

DISTRIBUTION, DEVELOPMENT, AND PRODUCTION OF *CALANUS FINMARCHICUS* (GUNNERUS) IN LINDÅSPOLLENE, WESTERN NORWAY, 1979

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The *Calanus finmarchicus* population in Spjeldnesosen, a 'poll' in the landlocked fjord system, Lindåspollene, in western Norway was investigated during 1979 and early 1980. The bottom water was renewed during the winter 1978–1979. This led to a well aerated water column in 1979 compared to earlier years. Differences were observed between the horizontal distributions of the various copepodid stages. This is thought to be due to migration away from the shore as the individuals grew older. One yearly generation with one spring spawning was observed. Residence times were estimated as 2, 4, 6, 13, and 250 days for copepodid stages I to V respectively. The estimated mortality was greater than 10 % per day when the younger stages were represented in the samples, and less than 1 % per day when stage V was dominant. Of about 72 000 ind./m² recruited to copepodid stage I, about 800 ind./m² of the total population survived until the end of 1979. Estimated production was 1 g dry weight/m² per year on the average for Spjeldnesosen, and 3.6 g dry weight/m² per year in the deep central area of Spjeldnesosen.

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INTRODUCTION

Due to movement of water masses the marine environment seldom gives good opportunities to carry out studies on the population dynamics of pelagic copepods. As a consequence, time series obtained in investigations on copepods are often a function of immigration and emigration as well as of recruitment and mortality. Furthermore, the time intervals between successive samples have often been too long to cover the rapid changes that may occur in a copepod population. The sampling necessary for studying population dynamics of copepods in the open sea is likely to require much time and effort. Population studies in more enclosed systems, such as fjords, are less expensive and may give time series less influenced by immigration and emigration. MATTHEWS & HEIMDAL (1980) found, however, that the production values estimated from a three-year study of *Calanus* in Korsfjorden (MATTHEWS & al. 1978), a relatively open fjord near Bergen, western Norway, were impossible for a static water column. Much of this production, according to MATTHEWS & HEIMDAL (1980), could only be explained as advective production.

Landlocked fjords, called 'polls' (see MATTHEWS & HEIMDAL 1980) provide good opportunities to study the population dynamics of pelagic copepods. In this environment transport of organisms due to currents is minimized and sampling is inexpensive. Spjeldnesosen (Fig. 1), one of the polls in the Lindås-poll

system was chosen as the sampling locality in this investigation on *C. finmarchicus*. Lindåspollene have been the sampling site for numerous studies, of which the ultimate aim is to develop a dynamic, mathematical model for the marine ecosystem (DAHL & al. 1973). Spjeldnesosen is, like other polls, almost completely surrounded by shore and the depth variations are large. This is likely to result in pronounced differences in the numbers of individuals obtained when sampling in the horizontal plane.

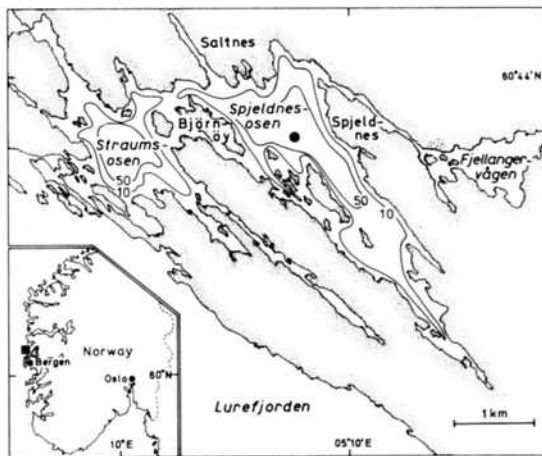


Fig. 1. Lindåspollene, western Norway, showing the sampling station for the time series investigation.

We, therefore, deal also with the horizontal distribution of *C. finmarchicus* in relation to the development of the population.

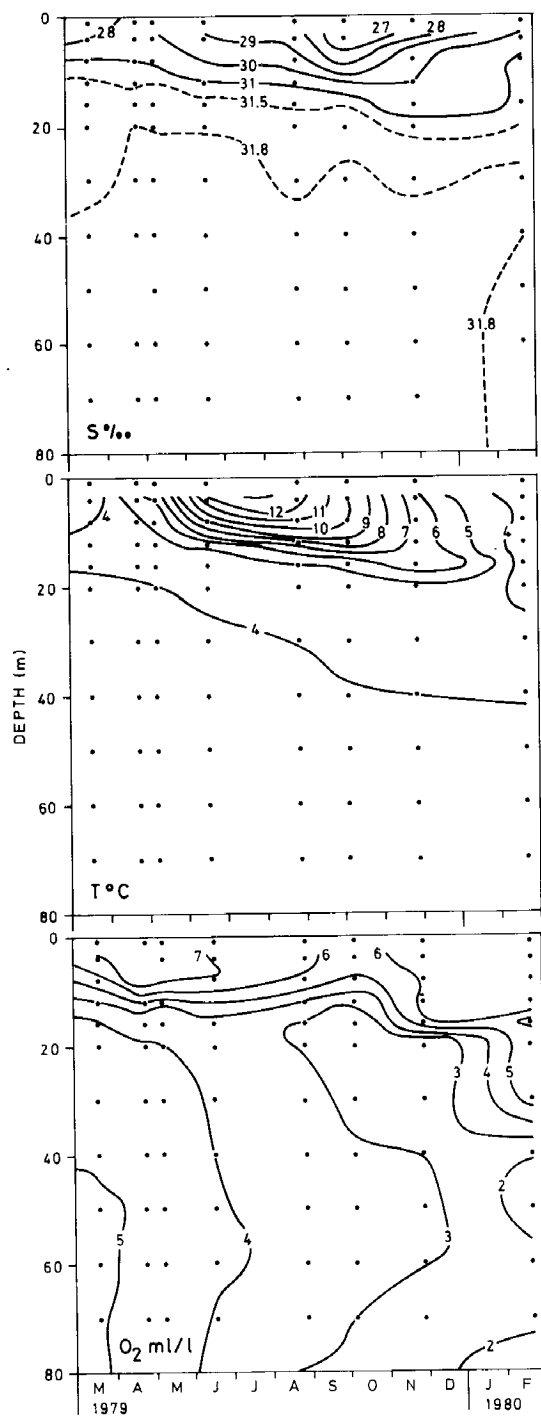


Fig. 2. Temperature, salinity and oxygen in Spjeldnesosen from March 1979 to February 1980.

C. finmarchicus is the dominant herbivorous copepod in the North Sea and along the Norwegian coast (e.g. LIE 1965; LONGHURST & WILLIAMS 1979; WIBORG 1954; WILLIAMS & LINDLEY 1980a). Despite several investigations on the life cycle, there have been few studies on *C. finmarchicus* dealing with the estimation of population characteristics such as recruitment, mortality, and residence times. Reports on laboratory rearings of *Calanus* are also seldom encountered in the literature. MATTHEWS (1966) has measured residence times for the copepodid stages at four different temperatures, and MATTHEWS & al. (1978) gave in situ estimates of recruitment, mortality and indirect estimates of residence times. WILLIAMS & LINDLEY (1980b) obtained residence times and estimated the production of *C. finmarchicus* on the Fladen Ground in the North Sea.

This paper is based on the results from two unpublished cand. real. theses (AKSNES 1981; MAGNESEN 1982).

MATERIAL AND METHODS

The sampling design is summarized in Table 1.

Time-series of copepodid-stage frequency were obtained between 9 April 1979 and 5 April 1980. This sampling was carried out at a single locality in the central deep part of Spjeldnesosen (Fig. 1). Two Juday nets with a diameter of 40 cm arranged 50 cm apart on a frame were used. The mesh size was 180 μ m. All samples were taken as vertical hauls from two metres above the bottom to the surface. The sampling frequency varied with the presumed stage composition of the population. Intensive sampling was carried out during a period of three weeks in April and May when we observed rapid changes in abundance and stage composition.

The horizontal distribution was investigated by sampling on 8 and 9 May 1979. These days three boats sampled (with single Juday nets) 81 different stations in areas deeper than 10 m (Fig. 4). These stations were chosen by a stratified random design described by MAGNESEN (1982).

The copepodid stages of *C. finmarchicus* were identified

Table 1. Sampling statistics.

Date	Number of hauls	Number of samples	Date	Number of hauls	Number of samples
1979			1979		
9 Apr.	2	4	11 May	6	12
24 »	2	4	12 »	4	8
26 »	2	4	23 »	2	4
28 »	6	12	2 Jun.	2	4
29 »	4	8	22 »	2	2
30 »	4	8	6 Jul.	2	2
2 May	2	4	14 Aug.	2	2
3 »	2	4	18 Sept.	2	2
4 »	4	8	7 Oct.	2	2
6 »	4	8	19 »	2	2
8 »	47	53	9 Dec.	2	2
9 »	42	44	1980		
10 »	2	4	21 Feb.	2	2
			5 Apr.	1	1

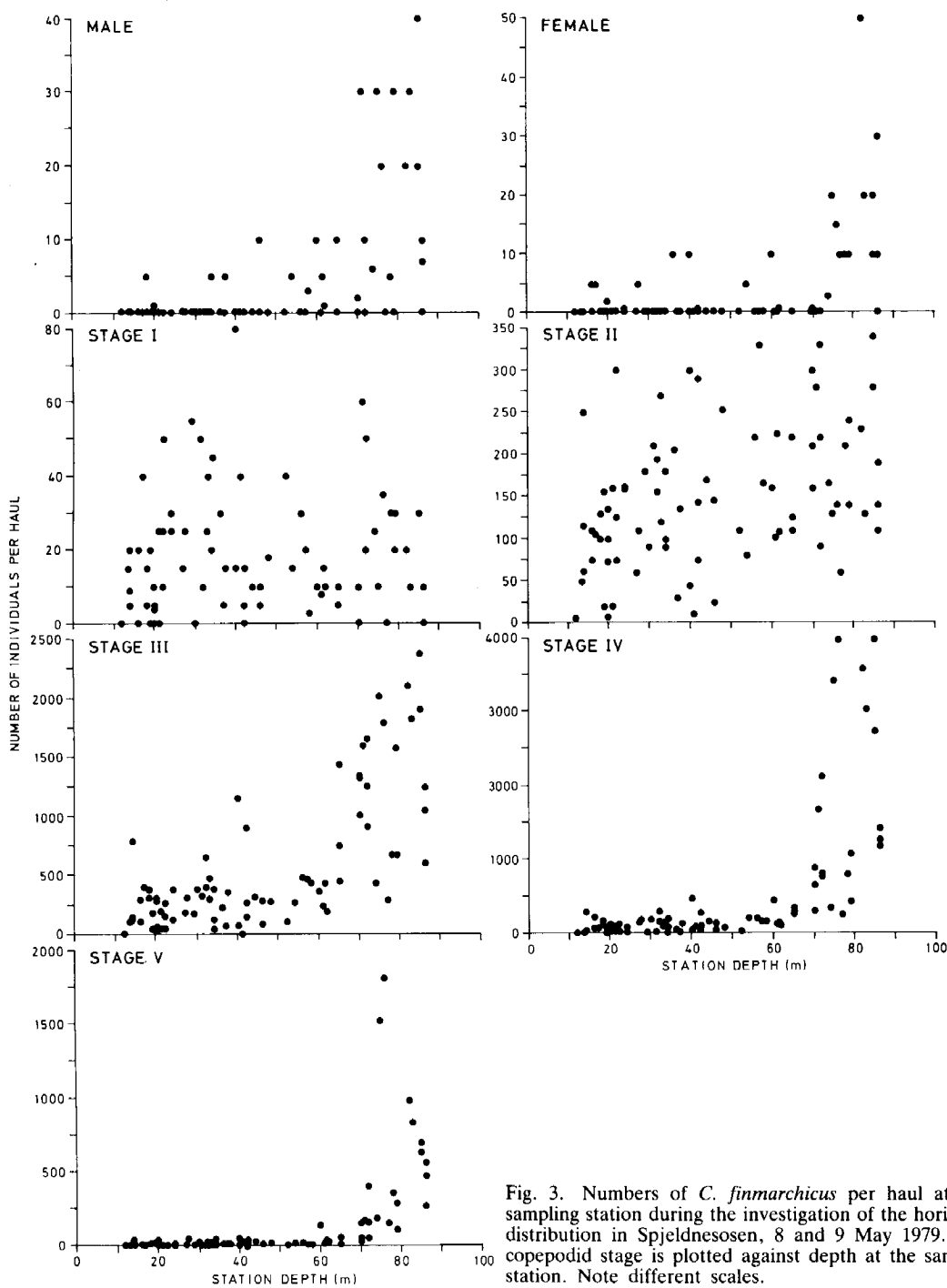


Fig. 3. Numbers of *C. finmarchicus* per haul at each sampling station during the investigation of the horizontal distribution in Spjeldnesosen, 8 and 9 May 1979. Each copepodid stage is plotted against depth at the sampling station. Note different scales.

and counted. The samples were subsampled with a Lea-Wiborg plankton divider (WIBORG 1951). No samples were fractioned beyond 1/10 of the original sample.

Methods given by MANLY (1974, 1977) were used to estimate the population characteristics. The following

estimates are obtained by using these methods: M : the number of organisms that enter a stage, μ : the mean time of entry to the stage, σ : the standard deviation of the time of entry to the stage, θ : the death rate, a : residence time for the stage.

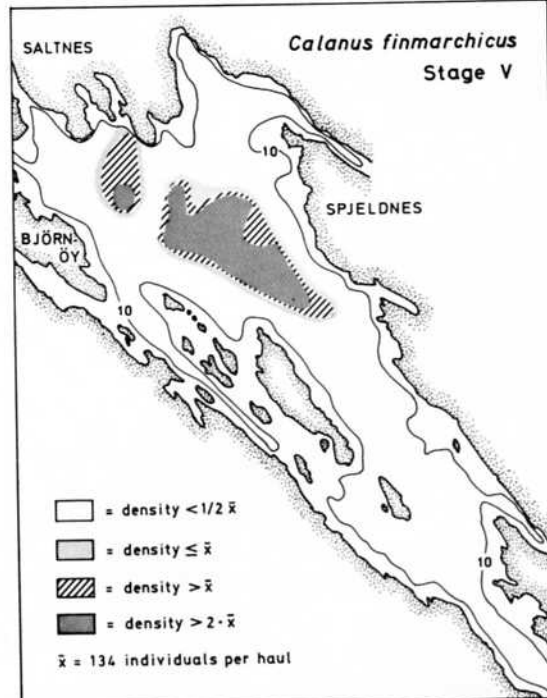
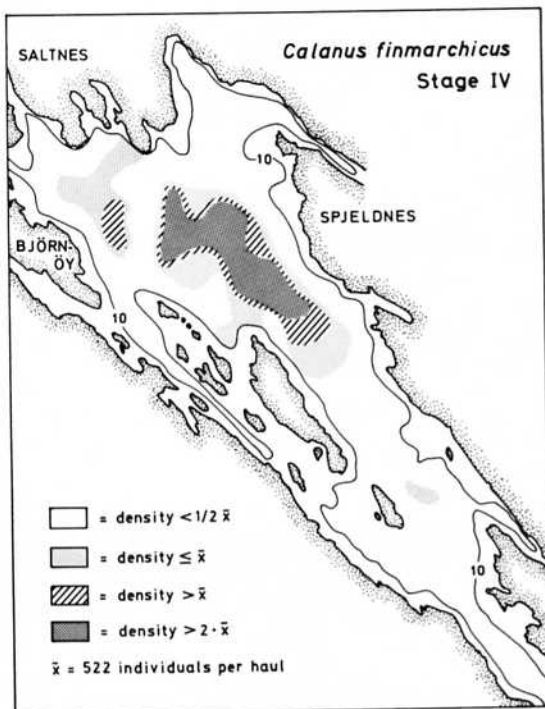
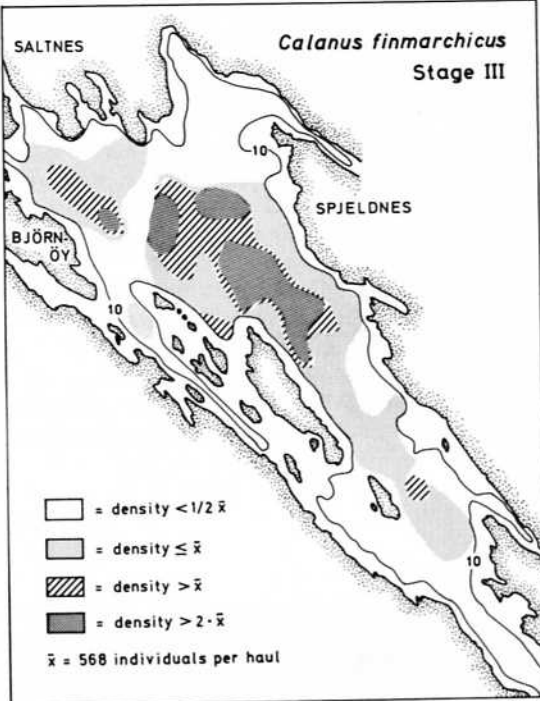
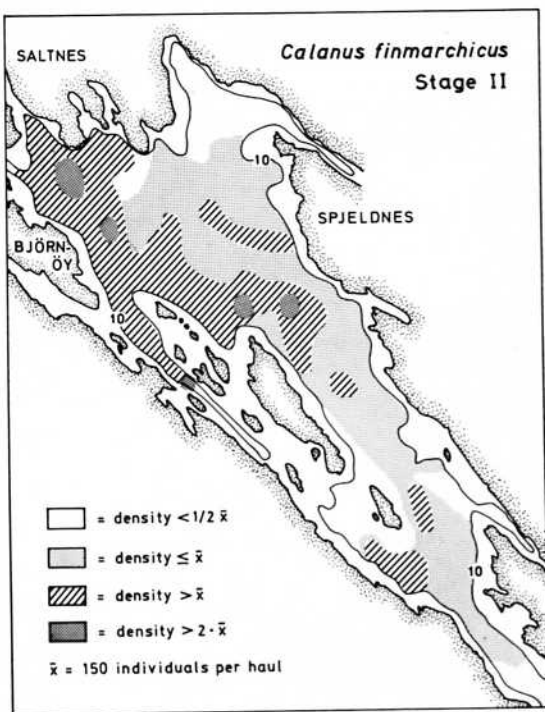


Fig. 4. The horizontal distribution of *C. finmarchicus* in Spjeldnesosen on 8 and 9 May 1979. Location of sampling stations and the distribution of copepodite stage II-V are shown. Densities refer to numbers per haul relative to the mean number of individuals (\bar{x}) for all stations.

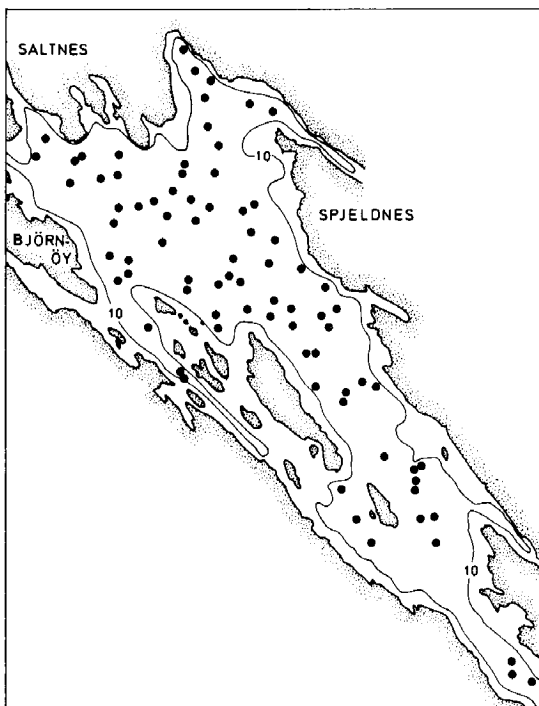


Fig. 4. (contd). Sampling stations.

With these characteristics the number of individuals in the stage under consideration and all later stages at time t is given by the equation (MANLY 1974):

$$N(t) = M \int_{-\infty}^t e^{-\theta(t-x)} f(x) dx \quad (1)$$

where $f(x)$ is the normal frequency distribution given by the two parameters μ and σ .

Least squares estimates of M , θ , μ , and σ were obtained by running a computer program (MATTHEWS & al. 1978) that minimized $\sum (\hat{N}(t) - N(t))^2$, where $\hat{N}(t)$ is the observed time series and $N(t)$ is the time series given by equation 1.

MANLY'S (1974) method gives indirect estimates of residence times by taking the differences $\mu_{i+1} - \mu_i$ where i is the stage number. For reasons explained later we chose his second method (MANLY 1977) for the estimation of the residence times for the first three copepodid stages. The estimates obtained by this method are based on calculated areas and means of the $N(t)$ -curves instead of the 'curve-fitting' procedure described above.

If there are no deaths in a particular stage i ($\theta = 0$) the relationship between the area A_i under the $\hat{N}_i(t)$ curve, the number entering (M_i) and the duration of that stage (a_i) simplifies to $A_i = M_i a_i$ (MANLY 1977). For stage V we chose this simplified expression to estimate the number entering this stage. This could be done since the observed mortality was low and a reasonable estimate of the residence time was obtained.

Production was estimated by the expression:

$$P = \sum_{i=1}^4 (M_i - M_{i+1}) w_i + M_5 w_5 \quad (2)$$

where w_i is the weight of stage i and M_i is the number of recruits to stage i .

The stage specific-weight values used in this study are 2, 5, 15, 40, and 250 μg dry wt/individual for stage I-V, which are approximate means of the values given by MARSHALL & ORR (1955), ELLINGSEN (1973), KIRKESÆTHER (1977), and WILLIAMS & LINDLEY (1980b). This will introduce bias into our estimates of biomass and productions, but enables valuable comparisons with other studies to be made.

HYDROGRAPHY

The vertical distribution of temperature, salinity, and oxygen during 1979 are plotted in Fig. 2. Below 20 m the annual variations in temperatures and salinities were small, with ranges of 3.5–4.2°C and 31.50–31.82‰ respectively. The oxygen values measured below 20 m decreased from March to November 1979, but never reached below 1 ml/l. Above 20 m the water column became stratified during the spring, and the oxygen values measured were always higher than 2.5 ml/l.

The hydrographical conditions in Lindåspollene have been investigated more or less continuously since early 1971 (LIE & DAHL 1981). Compared with earlier years the hydrographical conditions in 1979 were characterized by quite high oxygen values and low temperatures in the deeper part of the water column. This was due to renewal of the bottom water during the winter 1978–1979. No extensive renewal was detected during the following winter.

RESULTS

Distribution

The distribution of the population on 8 and 9 May 1979 is shown in relation to water depth in Fig. 3. Copepodid stage I seemed to be distributed independent of the depth at the sampling locality. For stage II–V progressively more of the individuals were found at the deeper stations. Fig. 4 shows that the younger stages had a wide geographical distribution and that the copepodid stages IV and V were restricted to the central parts of the poll. Later in the year very few individuals were found in the shallow area, and LIE & al. (1983) found in October 1979 that most of the individuals were below 65 m. Because of this concentration of individuals in the central deep part of the poll, especially in areas deeper than 70 m, we divided Spjeldnesosen into two strata. Stratum 1 covered the area with depths ranging from 10 to 70 m and stratum 2 covered the area with depths greater than 70 m. The abundances found in these two strata together with stratified mean values are given in Table 2.

Table 2. The abundance of *C. finmarchicus* in two strata in Spjeldnesosen 8 and 9 May 1979. A stratified mean is given in column 3. Numbers indicate ind./m².

Stage	Stratum 1 10-70 m	Stratum 2 70-89 m	Stratum 1 + 2 10-89 m
I	145	150	147
II	1 120	1 550	1 190
III	2 870	10 040	4 100
IV	1 300	13 540	3 400
V	160	4 020	830
VI female	12	100	27
VI male	7	90	22

Table 3. Vertical distribution of *C. finmarchicus* in Spjeldnesosen on 5 and 6 May 1979. Numbers are means from four nets.

Depth interval	Stage	5 May		6 May	
		Day	Night	Day	Night
0-25 m	I	20	40	10	40
	II	210	400	155	180
	III	100	2 020	98	2 800
	IV	35	1 920	30	3 640
	V	5	600	0	1 000
	VI	0	20	0	0
25-89 m	I	0	5	0	0
	II	175	75	330	25
	III	1 330	380	3 430	290
	IV	1 270	485	3 370	495
	V	540	230	870	275
	VI	25	15	20	10

Vertical hauls taken at 89-25 and 25-0 m by day and by night on 5 and 6 May gave the results shown in Table 3. During day-time the copepodid stages III, IV, and V were mainly found deeper than 25 m. At night-time the numbers of these stages above 25 m increased, indicating diel vertical migration.

Development

Table 2 shows that the samples collected in stratum 2 greatly overestimated the average abundance estimates for Spjeldnesosen. The time-series counts obtained from sampling in this stratum were therefore adjusted. The count for each stage was multiplied with the proportion between the stratified mean and the abundance in stratum 2. The new time series (Fig. 5) obtained are probably less biased with regard to the description of the population's development in Spjeldnesosen.

The young stages were not present in significant numbers for more than three to four weeks. This means that sampling in 1979 covered only one spawning period, and that the spawning did not last for more than about three weeks. The generation had an intensive development period lasting from mid-April until mid-May. Later the samples were dominated by stage V. The mature stage VI was not observed in significant numbers before February 1980. Due to lack of sampling between 9 December 1979 and 21 February 1980 we do not know when the juveniles matured. The low counts of adults in February and April 1980 suggest that they suffered from high mortality or that they migrated out of the

Table 4. Nested analysis of variance and estimated components of variance performed on logarithm transformed abundance of stages I-V of *C. finmarchicus*.

Stage	Source of variance	d.f.	MS	F	P	Variance component Value	%
I	Between:						
	Low and high tide	7	0.0159	1.1	n.s.	0.0002	1
	Hauls	14	0.0151	0.9	n.s.	0.0000	99
Nets	28	0.0160			0.0160		
II	High and low tide	7	0.0145	0.6	n.s.	0.0000	100
	Hauls	14	0.0236	2.0	< 0.1	0.0060	
	Nets	28	0.0116			0.0116	
III	High and low tide	7	0.0424	1.6	n.s.	0.0039	21
	Hauls	14	0.0270	11.6	< 0.01	0.0123	79
	Nets	28	0.0023			0.0023	
IV	High and low tide	7	0.0591	1.8	< 0.1	0.0067	28
	Hauls	14	0.0322	12.6	< 0.01	0.0148	72
	Nets	28	0.0026			0.0026	
V	High and low tide	7	0.0702	3.7	< 0.05	0.0128	45
	Hauls	14	0.0190	1.6	n.s.	0.0035	55
	Nets	28	0.0121			0.0121	

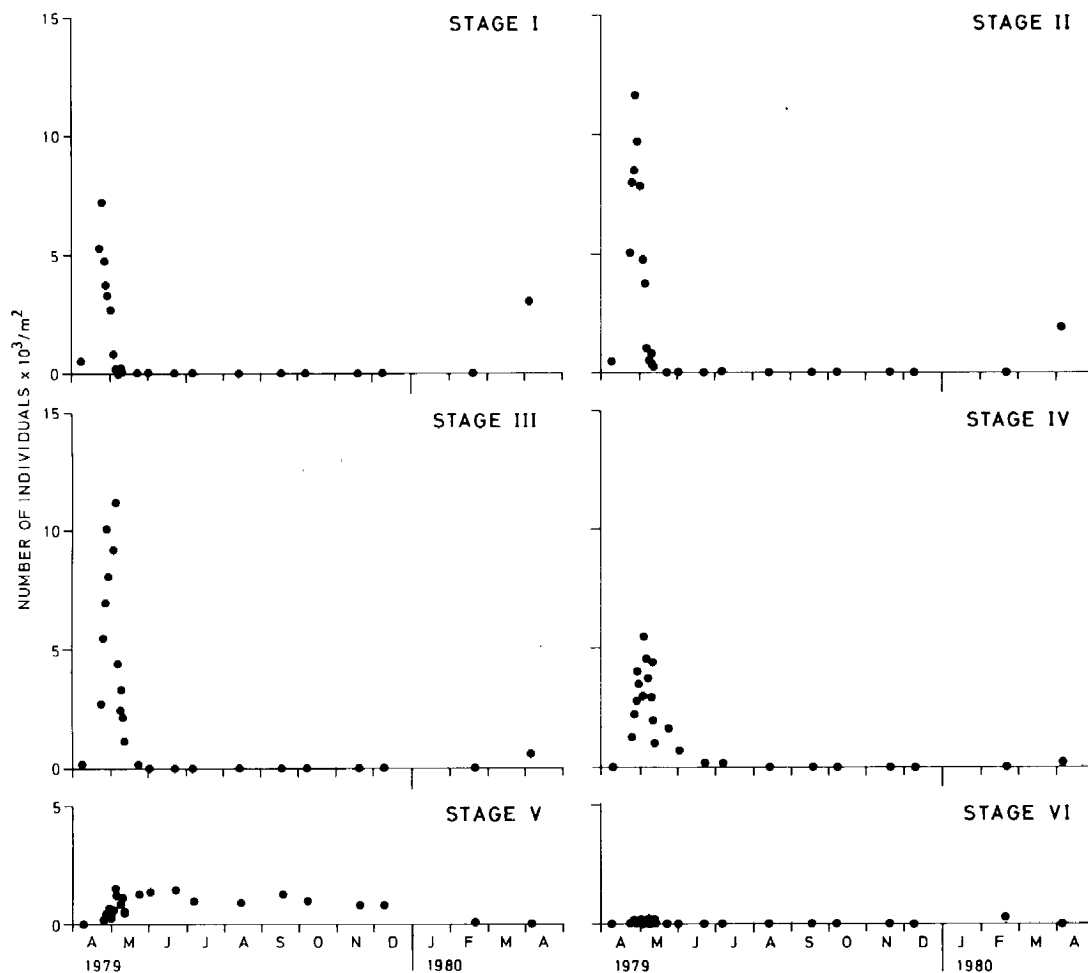


Fig. 5. Development of *C. finmarchicus* in Spjeldnesosen 1979–1980. Numbers refer to the average numbers of individuals of each copepodid stage per m^2 in the poll as a whole.

sampling area. On 5 April we observed the first copepodids produced in 1980.

Population dynamics

We have made one fundamental assumption regarding the *C. finmarchicus* population, namely that all changes in total numbers of the population are caused by recruitment and mortality. More precisely, we have assumed that migrations out of or into the two neighbouring polls balanced each other. We consider tides to be the main factor that could make this assumption invalid. Sampling was therefore performed at high and low tide on seven different days. The counts from these samplings have been subject to an analysis of variance (Table 4). Due to the time interval of 6.5 hours between low and high tide, the variance component 'between tides' (Table

4) may also include a component associated with diurnal behaviour of the organisms. On the basis of differences in vertical distribution (Table 3) we expect that any possible tidal component would be greater in the case of the younger stages than the older ones. The opposite seems to be the case. The counts of stage V had a significant ($p = 0.05$) variance component 'between tides', but it is hard to believe that the counts of a stage found mostly below 25 m should be influenced by a tidal amplitude of about 0.5 m. This variance component is more likely to be due to diurnal behaviour. For stage I to IV there is no reason to conclude that samples at low and high tide differed from each other more than samples taken 10 minutes apart. It is therefore concluded that the tides did not influence abundances to any significant degree.

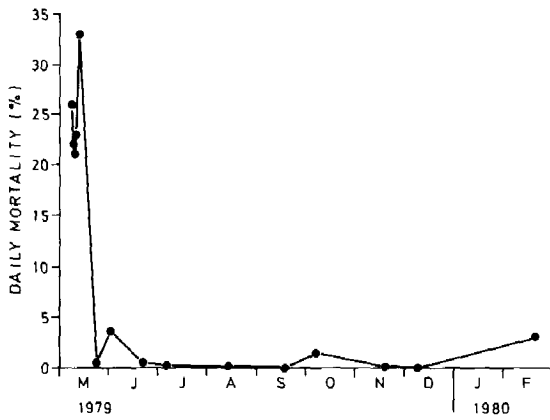


Fig. 6. The daily mortality rate (%) of *C. finmarchicus* in Spjeldnesosen 1979–1980.

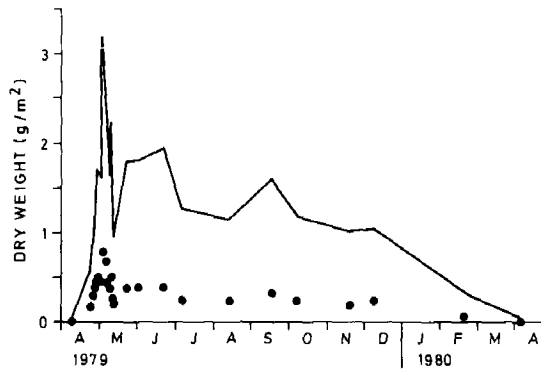


Fig. 8. Estimated biomass of *C. finmarchicus* in Spjeldnesosen 1979. Solid line show values for the deep area only, circles average values for the whole poll (areas deeper than 10 m).

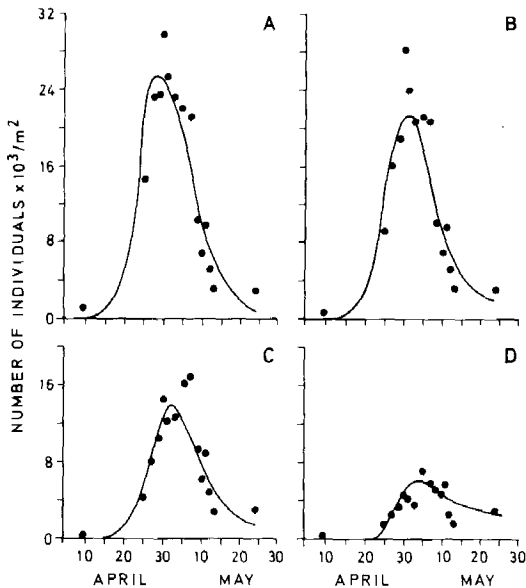


Fig. 7. Cumulated observed numbers (circles) of *C. finmarchicus* in Spjeldnesosen 1979, and predicted population curve based on the population characteristics estimated according to MANLY (1974). A: stages I + II + III + IV + V, B: stages II + III + IV + V, C: stages III + IV + V, D: stages IV + V.

Since the naupliar stages were not included in this study the individuals at copepodid stage I represent the recruits to the population. On 6 May the number of this stage was reduced with about 95 % relative to the maximum number observed on 26 April. Recruitment thus seems to have ceased by 6 May and changes in total numbers after this date were presumably caused by mortality. This mortality (Fig. 6) was far from constant. During May it fell rapidly from rates above 20 % per day to rates near 1 % per

day. This means probably that the older stages had lower mortality than the younger ones. Because of the better survival of the older stages the Manly model (represented by equation 1) was fitted to the observations of the younger stages excluding the last observation points. The estimates of the population characteristics are given in Table 5 and the fit of the Manly model to the observed data is shown in Fig. 7.

As mentioned earlier, MANLY'S (1974) method gives estimates of residence times by taking the differences $\mu_{i+1} - \mu_i$, where i is the stage number. Unfortunately, when stages are short-lived relative to the precision of μ the estimates of residence times will be imprecise and negative values may occur. The residence times for stages I, II, and III were therefore estimated by MANLY'S (1977) second method. In using this method we had to assume that the mortality was approximately the same for these stages. The residence time for stage IV could not be estimated by this method because of the much lower mortality estimated for this stage. In this case, however, the estimate $\mu_5 - \mu_4$ is reasonable. The duration of stage V was found by visual evaluation of Fig. 5.

Of the total recruitment of 72 000 ind/m², about 800 ind/m² probably reached the adult stage. This figure is not really an estimate of the recruitment to stage VI, but rather an estimate of the number alive in December 1979. The largest numerical loss from the population seems to have been from stages II and III.

Biomass and production

The estimated biomass during the year is shown in Fig. 8. The values for the central part of the basin ranged from 1 to 2 g dry weight (dw)/m² most of the year, while the average values for Spjeldnesosen

were significantly lower, ranging from 0.2–0.5 g dw/m². The highest biomass values occurred in early May 1979. The estimated total zooplankton biomass, based on the sampling at the 81 sampling localities, was 1.3 g dw/m² while it was 3.5 g dw/m² in the central basin (MAGNESEN 1982). Thus, *C. finmarchicus* seems to have accounted for more than 50 % of the zooplankton biomass in central parts and for about 25 % of the total biomass in Spjeldnesosen at this time. The calculated biomass was fairly constant from late May to December, due to the low mortality of stage V and to the fact that we used the same weight values for this stage throughout the year.

We estimated the production of *C. finmarchicus* in 1979 to have been approximately 1 g dw/m² per year. Production in the central area, calculated on the basis of the uncorrected time series, was about 3.6 g dw/m² per year.

DISCUSSION

Distribution

The horizontal distributions of the developmental stages raise the following question: What mechanisms have caused the apparent concentration of the older stages in the central basin? Stage I, and to some extent stage II, seemed to be almost randomly distributed in Spjeldnesosen while the older stages had high abundances in the central deep basin. We are inclined to consider two possible explanations, or a combination of them, for this distribution pattern. First, the distribution could have been caused by migration or transport from the shallower into the deeper areas. Secondly, it could have been caused by a higher mortality in the shallower areas. We have no observations to reject either of these hypotheses, but our time-series data indicate migration or transport. This will be discussed below.

The equation (MANLY 1977):

$$A_i = M_i (1 - e^{-\theta_i a_i}) / \theta_i \quad (3)$$

gives the relationship between the population characteristics recruitment (M_i), mortality (θ_i), and residence time (a_i) and the area (A_i) under the $N_i(t)$ curve for stage i . Assuming that the $N_i(t)$ is the result of recruitment and mortality (no immigration or emigration) it follows that

Table 5. Estimated population characteristics for *C. finmarchicus* in Spjeldnesosen 1979. The number of recruits (M) to the 1 m² water column, instantaneous mortality (θ), time of peak recruitment (μ) in days from 1 January 1979, spread of recruitment (σ) in days, and residence times (a) as estimated by MANLY'S (1974, 1977) methods. Estimates obtained according to MANLY (1977) are marked +. The residence time for stage V was obtained by visual assessment of the frequency curves.

Stage	Estimates of population characteristics				
	M	θ	μ	σ	a
I	72 000	0.16	117.5	5.2	1.8 ⁺
II	66 000	0.18	118.4	5.2	3.5 ⁺
III	35 000	0.15	119.2	5.2	6.0 ⁺
IV	8 000	0.04	117.5	2.8	13.0
V	1 100 ⁺	< 0.01	130.5	15.5	250.0

$$M_i = M_{i-1} e^{-\theta_i - 1 a_i - 1} \quad (4)$$

Equations 3 and 4 have been used to investigate possible values for residence time and mortality for the first three stages using the uncorrected time-series. The areas under the uncorrected $N(t)$ curves for stages I, II, and III are $A_1 = 92\ 300$, $A_2 = 182\ 900$ and $A_3 = 376\ 400$ respectively. We assume constant mortality for these stages, i.e.

$$\theta = \theta_1 = \theta_2 = \theta_3$$

We have calculated this mortality ($\theta = 0.28$) from the observed decrease in the total numbers (uncorrected time-series) from 8 to 12 May, after significant recruitment to stage I had ceased.

Equation 3 gives

$$a_3 = \frac{\ln(1 - \theta A_3 / M_3)}{-\theta}$$

and by combining stages I and II we obtain

$$M_1 = \frac{(A_1 + A_2)\theta}{1 - e^{-\theta(a_1 + a_2)}}$$

Equation 4 gives

$$M_3 = M_1 e^{-\theta(a_1 + a_2)}$$

By combining these equations we can express the duration of stage III as a function of the areas under the $N(t)$ curves, the mortality, and the duration of stage I and II:

$$a_3 = - \frac{\ln \left[1 - A_3 / (A_1 + A_2) e^{-\theta(a_1 + a_2)} + A_3 / (A_1 + A_2) \right]}{\theta}$$

The expression in square brackets has to be positive and this leads to:

$$a_1 + a_2 < 1.9$$

This means that the residence time for stages I and II combined, had to be less than two days. A combined residence time in the range 1.5–1.9 days gives residence time for stage III in the range 4.5–11.6 days. On the basis of earlier studies (see Table 6) both the short duration of stage I and II combined, and the proportion between stage I–II and III, seems very unlikely. If we reduce the area A_3 (i.e. removing an immigration component), more probable values can be obtained. From this analysis we are inclined to think that the uncorrected time series does include a considerable immigration component and that the observed horizontal distributions are partly a result of migration or transport, or both, of individuals into the deeper parts of Spjeldnesosen.

Avoidance of shore, also termed 'Uferflucht' (SIEBECK 1968), has been observed for limnetic copepods, and correlation has been detected between this behavioural pattern and daily vertical migration. According to SIEBECK (1980) there is hardly any zooplankton species which exhibits daily vertical migration and is prevalent near the shore or vice versa. It is known that *C. finmarchicus* at times exhibits diel vertical migration (MARSHALL & ORR 1955). Table 3 also suggests that the later copepodid stages, which were less abundant in shallower water, carried out diel vertical migration. There is of course no necessity of a causal relationship between the two behavioural patterns and it has been discussed whether or not avoidance of shore is a direct consequence of diel vertical migration. SIEBECK (1964, 1968, 1980) believes that avoidance of shore is a consequence of optical orientation away from the asymmetry produced by a raised horizon rather than of vertical migration.

Development

Our investigation indicated a one-year breeding cycle of *C. finmarchicus* with recruitment occurring during spring only. This is not in accordance with other studies performed at similar latitudes. Two or three periods of spawning have been observed in coastal waters along western Norway (RUUD 1929; RUNNSTRÖM 1932; WIBORG 1954; LIE 1965, 1968; MATTHEWS & al. 1978). Some studies, however, conclude that only a part of the spring generation takes part in spawning later in the year (WIBORG 1954; ØSTVEDT 1955; LIE 1965, 1968). LIE (1968) observed that the main part of the spring generation remained in an immature stage until the spawning

next spring. Under arctic and subarctic conditions *C. finmarchicus* produces only one generation per year (USSING 1938; MANTEUFEL 1941; DIGBY 1954; FONTAINE 1955; McLELLAN 1967). This was also found by TANDE (1982) in Balsfjorden near Tromsø.

The lack of summer and autumn spawnings in Spjeldnesosen was perhaps due to the hydrographical conditions. The poll was covered by ice until the beginning of March 1979. This might have led to a delayed phytoplankton spring bloom and thereby to a late spawning of the *Calanus* population. MATTHEWS (1969) found that the spring increase in the late stages took place in late March and early April in the North Sea and off the west coast of Norway. MATTHEWS & al. (1978) estimated that the heaviest recruitment to stage III (younger stages were not included in their study) in Korsfjorden occurred in the period from the end of March to the beginning of April, while our estimate is about one month later (1 May). It may also be of importance that the temperature in Spjeldnesosen during spring 1979 was relatively low (Fig. 2). A close relationship between temperature and development rate in different regions of the north-west Atlantic was found by MATTHEWS (1968).

Population dynamics

In early May, when the population consisted of young stages and it was living in the upper part of the water column, we observed a high mortality. Later in the year the estimated mortality was extremely low. At this time the population probably spent most of its time as stage V in the deeper parts of the water column. During an investigation on zooplankton in Spjeldnesosen 2–3 October 1979 (LIE & al. 1983) more than 80 % of the *Calanus* stock was found deeper than 60 m both day and night. In Korsfjorden, MATTHEWS & al. (1978) found a significantly higher mortality rate for *C. finmarchicus* stage V with a range of 2–37 % per day. For the larger species *C. hyperboreus* they estimated a mortality rate ranging from 0.3 to 0.7 % per day, which is closer to our mortality estimate for *C. finmarchicus* stage V. The lower mortality found in Spjeldnesosen compared to Korsfjorden may be due to the differences in community represented in these two localities. The communities of fjords consist of larger species which may increase the predation pressure to *C. finmarchicus*.

Table 6 summarizes estimates of residence times from this and earlier studies. The in situ estimates (MATTHEWS & al. 1978 and our results) show increasing residence times for successive copepodid stages. The laboratory results are not consistent, but a tendency for more isochronal development (con-

Table 6. The residence times (in days) of *C. finmarchicus* compared with other investigations. The values from MATTHEWS & al. (1978) are obtained as the difference $\mu_{4+1} - \mu_4$.

Authors	Temperature °C/ Season	Copepodid stage				
		I	II	III	IV	V
MARSHALL & ORR (1955)	14-15	3-5	2-4	3-11	3-13	4-19
MATTHEWS (1966)	0		16.0	18.0		
	5		8.4	10.5	11.8	16.7
	10		4.0	8.5	8.0	10.0
	15		4.0	8.2	8.9	9.3
WILLIAMS & LINDLEY (1980)	9	2	3	3-5	4-5	2-5
MATTHEWS & al. (1978)	Spring			2-9	5-12	-12-13
	Summer			-8-1	-1-11	61-159
Our results	Spring	2	4	6	13	250

stant residence times for the various stages at the same temperature) may be detected. MILLER & al. (1977) have described this kind of development for two species of *Acartia*. CORCKETT & McLAREN (1978) and KLEIN BRETELER & al. (1982) found that isochronal development may also occur in other calanoid copepods. Even if *Calanus* develop isochronally, an increase in the in-situ estimates of successive residence times seems reasonable, since the progressive downward movement of the various copepodid stages exposes them to lower temperatures, thereby retarding the development of the later stages.

The estimates of recruitment were much lower than the recruitment MATTHEWS & al. (1978) found for *C. finmarchicus* in Korsfjorden, where yearly recruitment to copepodid stage III (stage I and II were not included in their study) was about 1 500 000 ind./m². Two generations, one in spring and one in summer, were responsible for this high recruitment. Thus the recruitment, measured in ind./m², in Spjeldnesosen was only 5 % of that found in Korsfjorden, but, as earlier mentioned, much of the *Calanus* recruitment in Korsfjorden was probably caused by advection (MATTHEWS & HEIMDAL 1980).

Biomass and production

Results from investigations on zooplankton biomass in Norwegian fjords demonstrate that the biomass decreases towards the head of the fjord (GUNDERSEN 1953; LIE 1967; STRØMGREN 1974; FOSSHAGEN 1980). The estimate of total zooplankton biomass in Spjeldnesosen is greater than the estimates found by FOSSHAGEN (1980) in inner parts of the Ryfylke fjord system, but lower than the estimates from outer parts. The large biomass in the outer parts of fjords is dominated by *C. finmarchicus* and yearly biomass variations are often due to this species (GUNDERSEN

1953; LIE 1965; STRØMGREN 1974; MATTHEWS & BAKKE 1977; FOSSHAGEN 1980). MATTHEWS & BAKKE (1977) found the biomass of *C. finmarchicus* to be at least an order of magnitude higher than the biomass of the other species. Although this was not the case in Spjeldnesosen, *C. finmarchicus* was also among the dominant species in terms of biomass. In the inner parts of fjords and in polls the biomass is usually dominated by the smaller copepods (WIBORG 1944; JOHANNESSEN 1972; ELLINGSEN 1973). We think that the relatively high biomass of *C. finmarchicus* found in our study was due to the unusual hydrographical conditions in Spjeldnesosen in 1979. In years with poor oxygen conditions below 40 m (values less than 1 ml oxygen/l, and anoxic conditions in the deepest part of the poll) only small numbers of *C. finmarchicus* are found during the summer, although young copepodids are found during springtime (LIE & al. 1983).

During 1977 McLEAN (1979) estimated the total zooplankton production in Spjeldnesosen to be about 40 g ash-free dry weight/m² per year. Assuming little yearly variation, our production estimate for *C. finmarchicus* was only about 3 % of the total production. Since the production of *C. finmarchicus* mainly took place during 30 days in April-May, however (the population consisted mostly of stage V in June), it is of interest to examine production during this particular period. The primary production in Lindåspollene in April-May has been estimated to be around 360 mg C/m² per day (LÄNNEREGREN 1976). Using a conversion efficiency of 20 % (PAFFENHÖFER 1976) ingestion by *Calanus* would have been about 80 and 330 mg C/m² per day in Spjeldnesosen and in the central basin (depth between 70 and 89 m) respectively. It follows that during this period *C. finmarchicus* could have grazed about 25 and 90 % of the primary production in Spjeldnesosen and in the central basin respectively. The primary production calculated by LÄNNEREGREN

(1976), however, is probably an underestimate since it extended no deeper than 15 m. Nevertheless it is apparent that an appreciable amount of energy was transformed through the *C. finmarchicus* population during a 30 days period in late spring.

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