FINE-SCALE VERTICAL STRUCTURE OF A SUMMER ZOOPLANKTON COMMUNITY IN LINDÅSPOLLENE, WESTERN NORWAY

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During June 1981 zooplankton composition was investigated in samples collected with Clarke-Bumpus plankton samplers from 0.5, 2, 5, 10, 15, and 20 m depths. Most taxa were limited to specific depth zones. Diel variations in vertical range were observed for the majority of species inhabiting the uppermost part of the water column, whereas diel variations in median depth could be detected for only 3 out of 11 taxa. These were adult *Temora longicornis* and adult *Pseudocalanus elongatus,* which ascended during the night, and *Evadne nordmanni* which tended to descend during the night. A similarity analysis divided the samples into a surface layer group (0.5, 2, and 5 m) and a deeper group (10, 15, and 20 m) separated by the thermocline. The composition and distribution of the zooplankton living deeper down changed little with time, in contrast to the surface-dwelling zooplankton which was more variable. Multivariate analysis indicated that two factors were responsible for 79 % of the total variance in the species abundance data. In a stepwise multiple regression analysis, temperature and primary production were found to account for more than 75 % of the variations in the factors.

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INTRODUCTION

Many pelagic environments consist of a complex mixture of water-masses with different physical, chemical and biological characteristics. This makes studies of vertical structure and temporal changes difficult. Time series data obtained in a fluctuating environment can give a false impression of rapid changes in biological structure and processes. Land-locked fjords or polls (MATTHEWS & HEIMDAL 1980) are unique environments, being in many respects the marine equivalents of lakes. Their containment and restricted water exchange with the sea outside result in a fairly stable hydrographical regime. This represents a valuable research asset that facilitates detailed studies of vertical structure and temporal changes of the plankton.

A proper understanding of the vertical distribution of zooplankton is necessary in order to understand the functional properties of pelagic systems (LONGHURST 1981). Accordingly, there has been a growing interest in recent years in studies of vertical distribution, as reflected in an abundant literature (for example ORTNER & al. 1980; HERMAN & al. 1981; SMITH & al. 1981; HOPKINS 1982; HUNTLEY & BROOKS 1982; KRAUSE & TRAHMS 1982; BIRD 1983; CUMMINGS 1984; FIEDLER 1983; HERMAN 1983; HERMAN & PLATT 1983; OHMAN & FROST 1983; SOUTHWARD & BARRETT 1983; TURNER & DAGG 1983; ALCARAZ 1984; LONGHURST & al. 1984; SA-MEOTO 1984). Despite this considerable effort, knowledge of the factors which govern the vertical organization of zooplankton is still fragmentary.

The area for this study is Lindåspollene in western Norway (DAHL & al. 1973). This poll system has been the subject of extensive biological investigations during the last 15 years (for example LIE & al. 1983; SKJOLDAL & al. 1983). The water column in Lindåspollene is strongly stratified during summer. The input of nutrients into the euphotic zone from the deeper water is therefore restricted and recycling provides the major source of nutrients for the primary producers (LÄNNERGREN 1976; SKJOLDAL & al. 1983). Grazing and excretory activities of zooplankton attain special importance in regeneration of nutrients in such a stable water column.

Studies on the vertical distribution of size-fractions in the zooplankton in Lindåspollene have revealed highly stratified biomass distributions (LIE & al. 1983; MAGNESEN 1989a), and the diel variation in vertical distribution varied with size-class, as well as with season (MAGNESEN 1989b). Vertical stratification was also found by SKJOLDAL & al. (1983) for various zooplankton taxa in the uppermost 11 m of the water column in Lindåspollene.

The present study describes the vertical organization of the zooplankton community in the euphotic zone of Lindåspollene during a 23-day period in summer. Specifically, we compared the variability
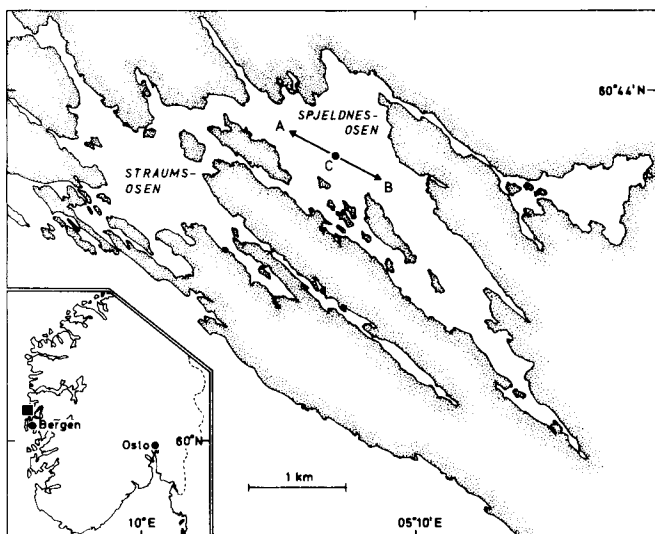
Fig. 1. Sampling location in Lindåspollene. A–B = cruise track, C = hydrographic station.

in day-time distributions over this period with the variability over a 24-hour cycle. Our study was part of a larger investigation on summer plankton dynamics that also encompassed nutrients, phytoplankton, bacterioplankton, and microzooplankton. We have used some of these data here, particularly chlorophyll and rates of primary production, as 'environmental' variables for comparison with the distributional patterns of zooplankton taxa.

MATERIAL AND METHODS

Zooplankton sampling and analysis

Zooplankton was sampled from the central part of Spjeldnesosen, the mid-basin of Lindåspollene (Fig. 1). The samples (Table 1) consist of a mid-day series (7, 10, 16, 22, and 29 June 1981), and a diel series (10 to 11 June 1981). On each sampling occasion three Clark-Bumpus samplers, equipped with 75 μm nets, were towed between anchored bouys. The samplers were set at 2, 10, and 20 m depth and towed in one direction, and on the return track at 0.5, 5, 15 m depth. The mid-day samples were usually collected between high- and low-water, but on 29 June the sampling started one hour prior to high tide (Table 1). During the diel investigation low tide occurred in the afternoon and high tide late in the evening (Table 1). The tidal amplitude in Lindåspollene is, however, usually less than 0.3 m.

The samples were always collected in calm weather. Sometimes the sky was cloudy, but no light measurements were taken. Earlier records indicate good correspondence between the irradiance in Lindåspollene and the official irradiance records for Bergen (Skjoldal & al. 1983). We have therefore used the official records (Anon. 1982), and the hourly values of illumination is given in Table 1.

Each sample was divided in two with a modified Folsom splitter (Motoda 1959) and one portion was preserved

Table 1. Depths, time of high and low tide, and hourly values of daylight illumination (KLXH) during the mid-day and the diel sample series in Lindåspollene in June 1981. Hours refer to local time (GMT plus 2 hours).

Time		Depth (m)						Tide		Light
		0.5	2	5	10	15	20	high	low	
Mid-day series										
7 June	1515	+	+	+	+	+	+	1810	1154	40.1
10 »	1210	+	+	+	+	+	+	0824		24.3
16 »	1145	+	+	+	+	+	+	0734	1354	23.7
22 »	1310	+	+	+	+	+	+	1734	1121	56.3
29 »	1130	+	+	+	+	+	+	1201		97.3
Diel series										
10 June	1210	+	+	+	+	+	+	0824		24.3
	1510	+	+	+	+	+	+		1504	25.2
	1915	+	+	+	+	−	+			2.8
	2220	+	+	+	+	+	+	2123		0.0
11 »	0155	+	+	+	+	+	+			0.0
	0450	+	+	+	+	+	+		0331	6.6
	0840	+	+	+	+	+	+	0940		42.9

with a neutralized formalin solution. The other portion was used for determination of dry weight (not reported here). The preserved samples were divided with the Folsom splitter, and the organisms in 1/4 to 1/128 (usually 1/16 or 1/32) fraction were identified and counted. This procedure gives a fair representation of the numerically dominant taxa, but rarely occurring taxa were lost.

Description of vertical distribution

Median depth and depths of the first and third quartiles of the vertical distribution were calculated as the depths above which 50, 25, and 75 % of the individuals, respectively, were found. Changes in the median depth are suitab-

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le for detecting synchronous, but not asynchronous migrations (Pearre 1979). Variations in the vertical range, however, may indicate asynchronous migrations within a population.

We have calculated a vertical-range index, according to the niche-breadth index of Pianka (1973). The index is used as a measure of 'mean number of depths' at which a species occurred, and was calculated as:

$$\text{vertical-range} = \frac{1}{\sum\limits_{i=1}^{n} p_i^2}$$

where p_i is the proportion of a species' abundance at a specified depth i. An index value of 1.0 means that all individuals of the species were found in one depth stratum, while a value of 6 means that a species has equal abundances at all six depths. Because of the unequal spacing between the sampling depths in this study, the vertical range index is only appropriate when comparing a species' vertical distribution through time, and not for comparing depth distributions between species.

Changes in median depth and vertical-range influence the overlap structure within the zooplankton community. We have used a niche-overlap measure, the α-index of Pianka (1973), to estimate the distribution overlap of one species with all the other species. This was calculated by averaging the overlaps between a given species and all other species. The overlap between species j and k is given by:

$$\alpha_{j,k} = \frac{\sum\limits_{i=1}^{n} p_{i,j} \cdot p_{i,k}}{\sqrt{(\sum\limits_{i=1}^{n} p_{i,j}^2 \cdot \sum\limits_{i=1}^{n} p_{i,k}^2)}}$$

where $p_{i,j}$ and $p_{i,k}$ are the proportional abundances of species j and k, respectively at depth i. This measure was used to see how alterations in individual species distributions over time affected the overlap between the species. A value of zero means no overlap with any other taxon, and a value of 1 means maximum overlap with all other taxa.

Multivariate analysis

Similarity between samples was described by cluster analysis. The analysis was performed on abundance data of 11 taxa (juveniles and adults combined) at six depths, from day-time samples collected on 7, 10, 11, 16, 22, and 29 June. Prior to clustering the abundances were root-root transformed, following recommendation by Field & al. (1982). Dendrogram construction was based on Bray-Curtis similarity index and a group-average sorting technique.

A factor analysis, described in the BMDP statistical software package (Dixon 1981), was used to estimate factors for the community composition and vertical distribution. Factor extraction was based on a correlation matrix subjected to principal component analysis after transformation (y = log (x + 1)) of the variables. The resulting first three factors were subjected to varimax factor rotation. After rotation the factor loadings were subjected to a stepwise multiple regression analysis to evalute possible correlations with environmental and biological variables (Skjoldal & al., unpubl. results).
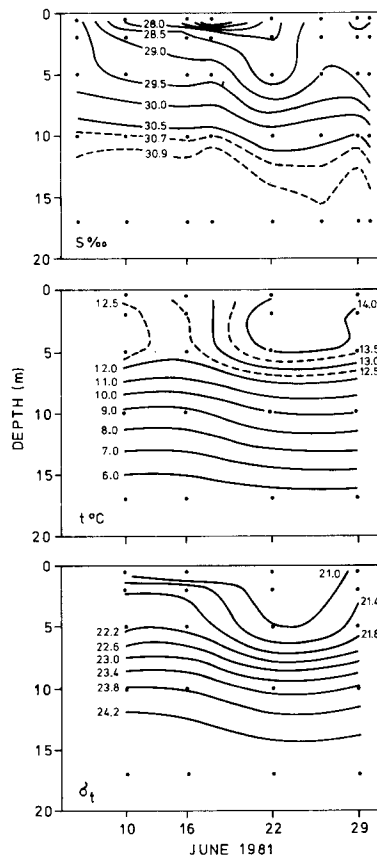

Fig. 2. Vertical distribution of salinity, temperature, and density in Spjeldnesosen during June 1981.

RESULTS

Hydrography

The surface salinity varied between 25.10 and 30.07 ‰ during the investigation (Fig. 2). At 10 m depth the salinity was about 30.5 ‰. A slight decrease in salinity occurred during the sampling period. The surface temperature increased from 12.3 to 14.5° C from 10 to 29 June (Fig. 2), while the increase at 5 and 10 m was about 1° C. Density calculations revealed the steepest density gradient between 5 and 10 m depth (Fig. 2). In the upper 5 m the salinity was low and the temperature was high on 22 June, and the water was fairly homogeneous. The oxygen conditions in June 1981 were characterized by a well aerated water column down to 25 m, but with low or no oxygen (< 0.2 ml/litre) below 30 m (Lie & al. 1983).
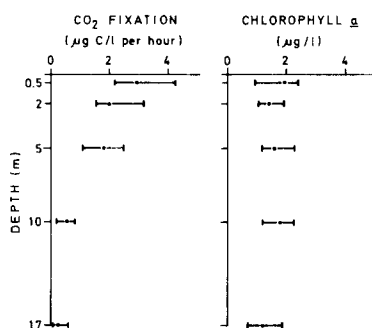
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Fig. 3. Vertical distribution of primary production (C-14 fixation) and chlorophyll a in Spjeldnesosen, June 1981. Mean and range of variation for observations on 7, 10, 12, 15, 23, and 26 June (H.R. Skjoldal, unpubl. results).

Chlorophyll a and carbon fixation

The rate of carbon fixation showed a general decrease with increasing depth, from about 1.5 $\mu C/$ litre per hour at 0.5 m to 0.03–0.3 μg C/litre per hour at 17 m (Fig. 3). Chlorophyll a, however, was distributed more uniformly in the water column with typical concentrations of 1–2 μg/litre (Fig. 3).

Vertical distribution of zooplankton

The vertical distribution of the taxa at the start of the investigation (7 June) revealed a tendency for each taxon to occur with maximum abundance within a narrow depth-range (Fig. 4). The median depths and interquartile distances were quite similar on 7 and 29 June (Fig. 5), suggesting that the vertical distributions of the different species changed little during the investigation period. The same overall picture was also obtained for the dates in between (not shown). This indicates a rather persistent pattern of vertical distribution throughout the period.

Mid-day series

The median depth for most taxa changed by 2 to 3 m during the mid-day series (Table 2). The smallest variation was found for *Temora longicornis* (Müller). This species was found almost exclusively at 10 m, however, and variations that did not alter the abundance at 5 and 15 m would have gone undetected. Adults of *Acartia longiremis* (Lillje-borg) and *Centropages hamatus* (Lilljeborg), *Podon* spp., adult *Oncaea* spp. (mainly *O. borealis* G.O. Sars) had the largest fluctuations in median depth, with variations between 4 and 7 m. Consistent differences in the median depths between copepodids and adults were only observed for *Pseudocalanus elongatus* Boeck and *Oithona similis* Claus (Table 2). For *P. elongatus* there was a tendency

Table 2. The means (m), the variance (var), and the range (d) calculated as maximum – minimum median depth for the mid-day (7–29 June 198) 1 and diel (10–11 June) series. Product moment correlation (r) between irradiance and median depth is given for the mid-day series. F is the ratio of the variance of the diel and mid-day sample series.

| Taxon	Mid-day				Diel			F
	m	var	d	r	m	var	d	
Podon spp.	2.9	3.45	1.9	0.65	2.4	0.56	1.3	0.2
Acartia longiremis, juv.	2.9	0.98	2.2	0.93	2.8	0.82	2.8	0.8
Acartia longiremis, ad.	5.8	4.06	5.3	0.22	4.4	1.03	2.8	0.3
Evadne nordmanni	4.1	0.76	2.1	0.51	5.1	5.77	5.9	7.6
Appendicularia, indet.	4.1	0.72	1.9	0.11	2.6	0.88	2.5	1.2
Paracalanus parvus, juv.	3.6	1.35	2.5	0.16	4.7	0.26	1.5	0.7
Paracalanus parvus, ad.	3.6	2.89	3.3	0.43	4.4	0.79	2.3	0.3
Copepoda, nauplii	5.1	2.39	3.2	0.23	6.9	0.91	3.2	0.4
Centropages hamatus, juv.	4.5	0.70	1.3	−0.01	4.6	0.59	1.9	0.8
Centropages hamatus, ad.	4.1	2.40	3.5	−0.39	4.6	2.14	3.7	0.9
Bivalvia, larvae	9.8	0.24	1.0	−0.87	10.4	0.34	1.4	1.4
Temora longicornis, juv.	10.0	< 0.01	0.2	0.18	10.2	0.24	1.3	47.3
Temora longicornis, ad.	9.9	0.03	1.6	0:36	9.5	2.43	4.9	81.0
Oithona similis, juv.	8.5	0.65	1.9	−0.53	9.4	0.30	1.4	0.5
Oithona similis, adv.	10.4	0.10	1.8	−0.77	10.8	0.08	0.8	0.8
Pseudocalanus elongatus, juv.	11.3	2.34	2.4	0.86	10.1	0.01	0.3	< 0.1
Pseudocalanus elongatus, ad.	14.3	0.49	2.0	0.53	12.0	1.26	3.7	2.6
Oncaea spp., juv.	18.0	0.20	1.2	0.40	17.8	0.41	1.7	2.1
Oncaea spp., ad.	14.7	13.19	7.3	0.25	16.3	3.78	5.3	0.3
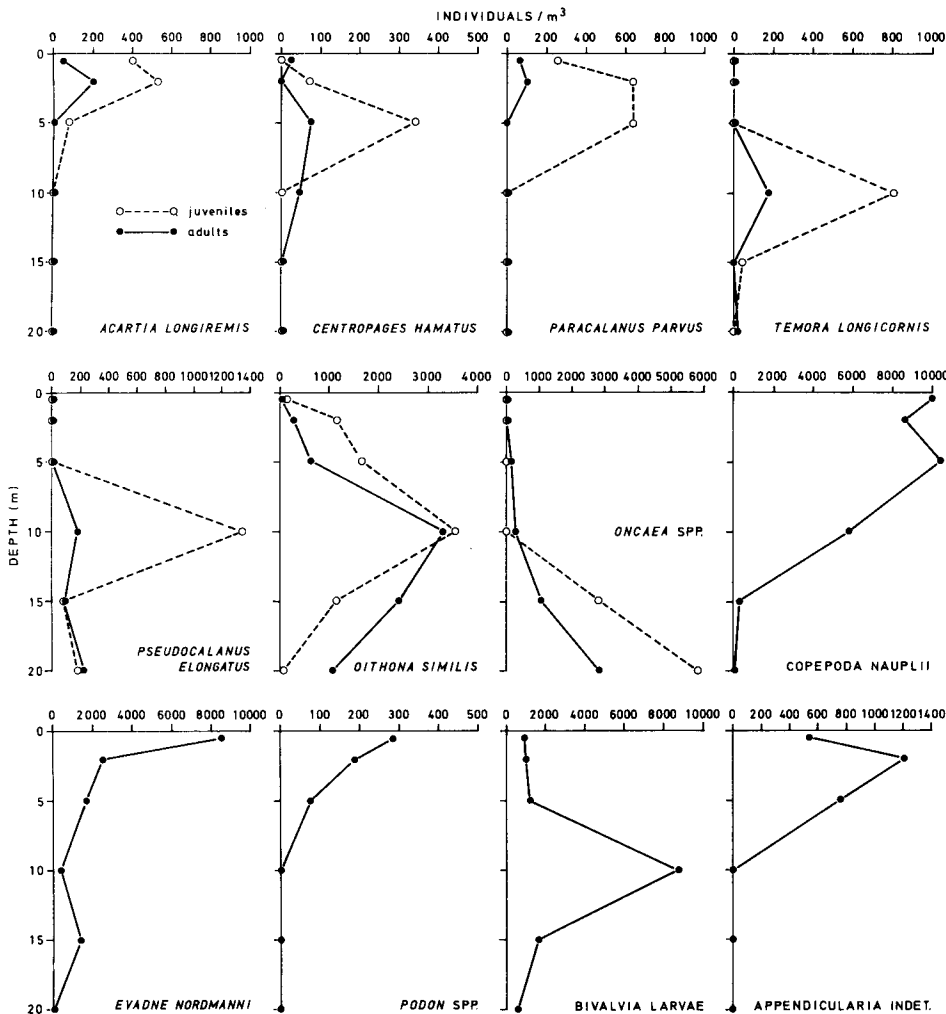
Fig. 4. Vertical distribution of zooplankton taxa (individuals/m³) in Spjeldnesosen at 1500 h on 7 June 1981. The copepods have been separated into juveniles (dotted line) and adults (solid line).

for the older copepodids (stages IV and V) to occur deeper than the younger stages, and for females to occur deeper than males (not shown). The mid-day median depths were not correlated to variations in surface irradiance (Table 2), except for significant positive correlation ($r > 0.86$, $p < 0.05$) for juveniles of *A. longiremis* and negative correlation for bivalve larvae.

The variations detected in the vertical-ranges among the mid-day series were small (Fig. 6, Table 3). The highest mid-day variation in vertical-range was found for bivalve larvae (coefficient of variation 54.2 %). This variation was due to an extension of the vertical-range towards the end of June. High

constancies in the vertical ranges were found for Appendicularia and *O. similis* with coefficients of variation of only 2.6 and 3.7 %, respectively.

Due to the high constancy in median depths and vertical ranges in the mid-day series, the values for overlap between taxa were also relatively constant through time (Table 3). The taxa living in the uppermost five metres overlapped more with the other taxa than did the taxa living mainly between 10 and 20 m. The average overlap index for the uppermost taxa was 0.50, and 0.34 for the species living deeper down. The average overlap for all taxa was in the range 0.37 to 0.45 for all the mid-day series (Table 4).
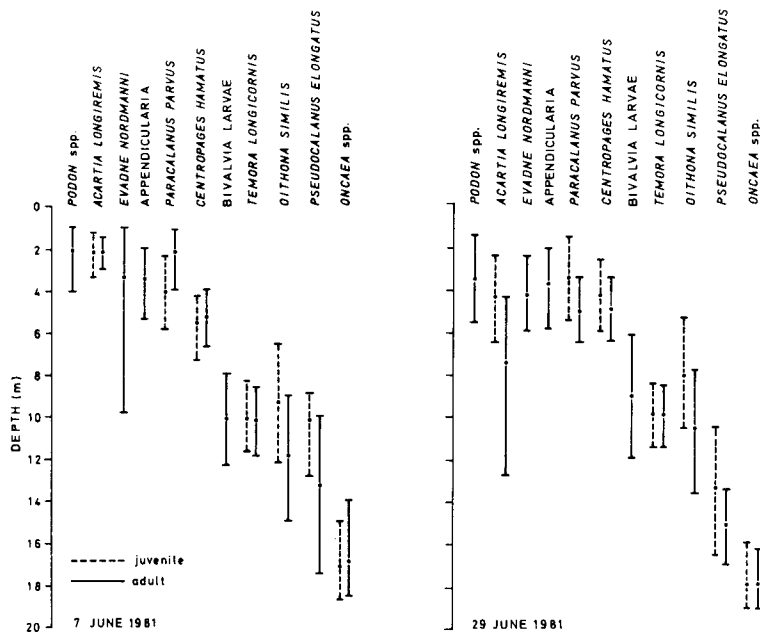
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Fig. 5. Median depth (points) and distance between first and third quartiles (vertical bar) of the vertical distribution of zooplankton taxa in Spjeldnesosen on 7 and 29 June 1981.

Table 3. The mean (m) and the variance (var) of the vertical range and the overlap for the mid-day (7–29 June 1981) and the diel (10–11 June) series. F is the ratio of the variance of the diel and mid-day sample series.

| Taxon	Mid-day		Diel		F
	m	var	m	var	
Vertical range					
Podon spp.	2.0	0.329	2.2	0.264	0.8
Acartia longiremis	3.2	0.295	2.7	0.256	0.9
Evadne nordmanni	3.1	0.193	3.8	1.609	8.3
Appendicularia, indet.	3.0	0.006	2.5	0.182	27.2
Paracalanus parvus	2.8	0.109	2.4	0.446	4.1
Centropages hamatus	2.3	0.349	2.2	0.336	1.0
Bivalvia, larvae	1.8	0.950	1.4	0.284	0.3
Temora longicornis	1.1	0.035	1.2	0.119	3.3
Oithona similis	3.3	0.015	2.7	0.279	17.7
Pseudocalanus elongatus	2.1	0.216	1.3	0.025	0.1
Oncaea spp.	1.7	0.175	1.5	0.070	0.4
Overlap					
Podon spp.	0.46	0.0022	0.42	0.0045	2.0
Acartia longiremis	0.52	0.0089	0.47	0.0027	0.3
Evadne nordmanni	0.52	0.0058	0.53	0.0073	1.6
Appendicularia, indet.	0.54	0.0006	0.44	0.0104	17.2
Paracalanus parvus	0.50	0.0027	0.41	0.0087	3.2
Centropages hamatus	0.47	0.0098	0.41	0.0111	1.1
Bivalvia, larvae	0.38	0.0098	0.36	0.0004	0.1
Temora longicornis	0.30	0.0043	0.36	0.0035	0.8
Oithona similis	0.53	0.0020	0.47	0.0034	1.7
Pseudocalanus elongatus	0.28	0.0088	0.35	0.0003	0.1
Oncaea spp.	0.14	0.0046	0.09	0.0010	0.1
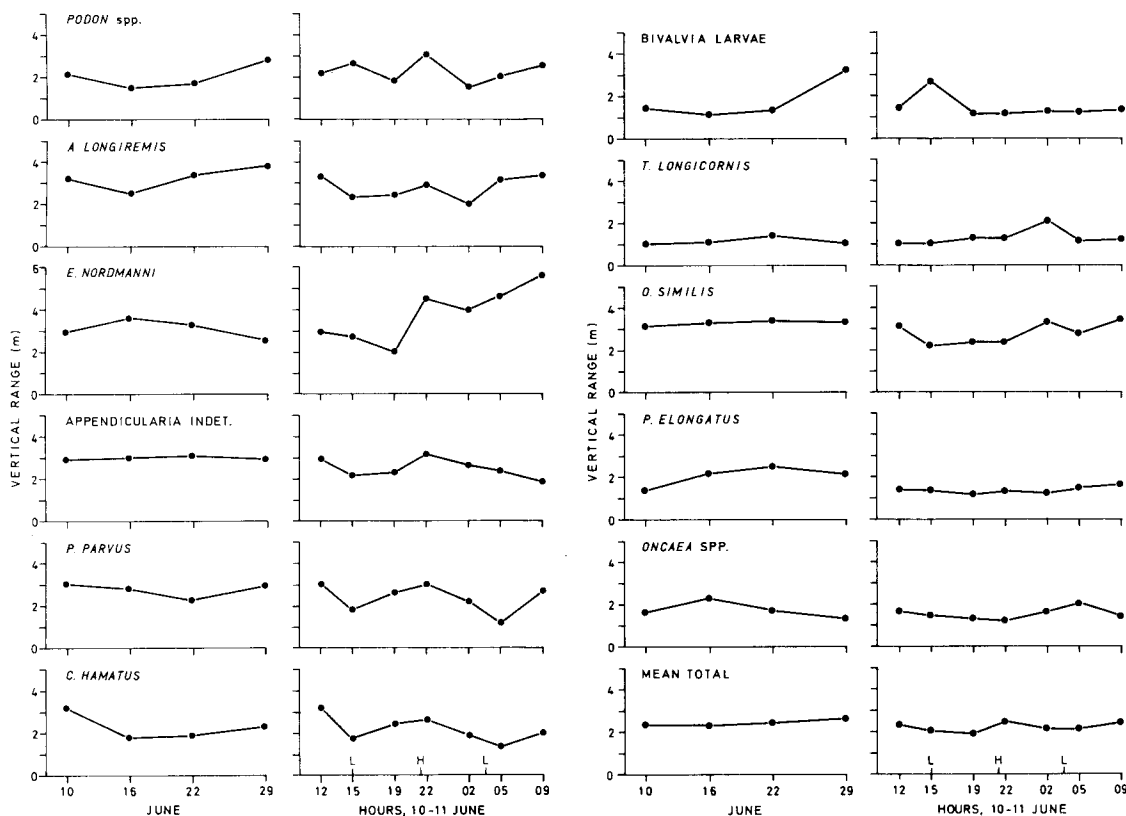
Fig. 6. Vertical range (relative measurement of span in vertical distribution; see Methods) of the zooplankton taxa in Spjeldnesosen for the mid-day (10–29 June 1981) and the diel (10–11 June) series. Time of low (L) and high (H) water is indicated.

Diel series

High ratios between the diel and mid-day variances of median depths were only obtained for *T. longicornis* and *Evadne nordmanni* Lovén (Table 2). The median depth for adult *T. longicornis* was about 10 m at daytime and 6 m at night (0200 h). *E. nordmanni*, however, moved downwards at night. At mid-day the median depth was about 4 m, while it was about 7 m at night (0200 and 0500 h), and 8 m in the morning (0900 h). The variance ratio of 2.6 for adult *P. elongatus* reflected an ascent of 4 m in the median depth at night (Table 2).

High diel to mid-day variance ratios in the vertical range were found for Appendicularia, *O. similis*, *E. nordmanni*, *Paracalanus parvus* (CLAUS) and *T. longicornis* (Table 3). The appendicularians had the largest vertical range at 1200 and 2200 h, while low values occurred at 1500 and 0900 h (Fig. 6). A similar pattern was found for *P. parvus* and *C. hamatus*, but the lowest values occurred at 0500 h. This gives the appearence of a 12-hour cycle (Fig. 6), where high values occurred at high tide and low

Table 4. Mean total overlap (α) calculated for zooplankton taxa in the mid-day and diel sample series (June 1981), and numbers of low (α_1; $\alpha < 0.3$), intermediate (α_2; $0.3 < \alpha < 0.7$), and high (α_3; $\alpha > 0.7$) values.

| Date | Hour | Total | Number of values | | |
		α	α_1	α_2	α_3
7	1515	0.37	32	8	15
10	1210	0.42	31	3	21
16	1145	0.42	26	12	17
22	1310	0.40	28	11	16
29	1130	0.45	22	15	18
10	1210	0.42	31	3	21
	1510	0.32	37	5	13
	1915	0.37	33	9	13
	2220	0.42	33	1	21
11	0115	0.46	24	11	20
	0450	0.36	31	10	14
	0840	0.37	26	12	17

values at low tide. The vertical range of *O. similis* was low in the afternoon and in the evening. *E. nordmanni* showed an increase in vertical range
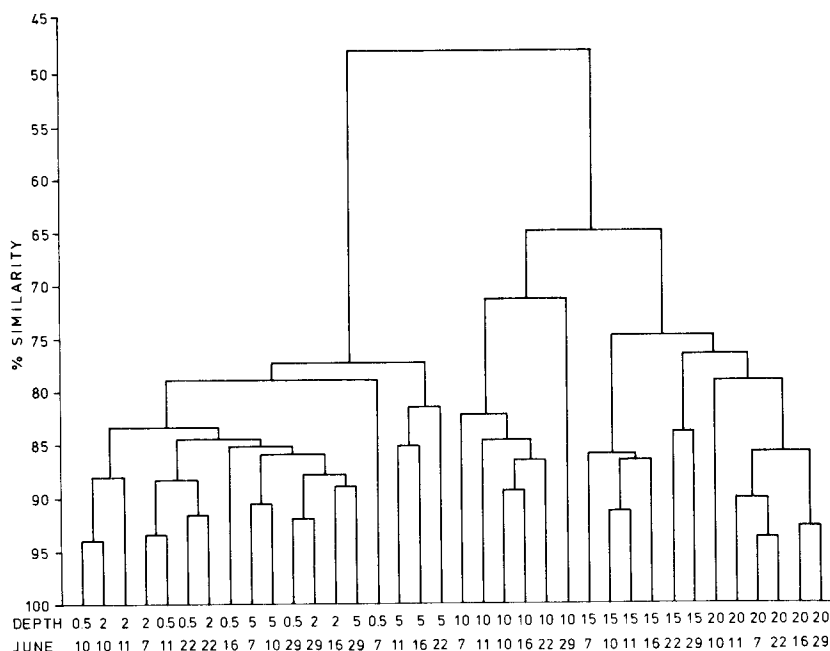
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Fig. 7. Similarity between zooplankton composition in samples collected in Spjeld-nesosen in June 1981. Dendrogram resulted from cluster analysis of zooplankton abundance data. Samples are identified by depth and date.

during the night, when the species migrated downwards. *T. longicornis* had its largest vertical range at 0200 h, when the species migrated upwards.

The taxa found in the uppermost 5 m had greater variations in the diel overlap values than the taxa found at 10 m and below (Table 3). Highest ratios between diel and mid-day variances in overlap between a given taxon and all the others taxa were found for Appendicularia, *P. parvus,* and *Podon* spp. These taxa were all found in the surface layer.

Minima in the mean total overlap values for all taxa occurred in the afternoon (1500 h) and in the morning (0500 and 0900 h, Table 4), while maxima were found at night (0200 h) and at mid-day. The values obtained at 1100 to 1200 h in the mid-day series were also relatively high. The lowest mean total overlap in the mid-day series was found at 1500 h on 7 June. This was at the same hour as the lowest mean overlap value was found in the diel series (Table 4). These results suggest a diel cycle in the overlap structure of the zooplankton community.

The frequency distribution of the individual species overlap values for the mid-day and diel series showed that low values ($\alpha < 0.3$) and high values ($\alpha > 0.7$) occurred more frequently than intermediate values (Table 4). This applied both to the

mid-day and the diel series, and shows that most of the taxa were either fairly well separated vertically or overlaped considerably with the other taxa.

Similarity between depth strata

The cluster analysis separated the samples into two main groups (Fig. 7) consisting of the shallow samples (0.5, 2, and 5 m) and the deeper samples (10, 15, and 20 m). Within the shallow group, the 5-m samples from 11, 16, and 22 June, together with the 0.5 -m sample from 7 June, were the four least typical samples. No particular grouping was apparent for the remaining samples in the shallow group, although the 0.5- and 2-m samples showed high similarity on 10, 22, and 29 June. Among the deeper samples, however, there was a regular grouping starting with the 20-m samples, then including the 15-m subgroup, and then the 10-m subgroup (Fig. 7).

Factor analysis

The first two factors explained 49 and 30 % of the total variance in the zooplankton abundance matrix, respectively, while the third factor accounted for only 8 % of the variance. The sample loadings to factors 1 and 2 after rotation of the axes, resulted in two distinct groups of samples (Table 5). The

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Table 5. Factor analysis of zooplankton abundance data for the mid-day series (7–29 June 1981). The samples loadings to factors 1 and 2 (F1 and F2) are shown.

Date June	Depth (m)	F1	F2	Date June	Depth (m)	F1	F2
7	0.5	0.84	−0.12	16	0.5	0.90	0.05
	2	0.91	−0.11		2	0.96	−0.09
	5	0.94	0.03		5	0.74	−0.16
	10	−0.21	0.85		10	−0.04	0.89
	15	−0.01	0.90		15	0.02	0.93
	20	−0.17	0.88		20	−0.29	0.76
10	0.5	0.87	−0.16	22	0.5	0.92	−0.15
	2	0.95	−0.20		2	0.90	−0.26
	5	0.91	0.03		5	0.69	0.24
	10	−0.17	0.94		10	−0.06	0.95
	15	0.14	0.93		15	−0.15	0.89
	20	0.13	0.56		20	−0.26	0.84
11	0.5	0.88	−0.31	29	0.5	0.92	−0.21
	2	0.76	−0.40		2	0.97	−0.12
	5	0.44	0.02		5	0.91	0.03
	10	−0.15	0.91		10	−0.10	0.79
	15	−0.03	0.90		15	−0.09	0.79
	20	−0.18	0.86		20	−0.33	0.67

samples from shallow depth strata (0.5, 2, and 5 m) had high loadings to factor 1 and low and usually negative loadings to factor 2. The samples from the deeper depth strata (10, 15, and 20 m) had high loadings to factor 2 and low and usually negative loadings to factor 1. The correlation coefficient (r) between the sample loadings to factors 1 and 2 was high but negative (r = −0.94, p < 0.001).

The factor loadings for each of the 36 samples (six depths, six dates) to factors 1 and 2 were subjected to a stepwise regression analysis (DIXON 1981) with 16 environmental variables (Skjoldal unpubl. data). The variables were temperature, salinity, nutrients (silicate, nitrate, phosphate, ammonium), pH, particulate organic phosphorus, carbon, nitrogen, primary production, chlorophyll a, phaeopigment, in vivo fluorescence, and numbers of autotrophic and heterotrophic cell counts. The stepwise regression analysis indicated that temperature was the most important environmental variable, accounting for 78 and 75 % of the variation in factors 1 and 2, respectively. The variable extracted in the second step was primary production, which accounted for 6 and 7 % of the variation in factors 1 and 2, respectively. None of the other variables included in later steps accounted for more that 5 % of the variation. Temperature was positively correlated with factor 1, and negatively correlated with depth (r = 0.88 and −0.94, respectively).

DISCUSSION

This study, as other investigations in Norwegian fjords has shown that Podon spp., E. nordmanni, Appendicularia, P. parvus, A. longiremis, and C. hamatus have their population maxima in the warm surface water above the pycnocline during summer (WIBORG 1944; HANSEN 1952; JOHANNESSEN 1972; ELLINGSEN 1973; STRØMGREN 1973; ERIKSON 1978; MAGNESEN 1989b). P. parvus is generally reported from warm, near-surface waters (BIGELOW 1926; McLAREN 1963; ERIKSSON 1976; TURNER & DAGG 1983). We found T. longicornis and bivalve larvae in the pycnocline, while O. similis and P. elongatus occurred in or below, and Oncaea spp. mainly below the pycnocline. The vertical distribution of these taxa seems to be variable, since they may be found either above, in or below the pycnocline both in polls (LIE & al. 1983; MAGNESEN 1989b), in Norwegian fjords (HANSEN 1951; STRØMGREN 1973), off the west coast of Sweden (ERIKSSON 1973), and in the White Sea (AFRIKOVA 1975). In the White Sea SHUVALOV (1965) investigated some features of the biology of O. similis and concluded that although it is an eurythermal species, found at all depths, it was usually less abundant in the uppermost layer. It may therefore be concluded that the observed vertical distributions are comparable to other observations, but that the vertical distributions of most species may be variable, as

pointed out by TURNER & DAGG (1983). The high constancy in the median depths during our mid-day series indicates, however, that the species' vertical distributions may persist under stable conditions. In the coastal epiplankton off southern California FIEDLER (1983) observed that the fine-scale vertical distribution was sufficiently stable to influence zooplankton growth.

The vertical distribution may change due to relocation of water masses (BANSE 1964; STRØMGREN 1973), but it is questionable whether concentrations of copepods within restricted depth-ranges could be solely the result of passive transport (LEE & WILLIAMSON 1975). The vertical separation of the species may be maintained even in mixed water (SOUTHWARD & BARRETT 1983), but dominant species have been found to be differently distributed in stratified and well-mixed waters (TURNER & DAGG 1983).

The median depth distribution (Fig. 5), the overlap structure (Table 4), the clustering of the samples (Fig. 7), and the results from the factor analysis (Table 5) suggest that the species vertical distributions were discontinuous and consisted of two distinct species groups. This could, however, reflect the lack of samples between 5 and 10 m, or the use of fixed sampling depths. Thereby one looses the advantages of randomly selected samples in gradient analysis. The sensitivity of multivariate analysis to the sampling design was stressed in the study of benthic assemblages by LIE (1974).

In a review of vertical distribution of zooplankton CUSHING (1951) concluded that the daydepth was related to changes in light intensity. In the present study the correlations between irradiance and median depth were insignificant, except for two taxa. These taxa responded, however, differently to the changes in light intensity.

The vertical ranges of *P. parvus, C. hamatus* and partly of Appendicularia and *Podon* spp. were small at low-water, and at high-water large vertical ranges occurred (Table 1, Fig. 6). The largest mean vertical range for all taxa in the diel series was also observed at high-water. The increase in vertical range at high-water correspond with a high mean overlap value at mid-day on 29 June, but in the diel series it occurred at night (0200 h, Table 4). The large overlap value at night may be due to vertical migrations, since *T. longicornis* and *P. elongatus* migrated upwards, and the shallow-living *E. mordmanni* descended at night. It may therefore be argued that variation in vertical range was correlated with the tide, while the overlap between vertical distribution of all taxa in the diel series could be due to vertical migrations.

The vertical migration of small copepods in stratified waters has been doubted (BANSE 1964), but numerous observations of its existence at different times of the year are found (AFRIKOVA 1975; FURUHASHI 1976; KUIPER & al. 1982). *P. elongatus* was characterized as an active migrator in the White Sea by AFRIKOVA (1975). In Lindåspollene both *P. elongatus* and *T. longicornis* have been found to perform upward vertical migrations at night (WESTERGAARD 1975; BERG 1984; MAGNESEN 1989b). The apparent reverse migration of *E. nordmanni* has also been observed in Lindåspollene by MAGNESEN (1989b). Significant vertical migration in zooplankton biomass has not been observed in Lindåspollene during summer, but in spring and autumn a considerable part of the biomass has been found to migrate (LIE & al. 1983; SKJOLDAL & al. 1983; MAGNESEN 1989b).

The multivariate analysis revealed temperature as the major environmental variable structuring the zooplankton community. This is in accordance with observations from the English Channel (RUSSELL 1930) and the White Sea (KOSLOSOVA & al. 1977). During summer when food was scarce, however, feeding habits may be most important for separating numerically abundant taxa on a finer vertical scale (KOSLOSOVA & al. 1977).

In June most of the primary production was located in the uppermost 5 m (Fig. 3), and the highest zooplankton biomass was found at 10 m (LIE & al. 1983). The vertical distribution of zooplankton may be correlated with primary production (HERMAN & al. 1981; HERMAN 1983), or to the chlorophyll *a* maximum layer (ORTNER & al. 1980; BIRD 1983). In our study only 6 to 7 % of the variation in vertical distribution was due to variation in primary production. The significance of chlorophyll *a* was even less. The primary production during summer in Lindåspollene is thought to be mainly based on recycling processes in the uppermost part of the water column (LÄNNERGREN 1976). Close coupling between primary and secondary production (SKJOLDAL & LÄNNERGREN 1978), and low sedimentation rates during summer (WASSMANN 1983) indicate efficient use of nutrients and energy. The persistent zonation of the zooplankton species, and their small diel variations may reflect this high efficiency in the community.

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