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QUANTITIES OF ZOOPLANKTON AND PROPAGATION OF *CALANUS FINMARCHICUS* AT PERMANENT STATIONS ON THE NORWEGIAN COAST AND AT SPITSBERGEN, 1959—1962

By

ULF LIE[1]

Fiskeridirektoratets Havforskningsinstitutt

INTRODUCTION

Zooplankton has been collected at permanent oceanographic stations along the Norwegian coast since 1948. The purpose of these long-range plankton studies is mainly to follow the annual and seasonal changes in the food conditions for plankton-feeding fishes. Also, the samples provide material for an analysis of the abundance of eggs and larvae of commercially important fishes in Norwegian coastal waters.

The permanent stations were originally Sognesjøen, Ona, Skrova and Eggum (Fig. 1). Skarsvåg and Kongsfjorden at Spitsbergen were added in 1955 and 1957; the sampling at Ona was abandoned in 1957. Since 1948, zooplankton has also been collected at the weather ship "M" at 66°N, 02°E in the Norwegian Sea.

The hydrographical conditions at the various stations are representative of the conditions in the Norwegian coastal water at the corresponding latitudes. Hydrographic data from the permanent stations have been collected simultaneously with the zooplankton and processed at the hydrography section of the Institute of Marine Research, Directorate of Fisheries.

The zooplankton was completely identified and counted from 1948—1951 (WIBORG 1954), but has since been less thoroughly analyzed. The emphasis has been on measuring displacement volumes, the dominating species of zooplankton have been noted, and fish-eggs and larvae have been identified and counted. Since 1959 the percent composition of development-stages of *Calanus finmarchicus* has also been estimated.

WIBORG (1954) described the annual and seasonal changes in the quantities of zooplankton at the permanent stations from 1948 to 1951.

[1] Present address: Department of Oceanography, University of Washington, Seattle Washington 98105.

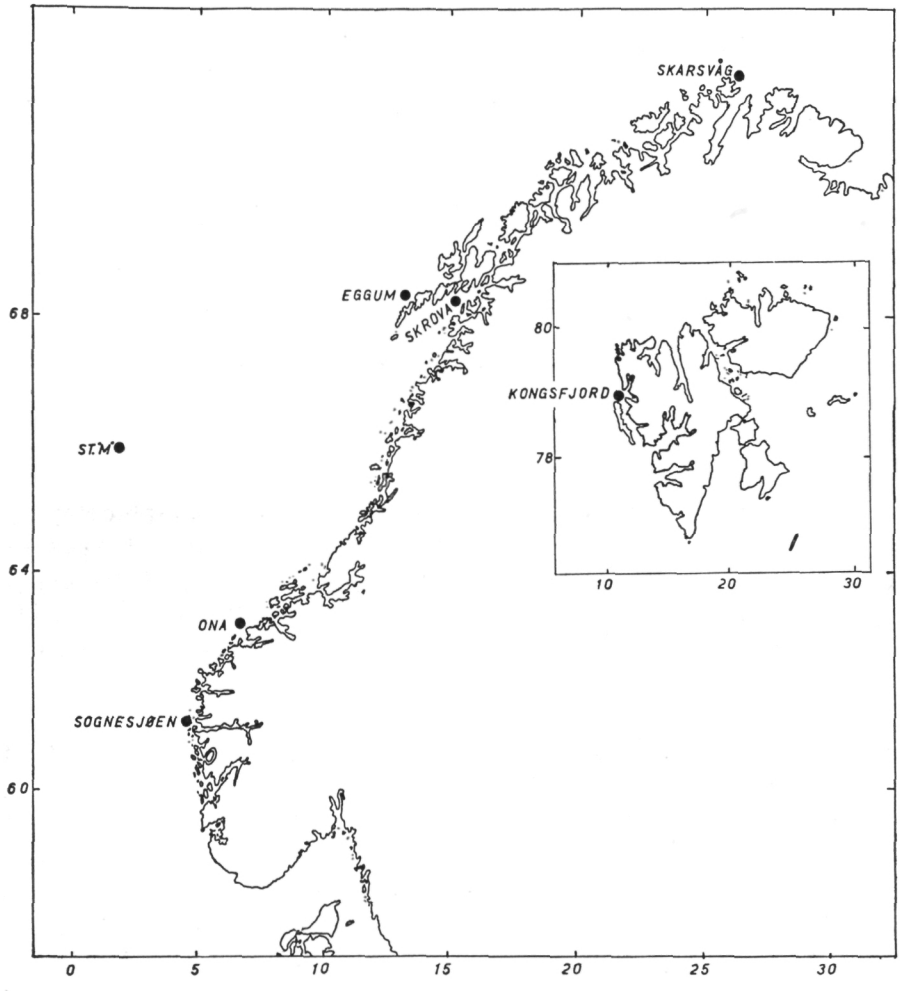

Fig. 1. Permanent zooplankton stations (from WIBORG 1958).

He also discussed the composition of the zooplankton and various aspects of the biology of the important species. The quantity of zooplankton at the permanent oceanographic stations until 1958 was reported by WIBORG (1958 and 1960).

The current paper reports on the zooplankton quantities and the propagation of *Calanus finmarchicus* at Sognesjøen, Skrova, Eggum, Skarsvåg and Kongsfjorden during the period 1959—1962.

MATERIAL AND METHODS

The present report is based on 734 samples from five stations. The material from Skrova is by far the most complete, averaging more than eight samples per month, while the average for the other four stations is less than four.

The majority of samples were collected with Nansen-nets with mouth diameter 70 cm and mesh size 0.2 mm. In 1961 and 1962 this gear was replaced by Juday-nets with 40 cm diameter in the upper ring, and the same mesh size as the Nansen-nets. When calculating the volume of zooplankton per square meter of surface, it has been assumed that the catch per unit area was the same for the Nansen-nets and for the Juday-nets.

Two samples were taken per station per sampling date: one sample from the 50—0 m layer, the second from the bottom to the surface. All the samples were preserved in 5—10 percent formalin.

The volume of the zooplankton was measured by the displacement method (WIBORG 1954). Presence of large quantities of phytoplankton may reduce the accuracy of the measurements considerably by clogging the sieves, but by washing the samples thoroughly before measuring volume, most of the phytoplankton can be removed.

The volumes of zooplankton per square meter of surface have been calculated and the monthly means of these values are presented in Figs. 2—6.

The propagation of *Calanus finmarchicus* has been studied by determining percentage distribution of the first 100 *Calanus* copepodites counted when examining the sample under a dissecting microscope. This method probably does not meet the requirements for random sampling; therefore, the data have not been used for any statistical evaluations. The bias introduced by the method of subsampling does not permit much emphasis on single observations of stage distribution, but demands consideration of trends in large numbers of samples.

The percentage developmental stage distribution as monthly means averaged for the years 1959—1962 at the various stations is presented in Figures 7—10.

VOLUMES OF ZOOPLANKTON AT THE PERMANENT STATIONS, 1959—62

Sognesjøen (Fig. 2)

Very few samples are available from this station, a circumstance which makes the study of seasonal changes in the biomass uncertain. The spring increase seemed to start in April, the maximum was reached

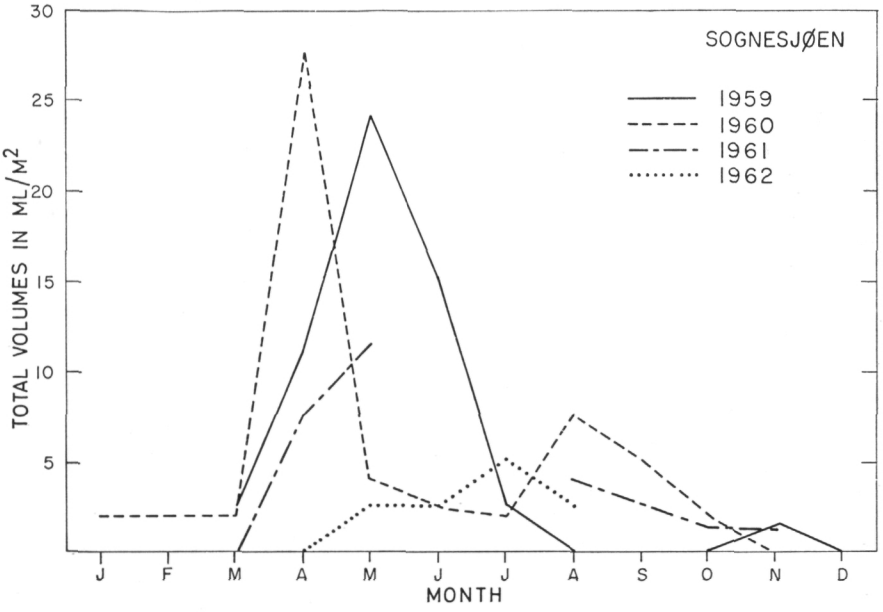

Fig. 2. Monthly mean total volumes in ml/m² of zooplankton at Sognesjøen, 1959—1962.

in April or May. A second, less pronounced peak could be detected in July—August.

WIBORG (1954, 1958, 1960) found the same general trend in the seasonal variations in biomass of zooplankton, and his data reveal considerable variations from one year to another. However, WIBORG also had relatively few observations from this station, which may account in part for the variations.

Skrova. (*Fig. 3*)

The quantities of zooplankton in the 50—0 m samples were very poor during the first three months of all the years investigated. The spring increase was observed from the middle of April, and for all years two significant peaks were found; one in May and one in June. A third, less pronounced peak occurred in September-October.

Fairly high densities of zooplankton were observed all year round in the 300—0 m samples. The minimum was found in March, and the same three peaks occurred as in the 50—0 m samples. The two separate peaks in May and June are not revealed by the monthly mean values per m².

From February on, an increasing proportion of the zooplankton was found in the upper 50 m layer, and during April, May, and June, more than 50 % of the total standing stock occurred in this layer. The relative

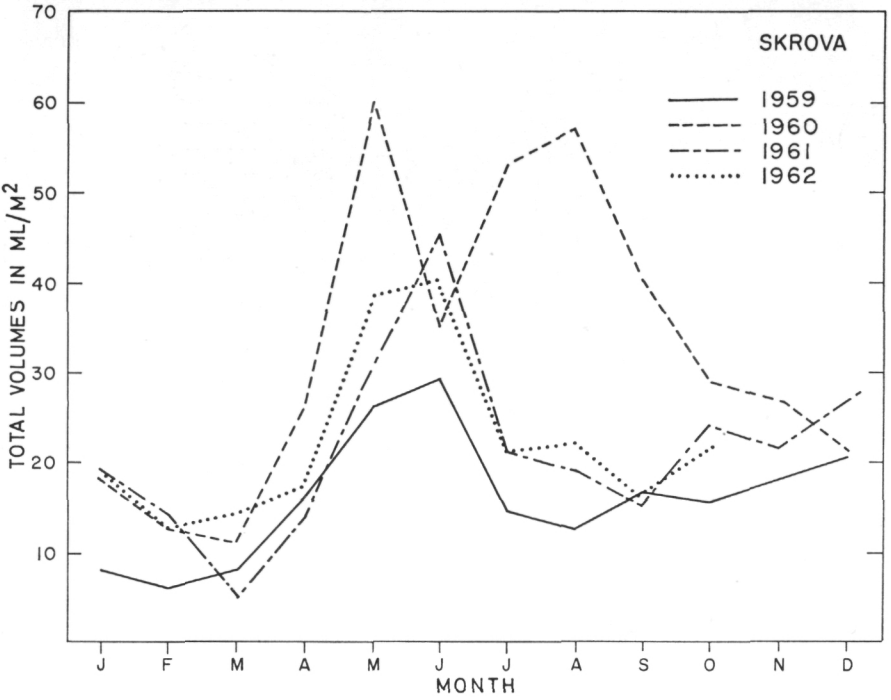

Fig. 3. Monthly mean total volumes in ml/m² of zooplankton at Skrova, 1959—1962.

density of zooplankton in the 50—0 m samples was also prominent during the peaks in September—October 1959 and 1961, but not in 1960. From October the amount of zooplankton in the upper 50 m layer decreased rapidly, and during December and January less than 5 % of the total biomass was found in this layer.

The variations in zooplankton volumes per square meter of surface from 1959 to 1962 (Fig. 3) correspond largely to those observed by Wiborg (1954, 1958, 1960). He demonstrated that considerable changes may occur at this station from one year to another as regards time for the peaks and the mean annual richness of zooplankton.

Eggum. (Fig. 3)

The spring increase in the 50—0 m samples at this station was always found in April, reaching a maximum of volume in May. In 1960, no other peaks were found, whereas a second peak occurred in August 1961 and June 1962.

The 200—0 m samples from 1960 revealed peaks in May and early July, and a slight increase in October. (Fig. 4). The same pattern was found in 1961, but as no samples were collected later than September,

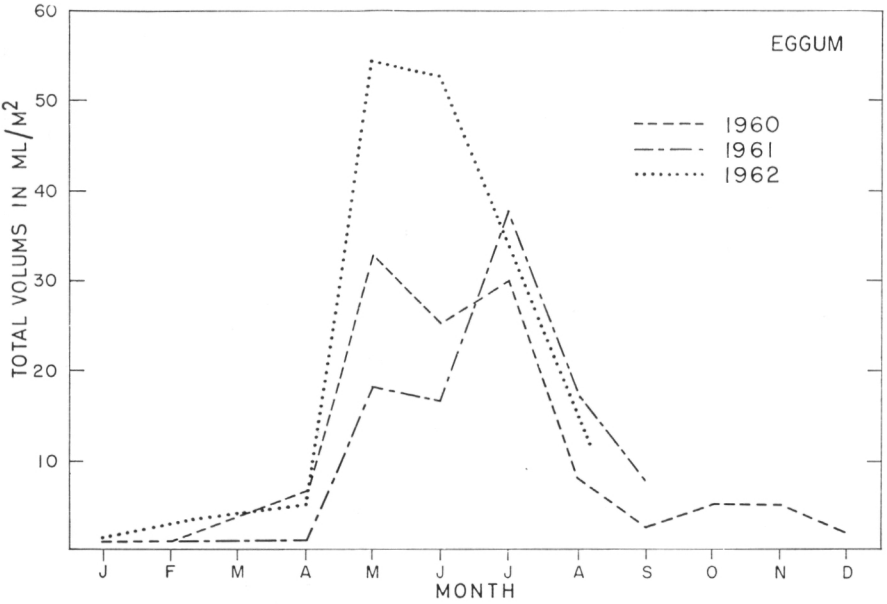

Fig. 4. Monthly mean total volumes in ml/m² of zooplankton at Eggum, 1960—1962.

an eventual third peak could not be detected. Also in 1962 the spring maximum in the 200—0 m samples was found in May, and a second peak seemed to occur at the end of June.

The zooplankton density in the winter season from September to April was extremely poor and no significant difference between the 50—0 and the 200—0 m samples was found. During the summer season, however, the volumes of the 200—0 m layer were considerably higher than the volumes of the 50—0 m samples.

WIBORG (1954, 1958) found largely the same pattern, and he emphasized the extensive variations from one year to another.

Skarsvåg. (Fig. 4)

The spring increase in the 50—0 m samples was observed from April—May. The maximum was as a rule found in July, but in 1962 it occurred as early as the middle of June. A small second peak could be detected in August—September 1960 and 1961. The volumes of the 260—0 m samples followed the same pattern.

The main part of the zooplankton seemed to be concentrated in the upper 50 m during the first half of the year, while the relative density of zooplankton in this layer decreases after the spring maximum when the plankton descends for overwintering in the deeper water layers.

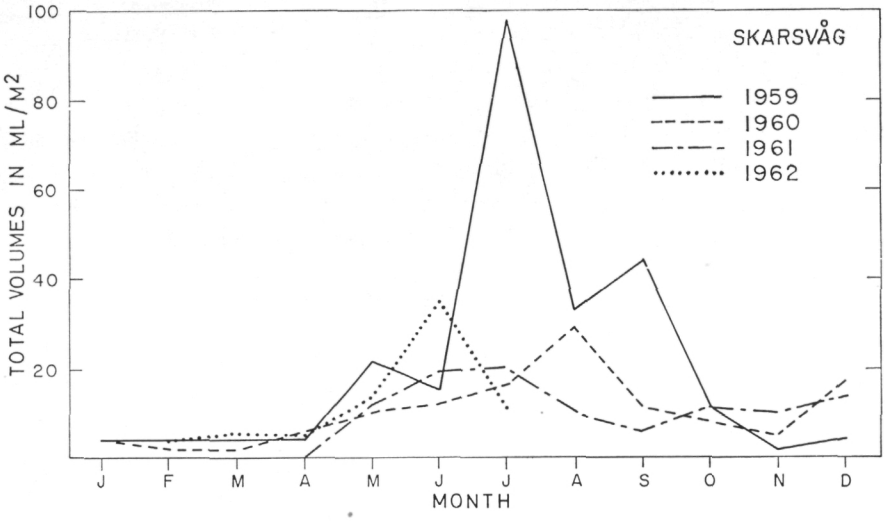

Fig. 5. Monthly mean total volumes in ml/m² of zooplankton at Skarsvåg, 1959—1962.

JASHNOV (1939a) found, at a corresponding latitude in the western Barents Sea, a minimum of zooplankton in March and a maximum in August, and no second peak was observed.

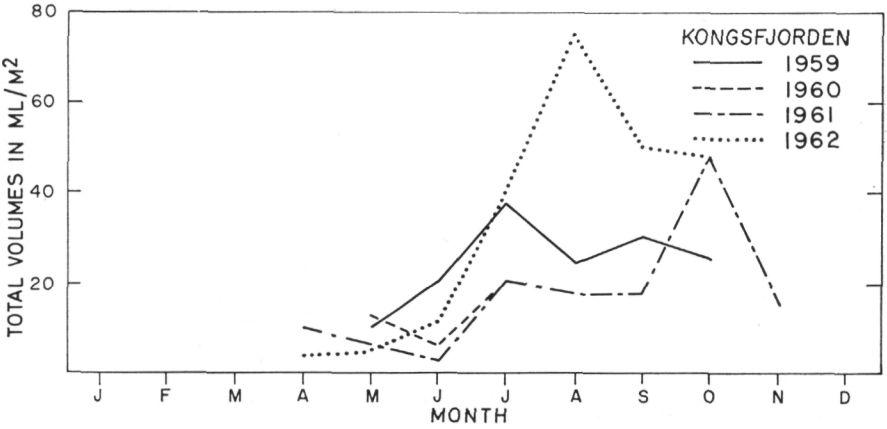

Fig. 6. Monthly mean total volumes in ml/m² of zooplankton at Kongsfjorden, 1959—1962.

Kongsfjorden (Fig. 6)

The scarcity of samples from this station prevents a complete discussion of the seasonal variations in the biomass of zooplankton. The spring increase started in June, but no general trend in the occurrence of the

maximum was revealed. However, high amounts of zooplankton were found from July, until the sampling was ended in October—November.

Up until June the main part of the zooplankton seemed to be concentrated in the upper 50 m, but from July onwards, the relative importance of the biomass of this water layer decreased steadily.

According to WIBORG (1960) the highest volumes of zooplankton were found during the last half of the year, both in 1957 and 1958.

PROPAGATIONS OF *CALANUS FINMARCHICUS* AT THE PERMANENT STATIONS, 1959—1962

Sognesjøen (Fig. 7)

The complete picture of the propagation of *Calanus finmarchicus* at Sognesjøen is rather uncertain due to the scarcity of samples. However, during all the years investigated there was a maximum of females at the end of February or the beginning of March, followed by high percentages of young copepodites during March. The main spawning evidently must have taken place in the first half of March. The percentage distribution of females, males, and young copepodites during the rest of the year indicates, as shown in Fig. 7, that spawnings also took place in early June and August.

High percentages of the copepodite stage V during summer and fall in the 200—0 m samples, indicate that only part of the spring generation

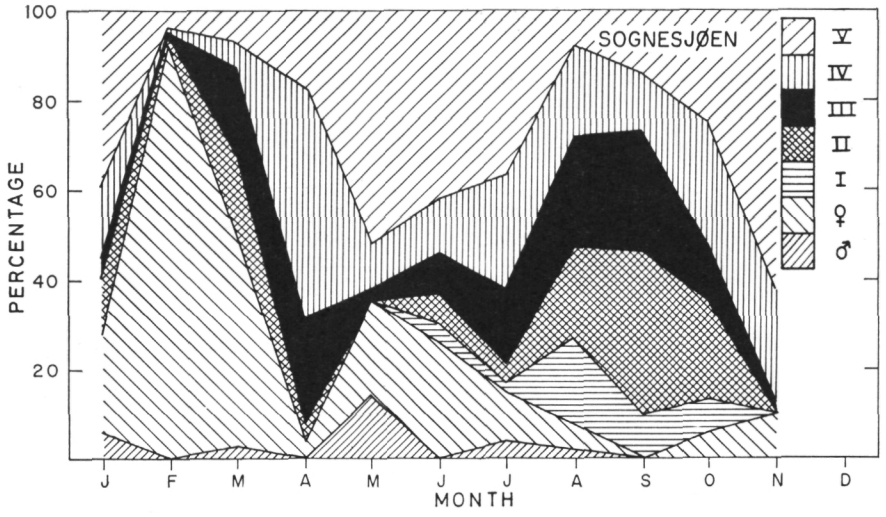

Fig. 7. Variations in the percentage distribution of males, females and copepodite stages I—V of *Calanus finmarchicus* at Sognesjøen. Monthly mean figures 1959—1962.

reaches maturity and spawns the same year, while the main part of the stock stays in the deeper waters as copepodite stages IV and V until next spring.

Three spawnings of *Calanus finmarchicus* in coastal waters of south-western Norway have been recorded by several authors (RUUD 1929, RUNNSTRÖM 1932, GUNDERSEN 1953, and WIBORG 1954), and WIBORG could even demonstrate that a fourth spawning occurred in 1949. WIBORG calls the spawning in March the "main spawning" and the later spawnings "minor spawnings", by which he probably implied that, as stated above, only a part of the spring generation takes part in the two latest spawnings.

However, as WIBORG based his terms "main" and "minor" spawnings on percentages, they do not reveal which of the spawnings actually was the most important because this will depend on the total number of animals present. In spring during the first spawning the stock is very small and, even if 100 percent of the population reaches maturity and spawns, the number of *Calanus* produced may still be smaller than the number produced by a lower percentage of adults in the autumn when the *Calanus* stock is larger. The percentage distribution of the development-stages does not therefore necessarily reveal the importance of the spawning. However, the spring spawning at all stations was followed by a sharp increase in the zooplankton biomass (Figures 2–6) which indicates that the first spawning really is the main spawning in the sense of production of new animals.

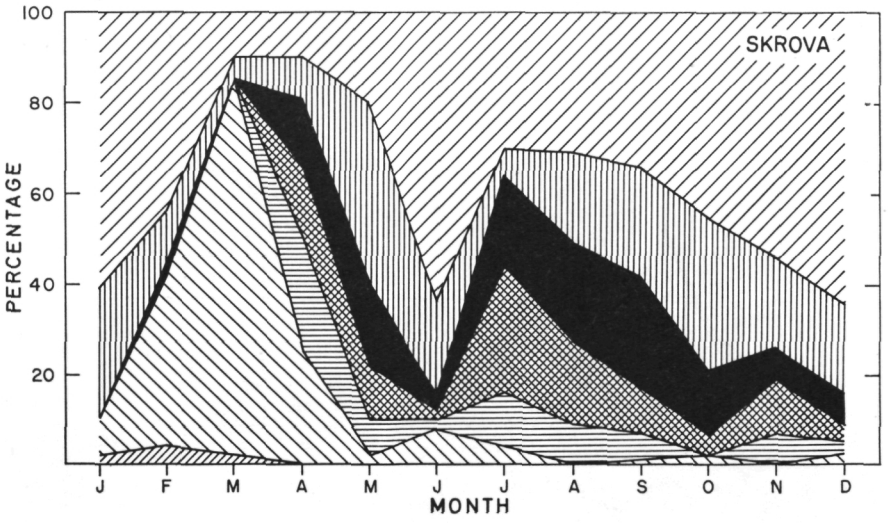

Fig. 8. Variations in the percentage distribution of males, females and copepodite stages I–V of *Calanus finmarchicus* at Skrova. Monthly mean figures 1959–1962. Symbols as in Fig. 7.

Skrova (Fig. 8)

During all the years investigated the maximum of females was found in the middle of March, and the corresponding copepodite stages I and II occurred from the end of March with a maximum in the middle of April, which indicates that the main spawning took place in the last half of March. A second peak of females occurred in June–July and high percentages of copepodite stages I and II were present from the middle of July, from which one may conclude that a second spawning of *Calanus finmarchicus* occurred in the first half of July. Fig. 8 indicates that some spawning may also have occurred in October.

High percentages of the copepodite stage V in the 300—0 m samples indicate that only a part of the spring generation spawned the same summer.

These results are in good agreement with WIBORG (1954), who stated that *Calanus finmarchicus* at Skrova spawned in April—May and in July—August. He also suggested that a minor spawning must have occurred in June. This suggestion was, however, built only on the occurrence of a small number of nauplii, and could not be followed through the copepodite stages.

Eggum (Fig. 9)

No samples from March 1961 and 1962 are available, but the occurrence of the copepodite stages I and II in April both years indicates that

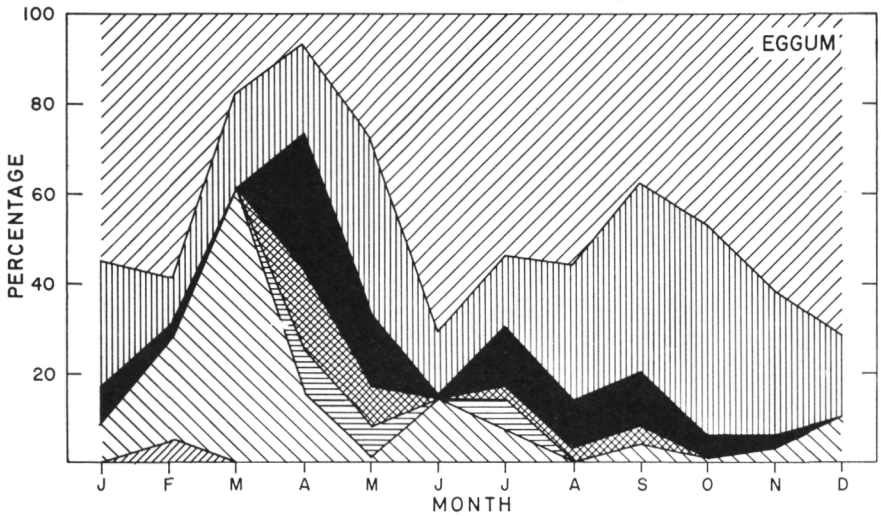

Fig. 9. Variations in the percentage distribution of males, females and copepodite stages I—V of *Calanus finmarchicus* at Eggum. Monthly mean figures 1960—1962. Symbols as in Fig. 7.

the maximum of females must have been in March, which was the case in 1960. A second peak of females was found in June—July of all the three years investigated. Both maxima of females were followed by high percentages of the copepodite stages I and II. High numbers of young *Calanus finmarchicus* were also found in September without a preceding peak of females. The material from Eggum 1960—1962, may then lead to the conclusion that there are two spawnings of *Calanus* per year; one in March and one in June—July. The young copepodites found in September may have been transported into the area from nearby populations, as suggested by WIBORG (1954). According to WIBORG there were three spawnings of *Calanus* at Eggum; in April, June and August—September. However, also in this material the last maximum of young copepodites was not preceded by a peak of females.

Skarsvåg (Fig. 10)

A maximum of females occurred each year in March—April, followed by high percentages of the copepodite stages I and II in April and May, so the spawning probably took place mainly in the first half of April. A second spawning occurred in July, as high percentages of females were found in July and the copepodite stages I and II in August.

High percentages of the copepodite stage V in the deeper water during the second spawning indicate that the spawning was of minor importance.

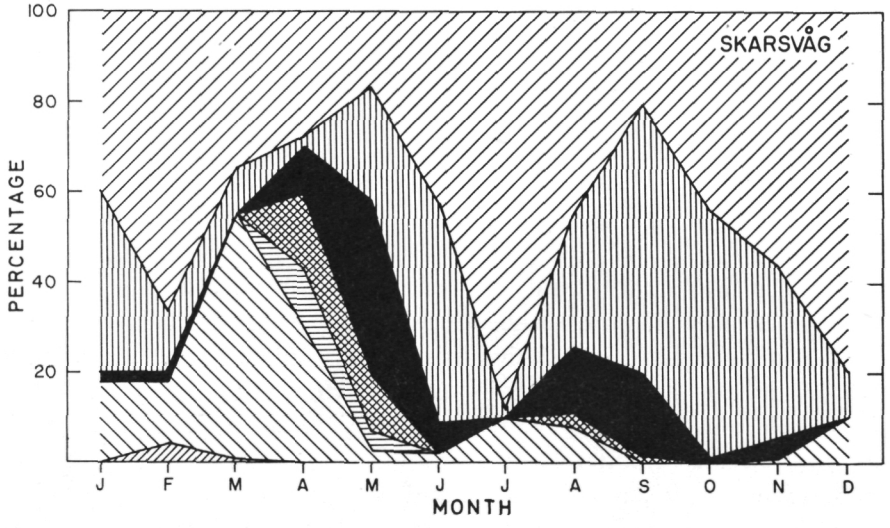

Fig. 10. Variations in the percentage distribution of males, females and copepodite stages I—V of *Calanus finmarchicus* at Skarsvåg. Monthly mean figures 1959—1962. Symbols as in Fig. 7.

No previous investigations on the propagation of *Calanus finmarchicus* from a comparable latitude in Norwegian waters have been made. According to YASHNOV (1939b) and MANTEIFEL (1939) there is only one spawning of *Calanus* per year in the southern Barents Sea and in the waters off the west Murman coast. However, according to MANTEIFEL (1941), copepodite stages I—III are found in some years from July to September in the Barents Sea without a preceding abundance of adults. MANTEIFEL concluded that these young *Calanus* were brought into the Barents Sea from Norwegian coastal waters, which supports the conclusion in the present paper that there is a second spawning in July in northern Norway.

Kongsfjorden

The scarcity of samples from this station allows no conclusions about the propagation of *Calanus finmarchicus*. The material indicates, however, that there is only one spawning per year and that no spawning takes place in the second half of the year.

DISCUSSION

At all stations along the Norwegian coast there were two pronounced maxima of volumes of zooplankton per year, while Kongsfjorden at Spitsbergen showed only one maximum. There was a significant delay in the occurrence of the spring maximum with increasing latitude, ranging from April at Sognesjøen to July at Skarvåg. A similar trend for the occurrence of the second peak could not be detected.

A complete comparison of the annual relative richness of the zooplankton from the different stations was not possible because the material collected during the winter season was too scanty for some of the stations. However, the material was fairly good for all the stations during the periode April to August, and in Table 1 is shown the mean zooplankton volumes for the different stations during this period of each year.

Table 1 indicates the relative richness of zooplankton at the different stations during the period April—August. However, one cannot draw any conclusions about the relative annual richness of the stations from the table because the plankton biomass during the last half of the year is considerably higher at Skarsvåg and Kongsfjorden than at the other stations.

The total annual biomass per station seems to be of the same order of magnitude at the four northern stations, while the biomass at Sognesjøen

Table I. Mean of monthly mean volumes in ml of zooplankton per m^2 surface from the permanent stations for the period April—August of the years 1959—1962.

Station	Year				Mean
	1959	1960	1961	1962	
Sognesjøen	10.5	8.6	No data	5.0	8.2
Skrova	19.5	46.4	25.6	27.5	29.8
Eggum	No data	20.4	32.9	31.8	28.2
Skarsvåg	31.9	12.2	12.1	15.9	18.0
Kongsfjorden	20.4	12.9	11.3	26.8	17.7

is considerable lower. This finding is supported by earlier investigations (WIBORG 1954, 1958, 1960).

WIBORG (1954) found that the richness of the zooplankton at Eggum during the spring and summer was comparable to the conditions at Georges Bank off the east coast of North America and in the Barents Sea. During the winter the zooplankton density at Eggum and Sognesjøen is extremely low, and WIBORG suggests that the strong north-going currents may carry the plankton away.

The data do not allow for conclusions as to which year was the richest because of the variation from one station to another with no general trend.

The data from the permanent stations during 1959—1962 revealed significant changes in the number of spawnings for *Calanus finmarchicus* and the time for their occurrence with increasing latitude. At Sognesjøen and possibly at Skrova three spawnings were observed, at Eggum and Skarsvåg two, and at Kongsfjorden only one. The spring spawnings occurred in the first half of March at Sognesjøen, in the last half of March at Skrova and Eggum, in the first half of April at Skarsvåg and some time between April and June at Kongsfjorden. A similar delay in the occurrence of the second spawning with increasing latitude could not be detected.

The spring spawning of *Calanus* was always followed by a sharp increase in the volumes of zooplankton, and the maximum volume was reached 1 $^1/_2$ to 2 months after the spawning. A similar increase in the volume after the second spawning was less pronounced. This may be attributed to the fact that only a small part of the stock of *Calanus* took part in the spawning, that plankton is transported into the area from nearby regions, and that neritic species are much more abundant during the late summer, reducing the relative importance of *Calanus finmarchicus*.

An attempt was made to determine the stage distribution of *Calanus* when maximum volume occurs. Although there are considerable variations from one year to another, it is probably permissible to conclude that maximum volume is found when the copepodite stages III and IV in southern Norway and IV and V in northern Norway comprise more than 50 % of the total number of *Calanus*. The relationships between the stage distribution of *Calanus finmarchicus* and the occurrence of maximum volumes should be studied more extensively, especially in boreal oceanic waters where the dominance of *Calanus* is more pronounced. The relationship might enable us to determine from a small number of samples the immediate future changes of the plankton biomass, which would be of main concern for the prediction of food availability for plankton feeding fishes.

SUMMARY

1. Zooplankton has been collected in vertical hauls from 1959 to 1962 as four permanent oceanographic stations along the coast of Norway and one from Spitsbergen. The volumes have been measured and the stage composition of *Calanus finmarchicus* determined.
2. A delay of occurrence of maximum volume with increasing latitude for the spring maximum of volume is evident, but a similar trend for the secondary maxima could not be demonstrated. The annual richness of zooplankton on the southernmost station (Sognesjøen) was considerably poorer than at the other four stations. At these the amount of zooplankton was of the same order of magnitude. There were large variations in amount of zooplankton from one year to another at all stations, and a general conclusion about the relative richness of the different years could not be made.
3. A significant delay in the time of spawning of *Calanus finmarchicus* and decreasing number of spawnings with increasing latitude was demonstrated.
4. Maximum of volume occurred about $1^1/_2$ to 2 months later than the spawning of *Calanus finmarchicus* when the copepodite stages III and IV in southern Norway and IV and V in northern Norway comprised more than 50 % of the stages. A method for prediction of biomass changes based on development-stage distribution of *Calanus* is suggested.

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REFERENCES

GUNDERSEN, K. R. 1953. Zooplankton investigations in some fjords in Western Norway during 1950—51. *Fiskeridir. Skr. Havundersøk., 10* (6):1—54.

JASHNOV, W. 1939a. [Plankton productivity of the southwestern part of the Barents Sea.] *Trans. Inst. Mar. Fish. U.S.S.R., 4*:201—224. [In Russian].

— 1939b. [Reproduction and seasonal variations in the distribution of different stages of *Calanus finmarchicus* of the Barents Sea.] *Ibid., 4*:225—244. [In Russian].

MANTEIFEL, B. P. 1939. [The zooplankton of the coastal waters of the western Murman.] *Ibid., 4*:259—294. [In Russian].

— 1941. [The plankton and the herring of the Barents Sea.] *Polar Sci. Inst. Seafish. and Oceanogr., 7*:125—218. [In Russian].

RUNNSTRÖM, S. 1932. Eine Uebersicht über das Zooplankton des Herdla- und Hjeltefjordes. *Bergens Mus. Aarb., 1931*, (Naturv. R.), (7): 1—67.

RUUD, J. T. 1929. On the biology of copepods off Møre 1925—27. *Rapp. Cons. Explor. Mer, 56*:1—84.

WIBORG, K. F. 1954. Investigations on zooplankton in coastal and offshore waters of western and northwestern Norway. *Fiskeridir. Skr. Havundersøk., 11* (1):1—246.

— 1958. Quantitative variations of the zooplankton in Norwegian coastal and offshore waters during 1949—56. *Ibid., 12* (1):1—17.

— 1960. Investigations on zooplankton in Norwegian waters and in the Norwegian Sea during 1957—58. *Ibid., 12* (6): 1—19.

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