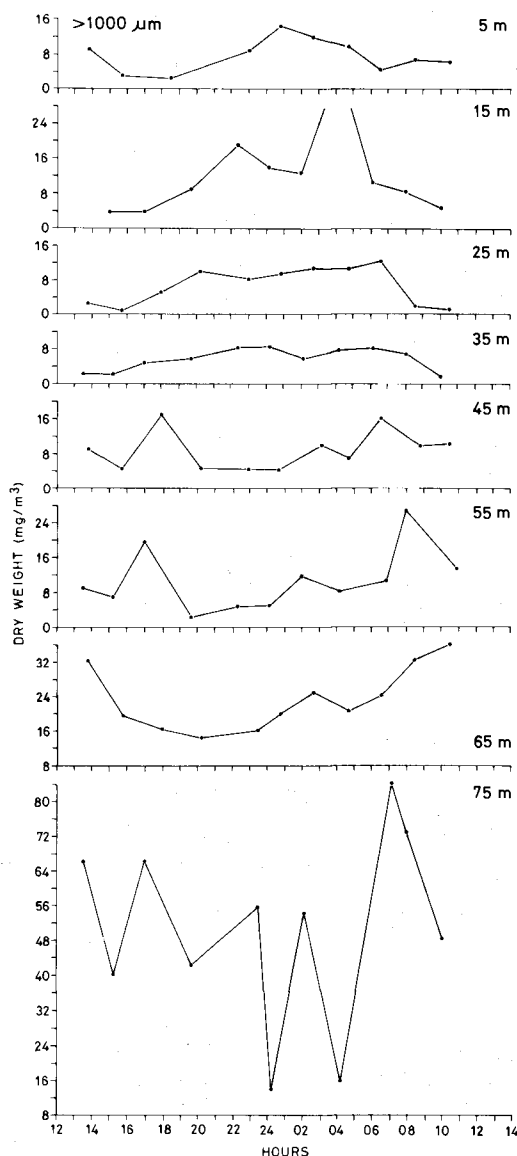


Fig. 4. Diel vertical distribution of the biomass (dry-weight) of the $> 1000\text{-}\mu\text{m}$ size-class of zooplankton in Lindåspollene, 2-3 Oct. 1979.

and *Bradyidius similis* (G.O. Sars) dominated in the samples deeper than 55 m, and *Acartia* spp. were particularly abundant in the uppermost layer. *Aglantha digitale* and *Sagitta elegans* were occasionally among the dominant species, particularly at intermediate depths.

The biomass of this size-fraction ranged from 0.22 g/m^2 to 0.56 g/m^2 (mean 0.35 g/m^2), comprising on the average 16.5 % of the total biomass (Table 2).

In the upper layers (5 m and 15 m) the highest biomass was recorded during late night or early

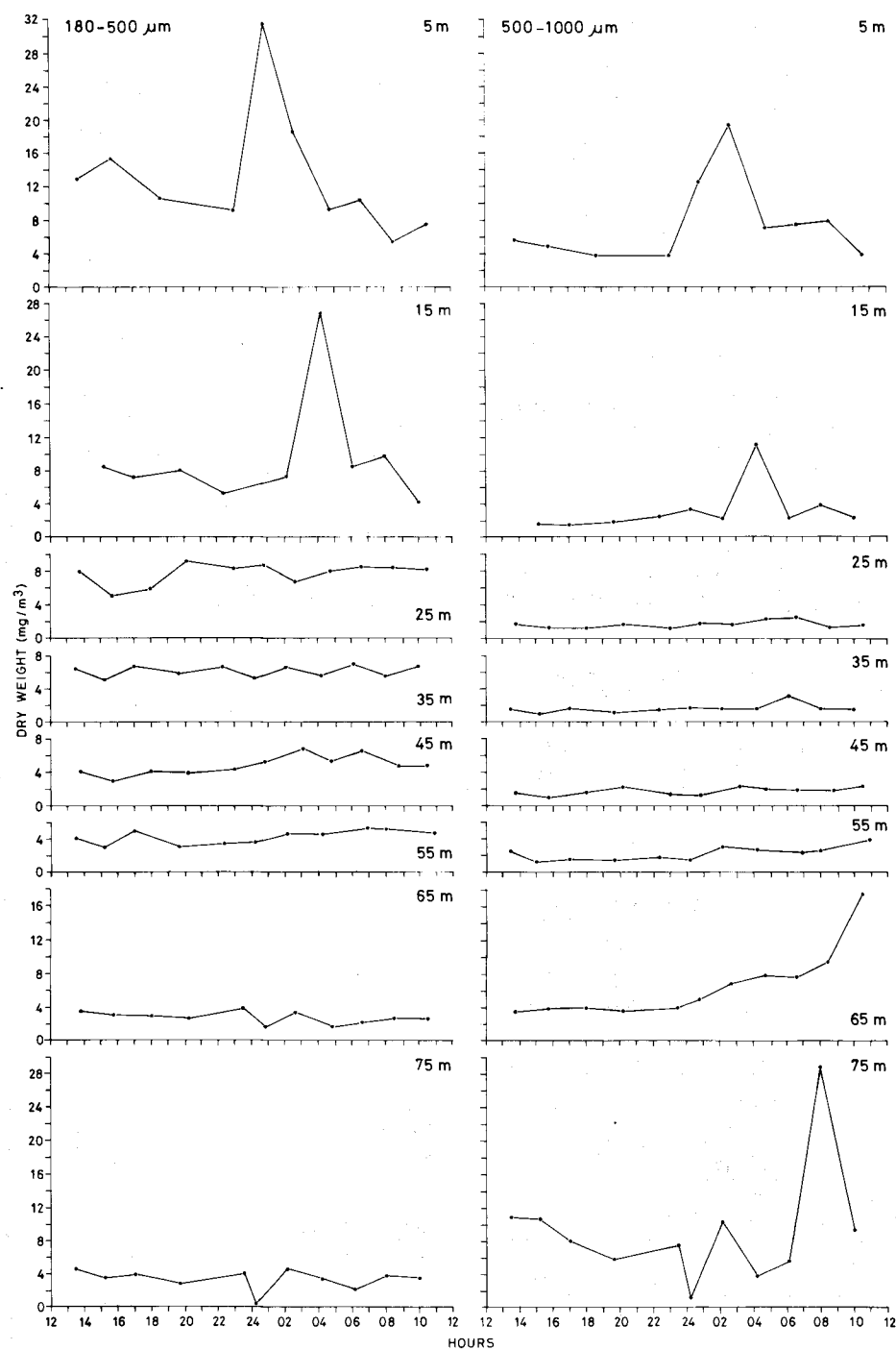


Fig. 5. Diel vertical distribution of the biomass (dry-weight) of the 180-500-µm and the 500-1000-µm size-classes of zooplankton in Lindåspollene, 2-3 Oct. 1979.

morning (Fig. 5), but there was no distinct diel variability in the biomass in the deeper strata. The biomass was highest at the top and at the bottom of the water column (Fig. 6), and the biomass at intermediate depths was low throughout the sampling period.

3) The 180–500- μ m size-fraction

This group of zooplankton organisms was strongly dominated by *Oncaea* spp. (Table 4). The species were among the numerically dominant species in 78 out of 87 samples, and in 71 samples it was ranked as number one in abundance. *Oithona similis* CLAUD and *Pseudocalanus elongatus* were ranked in a higher number of samples, but their ranking by abundance was significantly lower than that for *Oncaea* spp. The samples from 5 m depth were dominated by *Acartia* spp. and larvae of bivalves and gastropods.

Table 4. Zooplankton ranked among the four numerically dominant taxa in the size-group 180–500 μ m in 87 samples in Lindåspollene, 2–3 October 1979.

Taxa	Rank	Number of samples				Total
		1	2	3	4	
<i>Oncaea</i> spp.	71	3	2	2	2	78
<i>Oithona similis</i>	24	36	12	9	8	81
<i>Pseudocalanus elongatus</i>	8	13	28	32	8	81
<i>Acartia</i> spp.	3	4	1	–	–	8
Polychaeta, larvae	–	–	3	6	–	9
Bivalvia, larvae	–	1	2	7	–	10
Gastropoda, larvae	–	1	2	5	–	8
<i>Evadne nordmanni</i>	1	–	1	–	–	2
<i>Centropages hamatus</i>	–	1	1	–	–	2
<i>Temora longicornis</i>	1	–	–	–	–	1

The biomass of the 180–500- μ m size-fraction ranged from 0.43 g/m² to 0.64 g/m² (mean 0.50 g/m²), comprising on the average 24.2 % of the total biomass (Table 2). In the upper layers (5 m and 15 m) the highest biomass occurred during late night or early morning (Fig. 5), but no distinct diel trend could be detected at greater depths. The biomass decreased gradually from the 5-m layer downwards (Fig. 6), with a weak indication of an increase at 75 m depth.

12–13 May 1981

1) The > 1000- μ m size-fraction

This group was dominated by three species: *Sagitta elegans*, *Aglantha digitale*, and *Pleurobrachia pileus*. The number of *S. elegans* ranged from 150 individuals/m² at 1630 h to 415 individuals/m² at 0545 h (mean 289.3 \pm 59.4 individuals/m²). As indicated by the median depth distribution throughout the sampling period (Fig. 7), *S. elegans* carried out a distinct

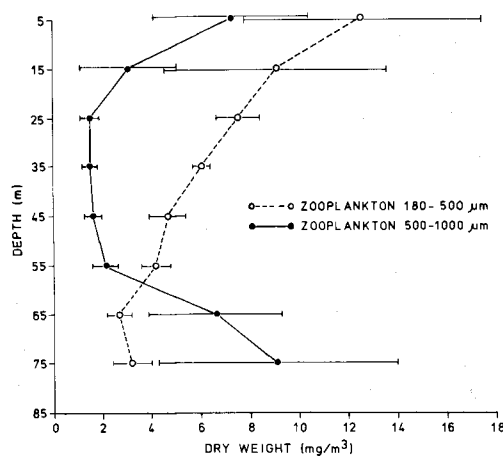


Fig. 6. Mean biomass (dryweight) with 95 % confidence intervals of the 180–500- μ m and the 500–1000- μ m size-classes of zooplankton in the various depth strata in Lindåspollene, 2–3 Oct. 1979.

diel vertical migration. The stock was strongly concentrated, more than 90 % of the individuals were always found within two neighbouring strata and the average interquartile range was 7.5 m. Less than 1 % of the individuals were found deeper than the 45 m sampling depth.

The number of *A. digitale* ranged from 203 individuals/m² at 0545 h, to 1014 individuals/m² at 0010 h (mean 619.9 \pm 189.4 individuals/m²). The species revealed a vertical migration similar to *S. elegans* (Fig. 7), but it remained 10–20 m deeper than the latter species. *A. digitale* was less densely concentrated than *S. elegans* but the average interquartile range was only 9.0 m. About 5 % of the individuals were caught deeper than 55 m.

The number of *P. pileus* ranged from 13 individuals/m² at 0010 h to 198 individuals/m² at 1630 h

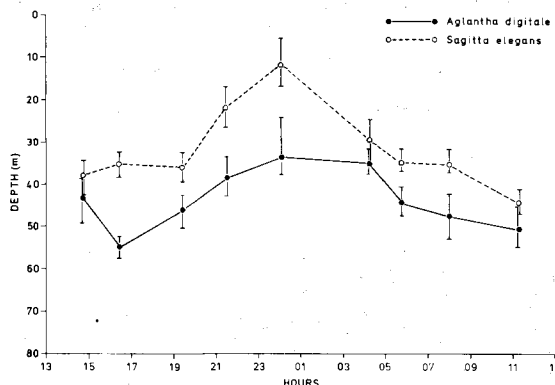


Fig. 7. Diel vertical distribution of *Sagitta elegans* and *Aglantha digitale* in Lindåspollene, 12–13 May 1981. Median depths with interquartile ranges.

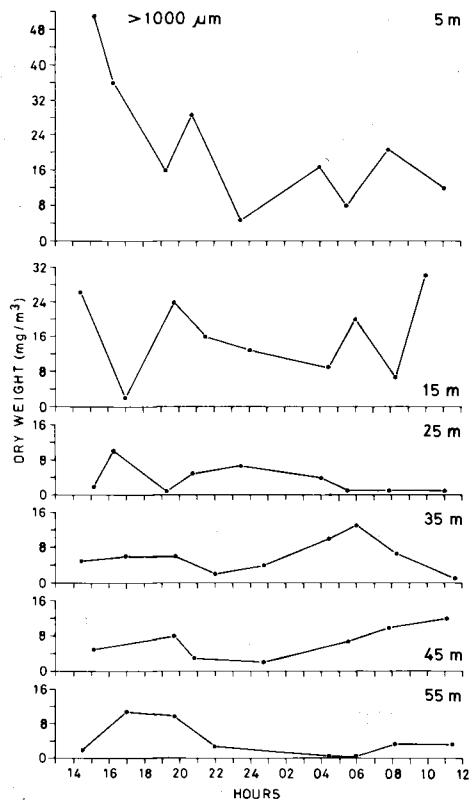


Fig. 8. Diel vertical distribution of the biomass (dry-weight) of the $> 1000\text{-}\mu\text{m}$ size-class of zooplankton in Lindåspollene, 12–13 May 1981.

(mean 74.7 ± 41.2 individuals/ m^2). The species occurred exclusively in the two upper strata. About 80 % of the total number of individuals were found in the samples from 5 m depth, but from 0010 h to

Table 5. Dry-weight in g/m^2 of zooplankton in Lindåspollene, 12–13 May 1981, with mean weight (\bar{X}), standard deviation (S.D.), and 95 % confidence intervals (C.I.) of the various size-classes.

Hours	180–500		Size-class (μm)		> 1000		Total
	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2
1450	0.81	40.70	0.25	12.56	0.93	46.73	1.99
1630	0.99	50.25	0.34	17.26	0.64	32.49	1.97
1930	0.98	50.52	0.31	15.98	0.65	33.51	1.94
2130	1.28	57.92	0.35	15.84	0.58	26.24	2.21
0010	1.17	65.36	0.31	17.32	0.31	17.32	1.79
0415	1.08	65.06	0.22	13.25	0.36	21.69	1.66
0545	0.90	51.43	0.35	20.00	0.50	28.57	1.75
0800	0.93	53.14	0.32	18.29	0.50	28.57	1.75
1115	0.84	44.44	0.31	16.40	0.81	42.86	1.96
\bar{X}	1.00		0.30		0.59		1.89
S.D.	0.15		0.04		0.20		0.17
\pm C.I.	0.11		0.03		0.15		0.13

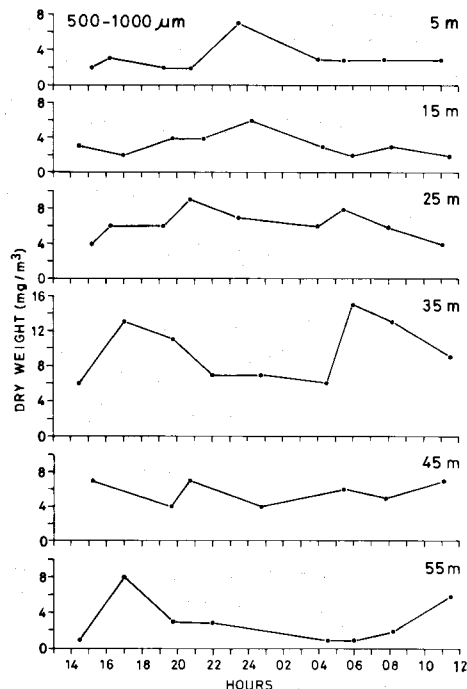


Fig. 9. Diel vertical distribution of the biomass (dry-weight) of the $500\text{--}1000\text{-}\mu\text{m}$ size-class of zooplankton in Lindåspollene, 12–13 May 1981.

0545 h more than 50 % were found in the 15-m depth layer.

The dry-weight of the $> 1000\text{-}\mu\text{m}$ size-fraction (Table 5) ranged from $0.31 \text{ g}/\text{m}^2$ at 0010 h to $0.93 \text{ g}/\text{m}^2$ at 1450 h (mean $0.59 \pm 0.15 \text{ g}/\text{m}^2$) comprising 31.2 % of the total biomass. The biomass was highly variable at all sampling depths, and no diel trend in the variability could be detected. The highest biomass was found in the two upper strata (Fig. 8), and the biomass in the two deepest strata was insignificant.

2) The 500–1000- μm size fraction

Acartia spp., *Evadne nordmanni* LOVÉN, *Centropages hamatus* (LILLJEBORG), and *Calanus finmarchicus* dominated in the upper layers of the water column (5 and 15 m), and *Pseudocalanus elongatus* and *Aglantha digitale* were particularly abundant in the deeper layers (Table 6).

The biomass of this size group ranged from $0.22 \text{ g}/\text{m}^2$ at 0415 h to $0.35 \text{ g}/\text{m}^2$ at 2130 and 0545 h (mean $0.30 \pm 0.03 \text{ g}/\text{m}^2$) comprising 15.8 % of the total biomass (Table 5). There was a weak tendency for a diel vertical migration (Fig. 9), but the major part of the biomass remained at 25 to 45 m depth throughout the sampling period (Fig. 10).

Table 6. Zooplankton ranked among the four numerically dominant taxa in the size-group 500–1000 μm in 45 samples in Lindåspollene, 12–13 May 1981.

Taxa	Rank	Number of samples				Total
		1	2	3	4	
<i>Pseudocalanus elongatus</i>	12	7	5	–	–	24
<i>Calanus finmarchicus</i>	–	8	12	–	–	31
<i>Acartia</i> spp.	14	2	3	–	–	19
<i>Aglantha digitale</i>	6	5	–	–	3	14
<i>Centropages hamatus</i>	–	6	4	–	1	11
<i>Evadne nordmanni</i>	2	2	2	–	–	6
<i>Temora longicornis</i>	–	2	3	–	1	6
<i>Bradydium similis</i>	–	–	2	–	4	6

3) The 180–500- μm size-fraction

This group was dominated by *Oithona similis*, *Pseudocalanus elongatus*, and *Oncaea* spp. (Table 7). *Evadne nordmanni*, *Acartia* spp., and larvae of bivalves were particularly abundant in the upper depth strata.

The biomass of the 180–500- μm size group ranged from 0.81 g/m^3 at 1450 h to 1.28 g/m^3 at 2130 h (mean $1.00 \pm 0.15 \text{ g}/\text{m}^3$) comprising 52.9 % of the total biomass. There was a distinct diel vertical migration in the upper 35 m of the water column (Fig. 11). About 70 % of the biomass was present in the two upper depth strata (Fig. 10).

12–13 June 1981

The composition of the zooplankton

The zooplankton $> 75 \mu\text{m}$ was identified and counted and the 20 major taxa are listed in Table 8. Copepoda nauplii and larvae of bivalves were particularly abundant, contributing more than 52 % of the total number of organisms/ m^3 .

Temora longicornis (MÜLLER) and *Paracalanus parvus* (CLAUS) revealed a weak ascending tendency at night, but there was no change in the modal depths for any of the 20 taxa during the 24 hours sampling period. In Table 8 the taxa have been arranged in accordance with increasing mean modal depth. *Podon* spp., Appendicularia indet., *Evadne*

Table 7. Zooplankton ranked among the four numerically dominant taxa in the size-group 180–500 μm in 45 samples in Lindåspollene, 12–13 May 1981.

Taxa	Rank	Number of samples				Total
		1	2	3	4	
<i>Oithona similis</i>	19	9	6	–	–	34
<i>Pseudocalanus elongatus</i>	9	2	13	5	–	29
<i>Oncaea</i> spp.	7	7	4	–	–	18
Bivalvia, larvae	1	11	4	–	1	17
<i>Evadne nordmanni</i>	–	6	6	1	–	13
<i>Temora longicornis</i>	–	–	1	6	–	7
Polychaeta, larvae	–	–	1	6	–	7
<i>Acartia</i> spp.	–	–	1	3	–	4

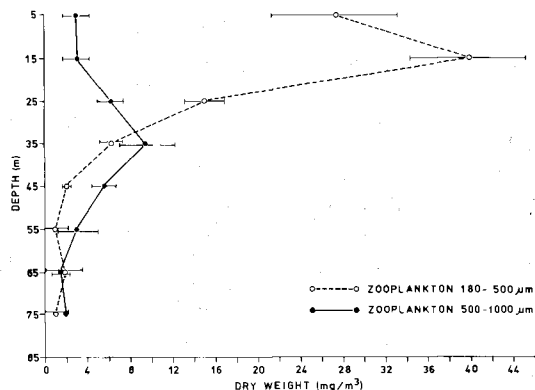


Fig. 10. Mean biomass (dry-weight) with 95 % confidence intervals of the 180–500- μm and the 500–1000- μm size-classes of zooplankton in the various depth strata in Lindåspollene, 12–13 May 1981.

nordmanni, *Acartia longiremis* (LILLJEBORG), *Paracalanus parvus*, and *Centropages hamatus* were concentrated in the upper 5 m of the water column, whereas *Oncaea* spp. and Polychaeta larvae occurred with their highest abundance below 20 m depth. Copepoda nauplii were abundant at all depths above 10 m, and *Oithona similis* was fairly abundant in the

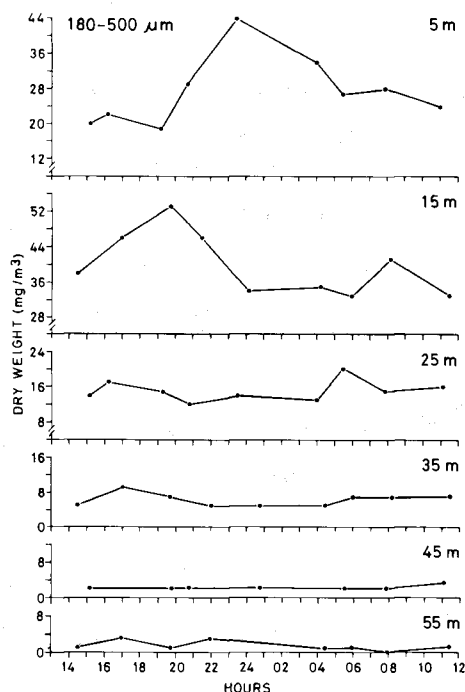


Fig. 11. Diel vertical distribution of the biomass (dry-weight) of the 180–500- μm size-class of zooplankton in Lindåspollene, 12–13 May 1981.

entire water column above 35 m depth. It is noteworthy that there was practically no overlap in the vertical distribution of *Pseudocalanus elongatus* and *Paracalanus parvus*.

The total number of organisms was particularly high at 10 m depth, but also the samples from 0.5, 2, and 5 m depths showed densities of about 25 000 individuals/m³. There was a distinct drop in the total number of organisms from 10 m to 15 m depth, but there was an increase again in 20 and 25 m depth due to the high number of *Oncaea* spp. at these depths.

The biomass

The total dry-weight of the zooplankton on the 0–45-m water column was 2.85 g/m², of which the 75–250- μ m size-class contributed 1.76 g/m² (60.5 %) and the > 250- μ m size-class contributed 1.09 g/m² (39.5 %). Both size-classes had their maximum biomass at 10 m depth, and lesser maxima at 20 and 25 m depth (Fig. 12).

The depth distribution of total biomass and total number of organisms showed considerable similarity (Fig. 13), but the figure indicates a shift in the ratio of the two quantities below 10 m depth. The mean individual dry-weight of the organisms at the various sampling depths was:

0.5 m	2 m	5 m	10 m	15 m
1.3 μ g	1.3 μ g	1.6 μ g	1.7 μ g	6.2 μ g
20 m	25 m	35 m	45 m	
4.6 μ g	3.7 μ g	20.4 μ g	90.9 μ g	

The high individual dry-weights at 35 m and 45 m, which correspond to the weight of adult *Pseudocalanus* (HASSEL 1980) or *Calanus* copepodite stage IV/V (WILLIAMS & LINDLEY) cannot be explained with reference to the small species in Table 8. However, the explanation may be that the deeper samples contained some large but rare forms which were excluded by the sub-sampling technique, or that the samples from these depths contained detritus or remnants of animals which were not counted.

DISCUSSION AND CONCLUSIONS

The species composition of the zooplankton in Lindåspollene did not change much from October 1979 to May 1981. The eight dominant species in the 500–1000- μ m size-class in 1981 were among the nine dominant species in 1979, but their order of importance had changed (rank correlation between the two data sets $r_d = 0.47$). Similarly, the eight dominant species in the 180–500- μ m size-class in 1979 were among the ten dominant species in 1981 (rank correlation $r_d = 0.64$). The major copepod taxa were *Pseudocalanus elongatus*, *Oithona similis*, *Oncaea* spp., *Calanus finmarchicus*, *Acartia* spp., *Centropages hamatus*, and *Temora longicornis*. Important non-copepod taxa were *Sagitta elegans*, *Aglantha digitale*, *Evadne nordmanni*, *Pleurobrachia pileus*, Polychaeta larvae, Mollusca larvae, and appendicularians. Most of these species or genera have been listed as the major taxa in coastal marine systems from many areas of the North-Atlantic

Table 8. Mean abundance (individuals/m³) of the major zooplankton taxa during the 24 hours sampling period in Lindåspollene, 10–11 June 1981.

Taxa	Sampling depths (m)									Total
	0.5	2	5	10	15	20	25	35	45	
<i>Podon</i> spp.	334	333	85	0	0	0	9	1	0	1 460
Appendicularia indet	2 162	1 865	712	144	24	0	43	9	1	10 359
<i>Evadne nordmanni</i>	5 309	4 351	1 548	1 449	1 083	230	123	54	13	36 379
<i>Acartia longiremis</i> , juv.	489	560	150	22	7	16	5	7	0	2 616
<i>Acartia longiremis</i> , ad.	150	229	226	0	36	58	18	4	1	2 280
<i>Paracalanus parvus</i> , ad.	50	102	121	0	0	0	3	2	0	841
<i>Paracalanus parvus</i> , juv.	535	760	1 697	18	0	0	0	1	0	9 791
<i>Centropages hamatus</i> , juv.	130	252	407	0	0	6	0	6	0	2 555
<i>Centropages hamatus</i> , ad.	4	13	44	0	0	0	3	0	0	250
Copepoda nauplii	13 123	16 806	18 290	18 226	783	237	176	84	13	227 560
<i>Oithona similis</i> , juv.	837	1 865	2 370	6 631	1 069	368	358	69	17	59 117
<i>Oithona similis</i> , ad.	77	123	539	5 944	1 381	1 307	1 271	478	25	60 471
<i>Temora longicornis</i> , ad.	19	89	303	1 008	20	6	12	9	4	6 950
<i>Temora longicornis</i> , juv.	0	0	25	3 241	23	0	11	3	4	16 576
Bivalvia, larvae	108	142	1 262	40 410	1 297	521	111	138	106	220 484
<i>Pseudocalanus elongatus</i> , juv.	0	12	12	5 305	169	197	35	21	7	29 116
<i>Pseudocalanus elongatus</i> , ad.	0	0	0	664	209	366	213	9	2	10 991
<i>Oncaea</i> spp., juv.	5	10	0	30	1 348	7 636	6 809	35	21	96 722
<i>Oncaea</i> spp., ad.	43	51	371	1 168	886	5 377	7 244	90	20	94 399
Polychaeta, larvae	12	13	14	32	103	259	821	341	8	20 547
Total number of individuals	23 387	27 576	28 176	84 292	8 437	16 584	17 256	1 361	242	

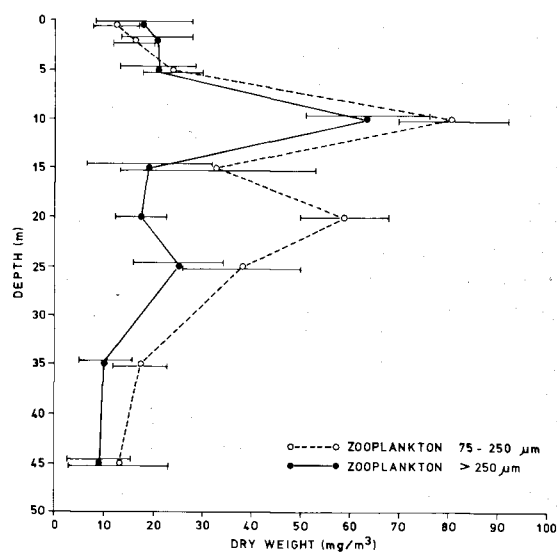


Fig. 12. Mean biomass (dry-weight) with 95 % confidence intervals of the $> 250\text{-}\mu\text{m}$ and the $75\text{-}250\text{-}\mu\text{m}$ size-classes of zooplankton in the various depth strata in Lindåspollene, 10-11 June 1981.

region (e.g. WIBORG 1944; MARSHALL 1949; DIGBY 1950; DEEVEY 1960; McLAREN 1969; KOSLOSOVA 1975; HERNROTH & ACKEFORS 1979). Therefore, there is now considerable information about the role these species play in the dynamics of pelagic ecosystems in coastal waters.

Previous studies of zooplankton in Lindåspollene (ELLINGSEN 1973; ELLERTSEN 1975; MAGNESEN 1982) have recorded the same species as dominants with the addition of *Paracalanus parvus*. The latter species is, however, a typical summer species in Lindåspollene (ELLINGSEN, loc. cit.), and in the present study it was fairly abundant in June 1981 (Table 8).

The role of *Calanus finmarchicus* in Lindåspollene is particularly interesting. The species was listed among the important species in 1970 (DAHL & al. 1973), in 1977 (McLEAN 1979), and in 1979 (AKSNES 1981; MAGNESEN 1982), and these years were characterized by massive renewal of the bottom water in the polls (LIE & DAHL 1981). It seems therefore that *C. finmarchicus* is introduced into Lindåspollene with water from the surrounding fjord system, but the species is not able to maintain itself within the polls. Aksnes & Magnesen (unpubl.) show that the species had a normal population development during a year of bottom-water renewal. Only one spawning per year was observed, whereas *C. finmarchicus* in West-Norwegian fjords spawns two to four times per year (RUNNSTRÖM 1932; GUNDERSEN 1953; WIBORG 1954; LIE 1967; MATTHEWS & al. 1978).

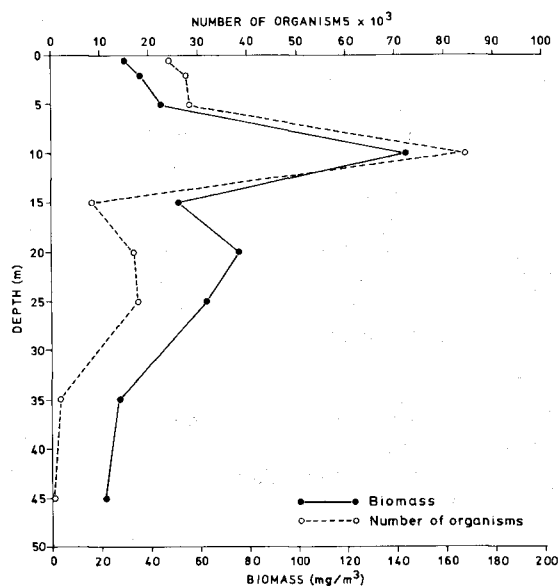


Fig. 13. Mean biomass (dry-weight) and mean abundance of zooplankton in the various depth strata in Lindåspollene, 10-11 June 1981.

Some *C. finmarchicus* are found in the surface waters of Lindåspollene also during spring-time of years without bottom-water renewal (ELLINGSEN 1973; ELLERTSEN 1975; McLEAN 1979). These are nauplii and young copepodite stages brought in with the tidal currents from the surrounding fjord system, but the species disappears from the zooplankton community during summer. Thus, although *C. finmarchicus* was among the most abundant species in May 1981 (Table 7), it was not recorded among the 20 major taxa in June 1981 (Table 8).

There were distinct differences among the size-classes of zooplankton in Lindåspollene with regard to vertical distribution and vertical migration. Thus, the $180\text{-}500\text{-}\mu\text{m}$ size-class in October 1979 and May 1981 was particularly abundant in the upper 15 m of the water column, and there was a diel trend in the distribution indicating vertical migration within this layer (Figs 5 and 11). The observations from June 1981 (Table 8) show that there were discontinuities within the upper layer, with different species inhabiting specific depths, but no diel migration could be ascertained. In a study of neuston from Lindåspollene ELLERTSEN (1975) found diel vertical migration within the upper 90 cm of the water column for some species (e.g. *Evadne nordmanni*, *Acartia* spp., *Centropages hamatus*, *Paracalanus parvus*), but not for others (e.g. juveniles of *Acartia* spp., *Oithona similis*, copepod nauplii). However, for the total number of organisms there was no significant difference between day and night samples.

In a review of zooplankton literature BANSE (1964) showed that salinity gradients of more than 0.2–0.3 ‰ per 10 m appears to prevent vertical migration of small copepods, and that the species of zooplankton in water masses with strong salinity gradients will remain within very restricted depth strata or salinity gradients. This view is supported by the data from June 1981 which showed no vertical migration and a strong vertical separation of the various species, and the salinity gradient in the upper 20 m was then about 0.1 ‰/m. On the other hand, the 180–500- μ m size-class which was dominated by small copepods (Table 8) displayed considerable diel vertical variability in biomass in the upper 20 m in October 1979, when the salinity gradient was about 0.3 ‰/m.

The 500–1000- μ m size-class of the zooplankton was distributed somewhat deeper than the 180–500- μ m size-class. In October 1979 about 45 % of the biomass was found in the deepest 20 m of the water column, and in May 1981 about 50 % of the biomass was found deeper than 40 m, i.e. in water masses with less than 0.5 ml O₂/l. There was a diel vertical migration in the upper 40 m of the water column, and the day-time biomass at 35 m was about twice as high as the night-time biomass (Fig. 9).

A comparison of the > 1000- μ m size-class shows that the biomass depth distribution and its diel pattern were quite different in October 1979 and in May 1981. In October 1979 about 65 % of the biomass was concentrated in the deepest 20 m of the water column, but a clear vertical migration could be ascertained above 65 m depth (Fig. 4). In May 1981 the major part of the biomass was concentrated in the upper 20 m of the water column, and there was no distinct vertical migration (Fig. 8). The difference in the distribution of the biomass was particularly related to the reduction of *Calanus finmarchicus*, which was a major contributor to the biomass in 1979 (Aksnes & Magesen unpubl.). The other two major species in the > 1000- μ m size-class, *Sagitta elegans* and *Aglantha digitale*, were also reduced during the same time-span, by 60 % and 25 % respectively, but the depth distribution and the vertical migration of these species were remarkably similar on the two sampling dates, in spite of the change in the hydrographic conditions (Fig. 2). However, the range in the depth distribution was considerably narrower in 1981, as demonstrated by the small interquartile ranges (Fig. 7).

PEARRE (1973) in a similar study of the vertical distribution of *Sagitta elegans* in Saanich Inlet, B.C., concluded that the magnitude of vertical migration was correlated with size and that the mean depth distribution increased with the size of the animal.

The *S. elegans* population in Lindåspollene displayed a synchronous and rather cohesive (sensu PEARRE 1979) diel vertical migration. Thus, in October 1979 the average proportion of the population caught deeper than 45 m was 9 % during the period \pm 4 hours from midnight compared to 25 % for the rest of the sampling period, and 46 % were caught in the upper 20 m at night compared to 22 % during the rest of the sampling period. During the migration about 20 % of the population crossed a range of temperatures from about 4 to 10° C and a salinity range from about 31.5 ‰ to 26.5 ‰. In May 1981, probably because of the poor oxygen conditions (Fig. 2), only about 1 % of the individuals was caught in the deepest 30 m of the water column. At midnight only 6 % of the population were found at 35 m depth or deeper, and 88 % were distributed in the upper 20 m of the water column. From 1450 h to 1930 h on 10 May only four individuals were caught in the upper 20 m, and from 0545 h to 1115 h on 11 May none. This could be explained by light-aided net avoidance, but the concurrent increase in the abundance of *S. elegans* in the deeper layers opposes the explanation. In a review of the zooplankton literature CLUTTER & ANRAKU (1968) found no observation in support of light-aided net avoidance. One must therefore conclude that at midnight about 90 % of the *S. elegans* population had moved into the upper 20 m layer, but the gradients in temperature and salinity were considerably less than in October 1979 (Fig. 2). It should be noted that *S. elegans* in May 1981 spent 14 out of 24 hours in water masses with less than 0.5 ml O₂/l.

In a study of the diel vertical migration of zooplankton in Oslofjorden HANSEN (1951) found a distinct diel vertical migration of *Aglantha digitale* but the species did not cross a 7 to 10° C temperature range and a 33 to 20 ‰ salinity range during its nocturnal ascent. Similarly, ARAI & FULTON (1973) demonstrated diel vertical migration of *A. digitale* in Saanich Inlet. In Lindåspollene both in October 1979 and in May 1981 the *A. digitale* population performed a synchronous and rather cohesive diel vertical migration with median depths ranging from 50–55 m at day-time to 25–35 m at night (Figs 3 and 7). At night (\pm 4 hours from midnight) the proportion of the population recorded in the deepest 30 m of the water column in October 1979 was 18 % compared to 50 % during the rest of the day, and in the upper 20 m the proportion was 25 % at night and 0 % during the rest of the day. At midnight 12 % of the population was found in the sample from 5 m depth. This shows that about 25 % of the *A. digitale* population must have crossed a considerable range of temperature and salinity during its vertical migra-

tion (Fig. 2). In May 1981 only 0.3 % of the individuals were caught in the deepest 20 m of the water column. At midnight 18 % of the population was located in the upper 20 m, but no individuals were caught in the 5 m sampling depth. At day-time 64–99 % of the individuals were recorded in the 45 m and 55 m sampling depths.

In studies of zooplankton vertical migration based on samples from discrete depths and with rather long time intervals between samplings, there is a possibility of constantly missing the peaks of the vertical abundance distribution and therefore significant vertical migration may go undetected because of low numbers and high variance. However, with 10-m depth intervals and about 2–3 hours time intervals as in the present study this seems highly unlikely, and the results for most of the categories studied in October 1979 and May 1981 indicate that the vertical migration patterns were detected. This is particularly true for the species populations studied (i.e. *Sagitta elegans* and *Aglantha digitale*) but the picture is less clear for the size-classes, which appear to have a 'migrating mode' and a 'stationary mode' (PEARRE 1973). Naturally, as the size-classes are composed of different species, each with its own diel pattern of distribution, one cannot expect the same clearly demonstrated vertical migration as for individual species. However, the results in the present investigations are sufficiently encouraging to pursue the research on the diel and seasonal vertical distribution of size-classes of zooplankton in Lindåspollene.

PEARRE (1973) argues that discrete, stratified samples cannot be used to detect vertical migration if individuals in the population have opposite migration directions at the same point in time. Discrete samples from a population with such migration behaviour, i.e. complete asynchronous behaviour, would result in a bimodal distribution with maxima near the top and the bottom of the water column (PEARRE 1979). Such distribution was found for the 500–1000- μ m size-fraction in Lindåspollene in October 1979 (Fig. 6). However, the qualitative composition of the zooplankton was not the same at all depths, thus *Calanus finmarchicus* and *Bradyidius similis* dominated in the deepest part, *Pseudocalanus elongatus* at intermediate depths, and *Acartia* spp. in the uppermost layer. Therefore, asynchronous migration in the entire water column is not very likely, but on the basis of the discrete, stratified samples in the present investigation one cannot conclude whether this phenomenon takes place within the 10-m depth strata or not. Studies are presently undertaken to test this by the use of zooplankton traps (VASS & al. 1981).

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