

DET KGL. NORSKE VIDENSKABERS SELSKAB
MUSEET

MISCELLANEA

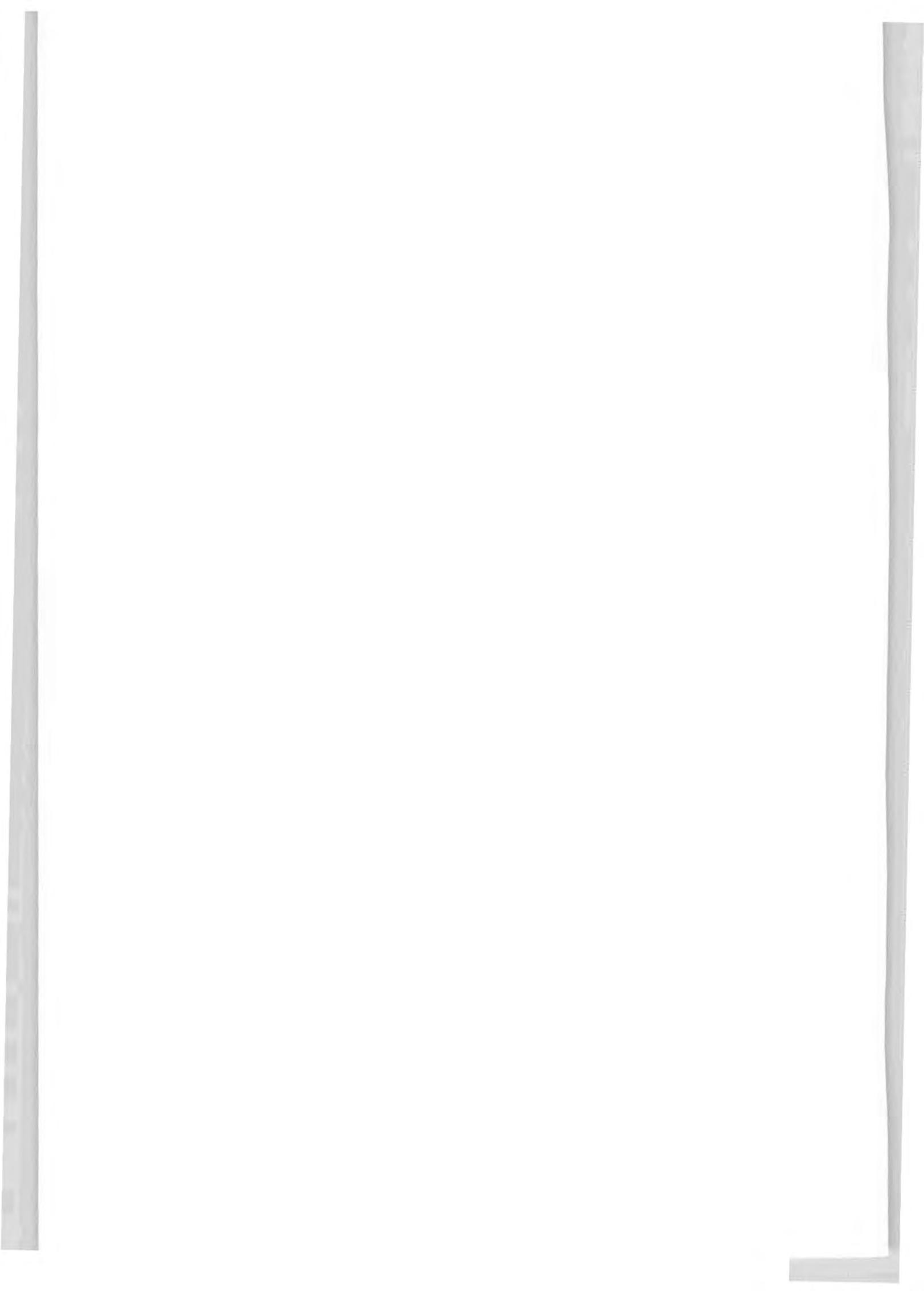
13



Tor Strømngren

ZOOPLANKTON INVESTIGATIONS
IN TRONDHEIMSFJORDEN, 1963-1966

TRONDHEIM 1973



K. norske Vidensk. Selsk. Mus. Miscellanea 13 - 1973

ZOOPLANKTON INVESTIGATIONS
IN TRONDHEIMSFJORDEN, 1963-1966

by

Tor Strømgen

University of Trondheim

The Royal Norwegian Society of Sciences and Letters, The Museum

ISBN 82-7126-014-6

ABSTRACT

Strømngren, Tor. 1973. Zooplankton investigations in Trondheimsfjorden, 1963-1966. *K. norske Vidensk. Selsk. Mus. Miscellanea* 13: 1-149.

Hydrographic and zooplankton data taken during a four year period in Trondheimsfjorden, Western Norway, are presented and discussed.

The upper layers of the fjord showed an estuarine circulation. In the deeper layers inflows occurred regularly. There were significant annual variations in these water movements.

The zooplankton volume varied greatly from year to year, and the major fluctuations seemed related to inflows and outflows in both surface and deep layers. The copepod *Calanus finmarchicus* dominated the zooplankton at all seasons, and the volume variations recorded were mainly due to this species. The autumn maxima in the upper layers, however, were strongly influenced by smaller autochthonous species.

Allochthonous species were of minor importance for the biomass. They occurred irregularly, and although immigrants might propagate, permanent stocks were not established.

The seasonal abundance, propagation, and vertical distribution of the different zooplankters in Trondheimsfjorden generally seemed to correspond with what is found on the open coast.

Tor Strømngren, University of Trondheim, The Royal Norwegian Society of Sciences and Letters, Zoological Department, N-7000 Trondheim.

CONTENTS

ABSTRACT	5
INTRODUCTION	7
MATERIAL AND METHODS	8
TOPOGRAPHY	12
HYDROGRAPHY	13
COMPOSITION OF THE ZOOPLANKTON	20
COMPOSITION OF THE COPEPODA	23
VOLUME VARIATIONS	30
COPEPODA CALANOIDA	37
COPEPODA CYCLOPOIDA	110
COPEPODA HARPACTICOIDA	118
OTHER ORGANISMS	118
TYPES OF COMPONENTS IN THE ZOOPLANKTON	137
SUMMARY	141
REFERENCES	143

INTRODUCTION

Extensive work on zooplankton has been done along the Norwegian Coast since 1900, but long term observations of zooplankton have never been carried out in a fjord. Investigations for a one year cycle have been done in Oslofjorden by Wiborg (1940), in Hardangerfjorden by Gundersen (1953) and Lie (1967), in Nordåsvannet, a landlocked locality near Bergen by Wiborg (1944), in Vestfjorden - Ofotfjorden by Sømme (1934) and partly Wiborg (1954), and in Dramsfjorden by Beyer (unpublished).

In the western coastal waters Wiborg (1954) made an extensive study for a four year period. His work has partly been continued by Lie (1965, 1966).

In addition must be mentioned the basic work of Ruud (1929) from the Møre Coast, the investigations in the Bergen area by Runnstrøm (1932) and at St. M in the Norwegian Sea, started by Østvedt (1955) and continued by Lie (1968). From Trondheimsfjorden a list of planktonic copepods was presented by Lysholm (1912). The localities referred to are indicated on the map, Fig. 1.



Fig. 1. Zooplankton investigations in Norwegian waters.

MATERIAL AND METHODS

The present investigation is based on zooplankton collected in Trondheimsfjorden. Samples were taken during the period February 1963 to July 1966 at permanent stations in the main fjord (Fig. 2).

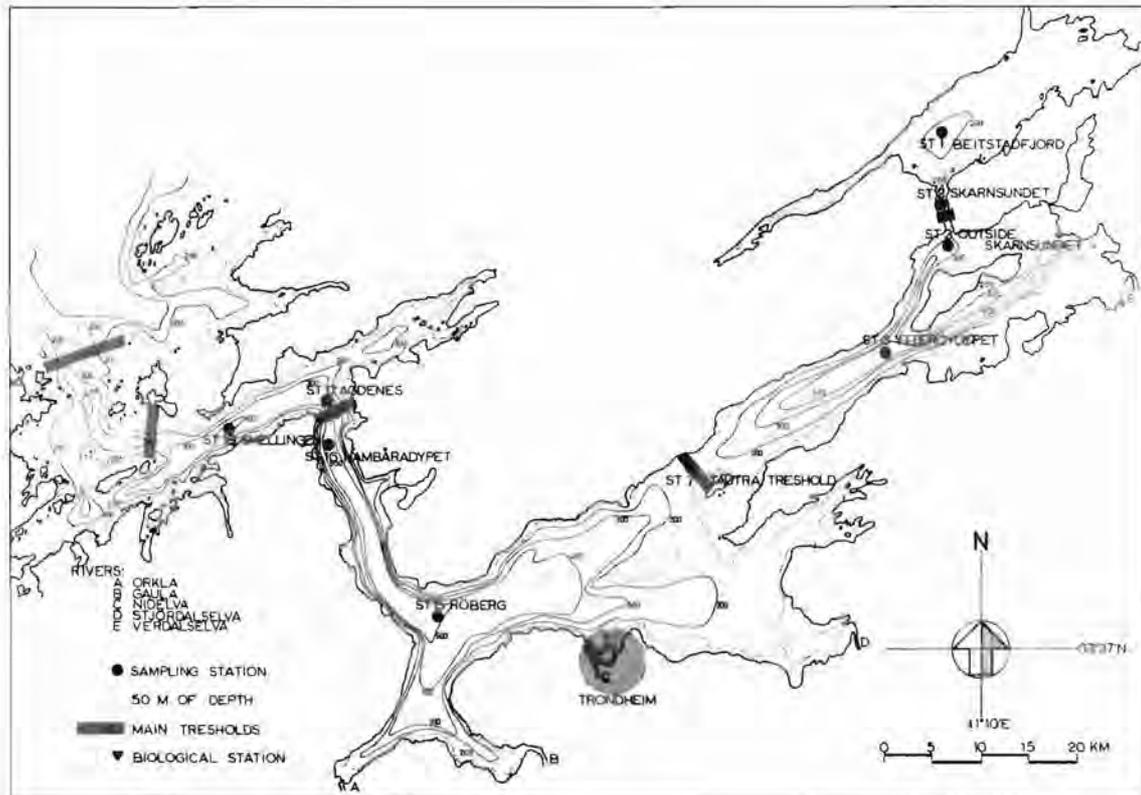


Fig. 2. Trondheimsfjorden, sampling stations and main thresholds indicated.

The stations are as follows:

- St. 1. Beitstadfjorden, depth 260 m.
- St. 2. Skarnsundet, depth 140 m.
- St. 3. Outside Skarnsundet, depth 280 m.
- St. 6. Ytterøydypet, depth 420 m.
- St. 7. Tautra threshold, depth 70 m.
- St. 15. Røberg, depth 510 m.
- St. 16. Hambåra, depth 600 m.
- St. 17. Agdenes, depth 300 m.
- St. 18. Smellingen, depth 410 m.

According to different methods and stations, the investigation may be divided into three periods:

1. February 1963 to February 1964. Samples were taken at stations 1, 2, 3, 6, 7, 15, 16, 17, and 18 in the main fjord. All hauls were vertical with a small Juday net with a diameter of 38 cm, equipped with a closing device. The net was closed at standard depths, near bottom - 100 m, 100 - 50 m, and 50 - 0 m. Mesh size of the walls of the net was 190 μ ; of the bucket approximately 440 μ .
2. February 1964 to July 1965. The number of stations were reduced to four, St. 1, 6, 15, and 18, each representing a main basin of the fjord. The closing depths were partly defined by hydrographic relations, near bottom - 100 m, 100 m - thermocline, thermocline - 0 m. The mesh size of the bucket was reduced to 190 μ .
3. July 1965 to July 1966. The number of stations were reduced to two, St. 6 and 15, representing the outer and inner fjord. The net was hauled from 100 m to the surface without a closing device. Mesh size was as during period 2.

Samples were taken monthly during winter and autumn and when possible with shorter intervals during spring and early summer (Tab. 1). Hydrographic data such as temperature, salinity, and oxygen, were collected at depths of 0, 5, 10, 20, 30, 40, 50, 60, 75, 100, 150, 200 m and further in steps of 100 m to bottom. Water samples were collected by Nansen reversing water bottles, equipped with two reversing thermometers each. The salinity was determined by the Standard Knudsen titration method and the oxygen concentration by the Winkler standard method. From May 1963 to July 1965 phytoplankton samples were taken quantitatively by water bottles at standard depths, 0, 5, 10, 20, 30, and 50 m, and qualitatively with a horizontal tow net near the surface (mesh size 78 μ). The samples from the tow net were used to check the breeding periods of the smaller copepods.

All hauls were single, and the conclusions based on such hauls must be considered with caution as the deviation from the mean is shown to be at least 30-40% (Gardiner 1931, Windsor & Walford 1936 and others).

Table 1. Sampling dates during 1963-1966

No.	1963												1964											
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
1	23			2 30		18	8 13	18	15		6	10 21	17		22		23	23	7	16	16	18		
2	23			2 30		18	8 13	18	15		5	9 20												
3	22			2 29		17	8 13	18	14		6	10 20												
6	22			3 29		17	8 12	17	14		5	9 20	16	3 21	4 21	22	24	6	15	15	18	17		
7	22			3 29		17	8 12	17	14		5	9 21												
15	21			5	2	19	10 14	19	17		3	7 18	19	2 24	5 20	24	21	4	17	13	19	10		
16	21			5	1	19	10 14	19	17		3	7 18												
17	40			6	3	20	11 15	20	18		4	8 19												
18	20			6	3	20	11 15	20	18		4	8 19	20		24		24	20	5	18	14	20		
1965																								
1	17			30		7 26	30				4		23	25	27					2	13			
8	21	16	17	31		13	6 25	29	19	19	30		1							1	30	26		
15	20	19	16			1 12	5 28		2 20	21	29		2		28		1 30	26			2	12		
18		10				2	12																	
1966																								

These figures are strongly affected by the tendency of certain species to occur in patches.

All hauls were taken during daytime, and the vertical distribution accordingly refers to daylight conditions.

The difference in mesh size from period 1 to period 2 greatly influences the number of small specimens and stages. But as the volume is mainly determined by relatively large specimens, this change in method is of less importance for the volume measurements. A number of parallel hauls were taken for control with both mesh sizes, but the deviation in volume expected for parallel hauls was not exceeded. The numbers of small specimens and stages found during period 1 must be interpreted with utmost care when compared with later periods, but may, however, be used as minimum values.

A problem with all vertical hauls is to sample the layer near the bottom adequately. Hauling was started when the wire length was the same as the depth recorded by the echo sounder. Effort was made to prevent drift of the ship, but when deep stations were sampled, even small deviations of the wire from the vertical would cause a significant error. Currents beneath the surface act in the same way. In order to sample the bottom plankton more adequately, the Beyer bottom sledge (Holme 1964) equipped with current meter and closing device, was used. However, at depths below 300 m it was impossible to control whether the sledge followed the bottom or fished pelagic. Nevertheless, the material gives a quantitative impression of the zooplankton, at least in the deepest 50 m.

Another source of error is the arrangement of the closing device. Undoubtedly, intricate arrangements mounted in front of the net significantly reduce the catch, but the simple closing mechanism used should hardly cause errors exceeding the normal deviation.

The vibrating movement of the wire when hauling probably caused a loss of plankton. This is supported by the observation that deep hauls from the bottom to the surface generally contain less plankton than divided hauls taken immediately after. This refers mainly to the plankton species inhabiting the upper zone of the water.

All samples were immediately fixed in 5% formalin and later transferred to 70% ethylalcohol.

The volume measurements were done by the displacement method with mechanical removal of interstitial water (Wiborg 1954). Gelatinous coelenterate material and large euphausiids etc. were removed before measuring. The percentage error involved in this method increases with decreasing volume and low values must be considered with caution. Large samples were subsampled in a whirling vessel, the Wiborg-Lea Plankton Divider (Wiborg 1951), before counting. Several parallel countings were made to check the method, and although no statistical treatment has been carried out, the results seem to support Wiborg's opinion that the instrument is reliable. Probably the error involved in this subsampling is small compared to the deviations introduced by the sampling method (Ackefors 1969). Subsamples with less than 300 individuals were controlled by parallel countings. Finally, the whole sample was examined cursorily for large and less numerous specimens.

Length measurements of copepods refer to carapace. The measurements were made with a Zeiss stereo microscope with built in micrometer. Each division equalled 0.040 mm for the large specimens, 0.025 mm for the small.

The relative volume of the copepods was estimated by measuring the length and diameter of the cephalothorax of each species and stage. If the cephalothorax is regarded as a cylinder, a volume may be calculated (Wiborg 1954). The volume of *Calanus finmarchicus*, copepodite stage V, was chosen to represent 100 units, and the rest were given values according to this. To obtain average values relevant to Trondheimsfjorden, measurements were carried out, if possible, on 25 individuals of each stage

of the important species from St. 18 and 1 in January, April, July, and September 1963. For species occurring singly or in very small numbers, the relative volume is estimated without individual measurements.

Product-moment correlation coefficients were calculated for the numerical variation of each possible pair of copepod species, noncopepod groups or species, important phytoplankton groups or species and temperature and salinity for the whole sampling period at St. 18, 15, 6, and 1 separately. The number of observation points included in the correlation analysis were 24, 44, 44, and 25 at St. 18, 15, 6, and 1 respectively.

TOPOGRAPHY

The main fjord penetrates 145 km inland with a moderate number of side branches. The broadest part of the fjord is approximately 16 km. A multitude of islands are scattered about at the mouth of

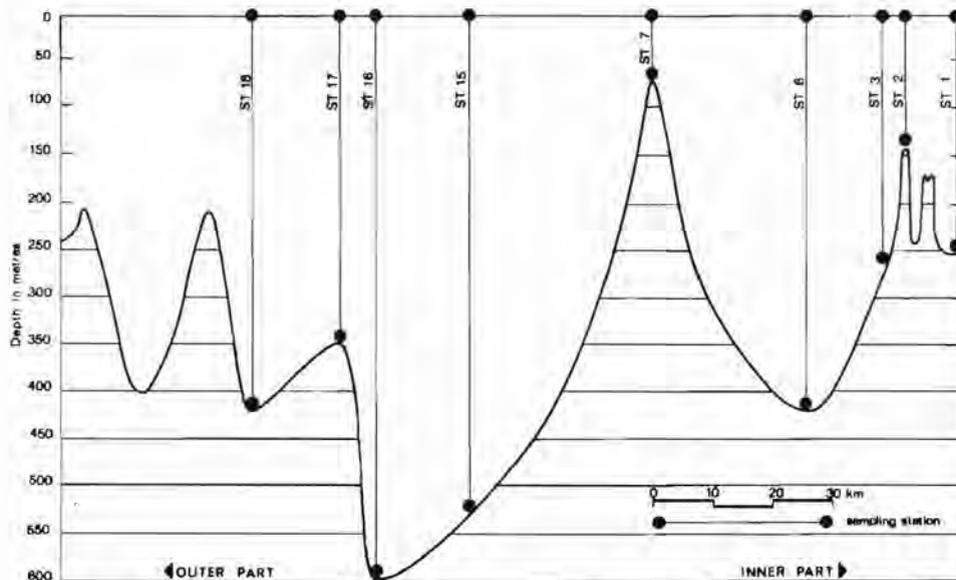


Fig. 3. Trondheimsfjorden, longitudinal section with sampling stations indicated.

the fjord, but very few islands are found within the fjord proper. Bathymetrically the main fjord consists of five main basins, separated by sills as indicated in the bathymetrical chart, Fig. 3. The bottom line is taken along the maximum depth of the fjord. The greatest depth in each basin is as follows, from the outer to the inner part: 410 m (inside Fjellværøy), 420 m (St. 18), 600 m (St. 16), 420 m (St. 6), 260 m (St. 1).

The outer sill at Fjellværøy, depth 207 m, separates the fjord area from the Norwegian Sea. The sill at St. 17, Agdenes, indicates the border between the fjord proper and the outermost part which is more influenced by coastal water. The Tautra threshold, with depth approximately 70 m, is found in the middle of the fjord between the third and the fourth basin. This threshold divides the fjord proper into an outer and an inner part. The outer part of the fjord proper lays in an eastward direction, while the inner part is directed more northerly. Thus the dominating wind directions may have different effects on the surface water and the distribution of the planktonic organisms in the outer and inner fjord. The innermost basin, Beitstadfjorden, is connected with the rest of the fjord by a rather narrow channel of 140 m depth.

HYDROGRAPHY

A survey of the hydrography of Trondheimsfjorden during 1963-66 is given in Figs. 4-11 showing isopleths for temperature, salinity, and oxygen. A more detailed description of the hydrography of Trondheimsfjorden is given by Wendelbo (1970).

The main hydrographic changes in the fjord generally follow the same trend each year. In the months January, February, and March, cooling of the surface water combined with reduced freshwater supply lowers the stability and causes normally a vertical winter mixing in the upper 5-50 m, as demonstrated by the temperature and oxygen isopleths. At the outer stations the winter mixing may be traced even below 100 m by increase in the oxygen level. The vertical mixing is reduced inwards due to greater stability in the inner fjord. A similar effect was found in the Oslofjord (Gade 1968), where a tendency for greater vertical

exchanges in the outer part was a general feature. In 1966 the winter cooling was extraordinarily strong. The stability was low and a deep winter mixing occurred even at the inner stations. The vertical mixing in the upper layers was followed by a deep inflow indicated by oxygen increase in the bottom layers.

The winter mixing normally supplies the uppermost layers with saline and relatively warm water with temperature above 7° . During the following months, April, May, and June, the supply of fresh water increases, mainly due to ice melting.

The surface salinities in April were highest in 1963 and 1966, probably corresponding to the small freshwater supply in early spring those years. The minima in surface salinities were observed in May-June, corresponding to maximal river discharge.

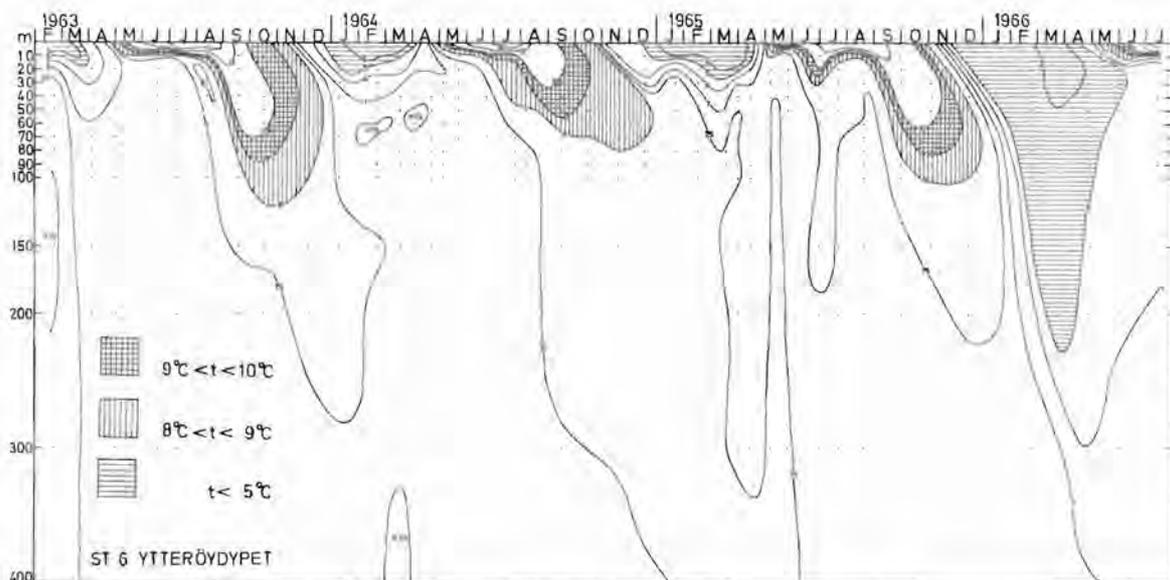


Fig. 4. Temperature isopleths 1963-66 at St. 6. (Modified from Wendelbo 1970).

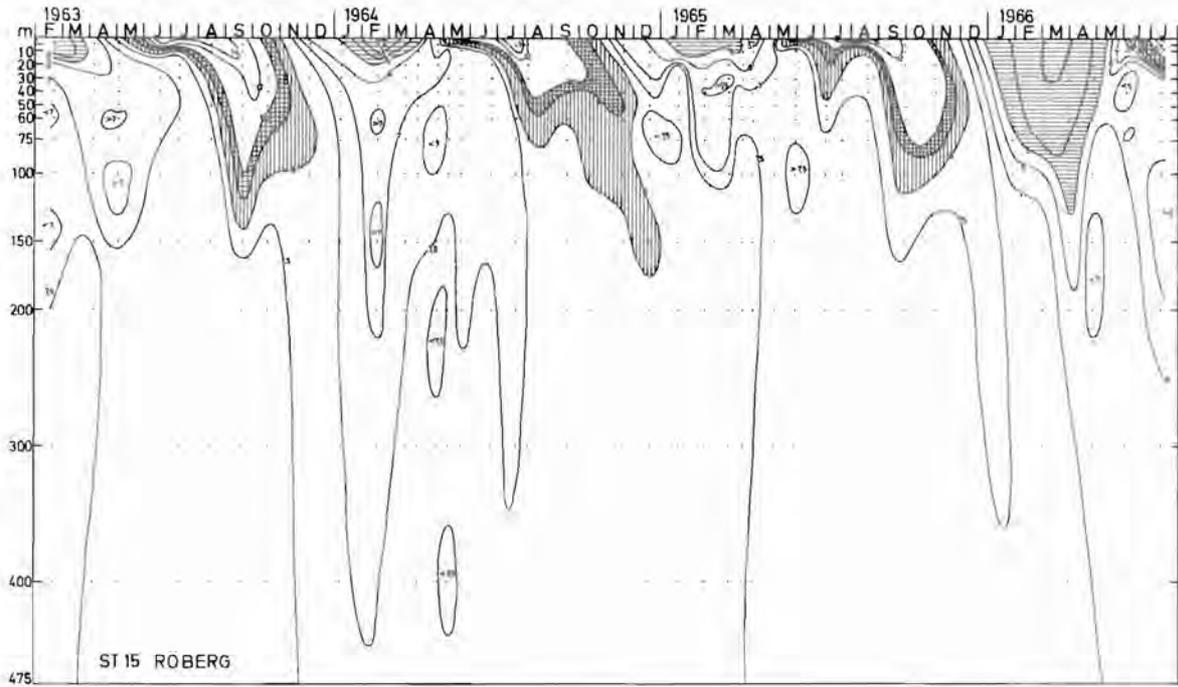


Fig. 5. Temperature isopleths 1963-66 at St. 15. Symbols as in Fig. 4. (Modified from Wendelbo 1970).

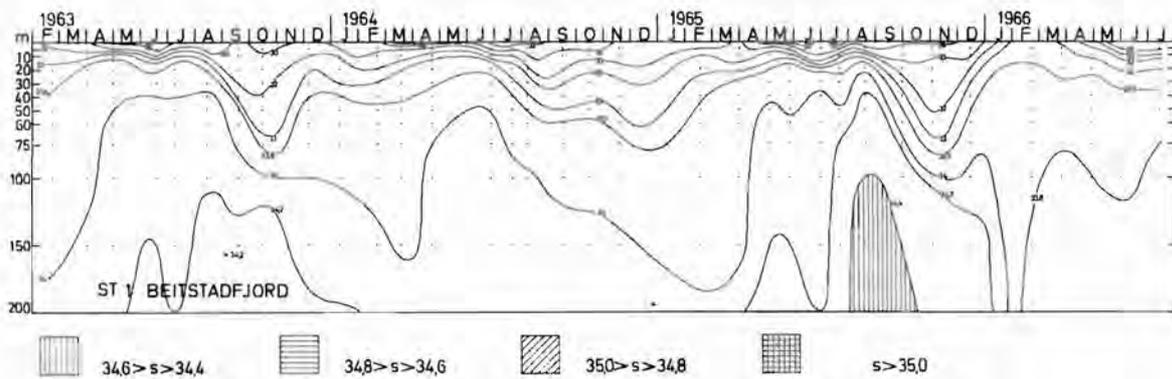


Fig. 6. Salinity isopleths 1963-66 at St. 1. (Modified from Wendelbo 1970).

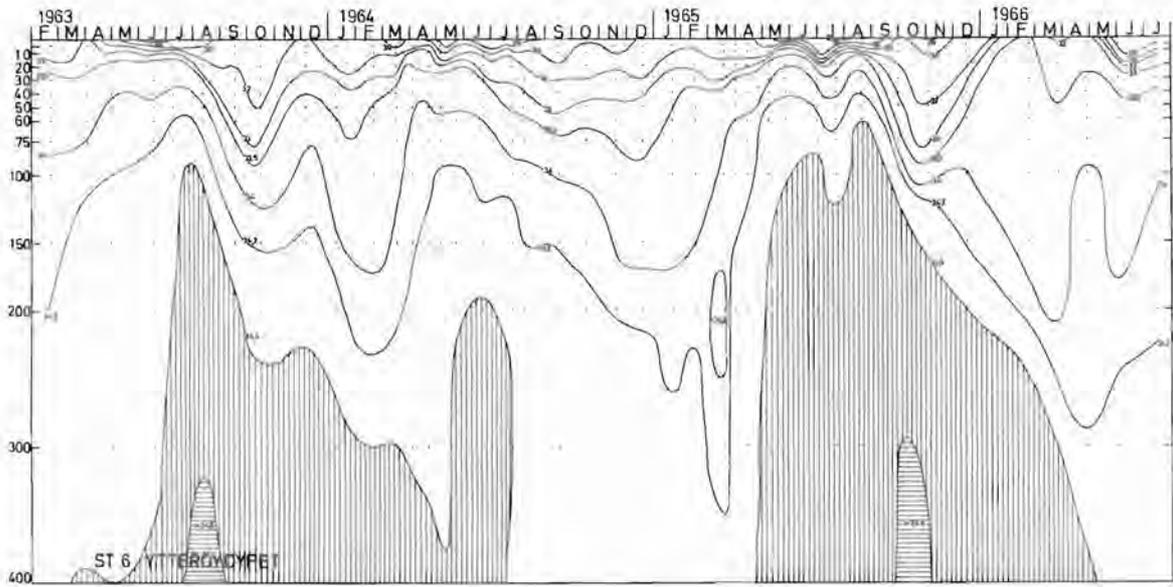


Fig. 7. Salinity isopleths 1963-66 at St. 6. Symbols as in Fig. 6.
(Modified from Wendelbo 1970).

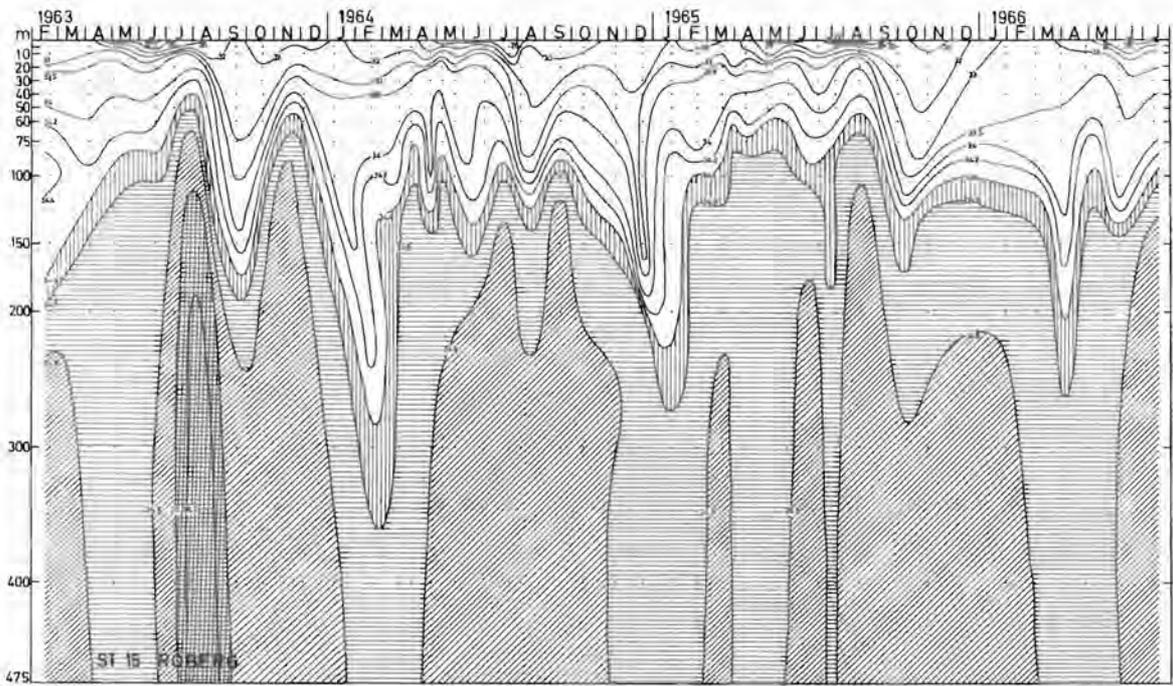


Fig. 8. Salinity isopleths 1963-66 at St. 15. Symbols as in Fig. 6.
(Modified from Wendelbo 1970).

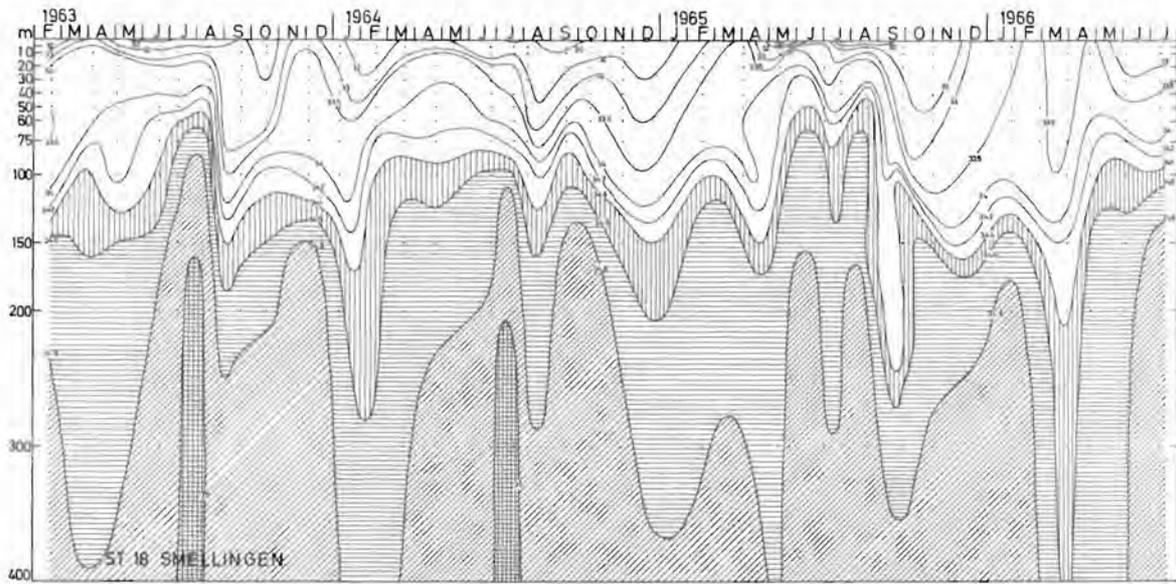


Fig. 9. Salinity isopleths 1963-66 at St. 18. Symbols as in Fig. 6.
(Modified from Wendelbo 1970).

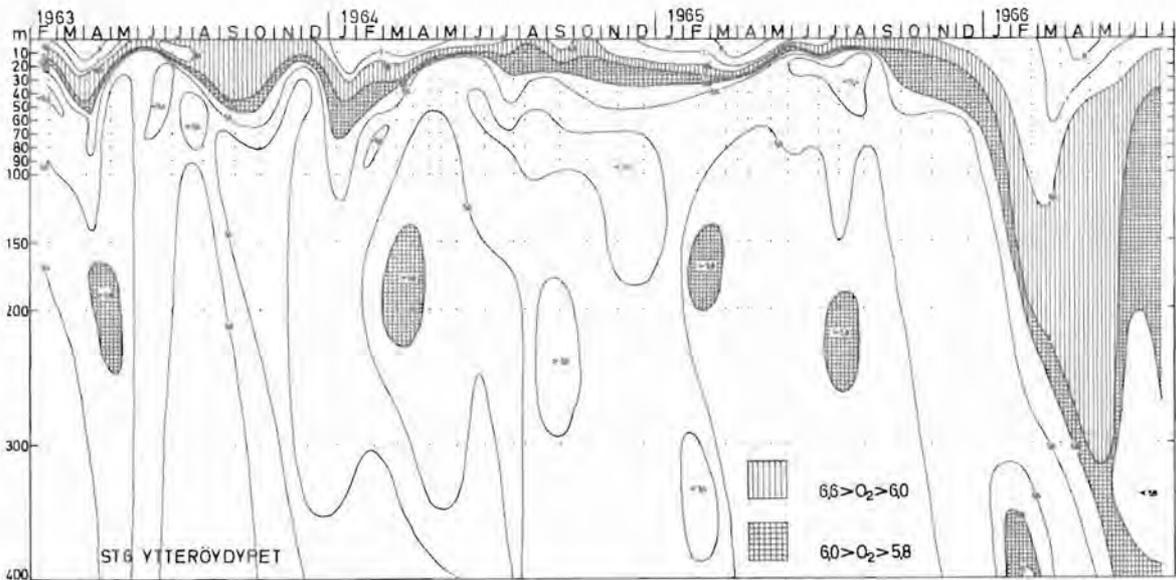


Fig. 10. Oxygen isopleths 1963-66 at St. 6. (Modified from
Wendelbo 1970).

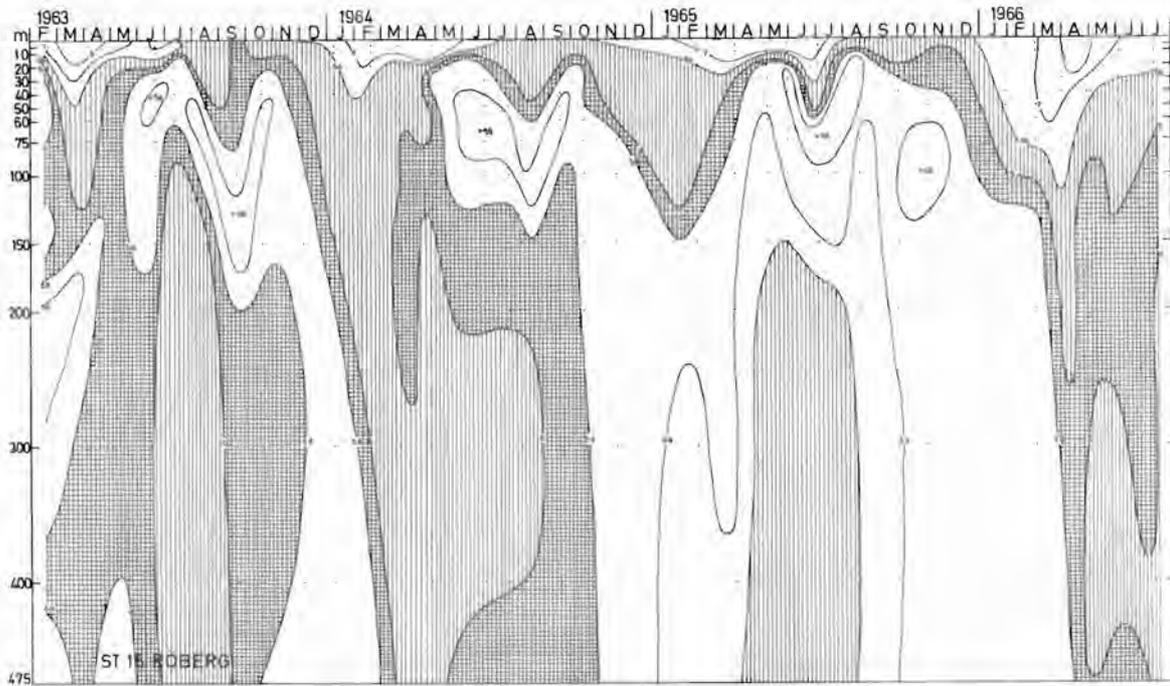


Fig. 11. Oxygen isopleths 1963-66 at St. 15. Symbols as in Fig. 10.
(Modified from Wendelbo 1970).

The reduction of surface salinity and the start of the vernal warming increase the stability and the halocline becomes more distinct.

Below the halocline an ingoing counter current is induced and an introduction of saline water is demonstrated by the rise of the $34.6^{\circ}/\text{oo}$ isopleth at St. 18 and 15, and of the $34^{\circ}/\text{oo}$ isopleth at all stations.

In July, August, and September the summer heating of the upper layers reaches its maximum, and gradually the deeper layers increase in temperature due to diffusion and vertical mixing.

The stability in September is very low. The salinity in the upper layers is reduced, and a transport of less saline water from the coast is indicated. Simultaneously the mean temperature of the upper 100 m increases due to an advective supply of heat. A similar temperature effect is described from Hardangerfjorden (Sælen 1969).

The freshwater supply to the surface layer in autumn is variable, and in 1963 small quantities were recorded compared to 1964,

as indicated by surface salinities. In 1963 a relatively strong westerly wind seems to have caused an ingoing surface current at the outer stations, while in 1964 the brackish water runoff seemed to be strong enough to persist in spite of the wind. In October-December the upper layers were still unstable. The surface salinity increased, and the winter cooling started.

In the deeper layers of Trondheimsfjorden several inflows seem to take place throughout the year, as demonstrated by the salinity and the oxygen isopleths (Figs. 6-11). The early spring inflows have been discussed earlier. These inflows are not characterized by high salinity; the inflows later in the year, however, are more saline. At the outer stations 18 and 15 the deep autumnal inflows may be traced by salinities of approx. $35^{\circ}/\text{oo}$. When passing the Tautra threshold the salinity is reduced, and at St. 6 salinities above $34.6^{\circ}/\text{oo}$ and $34.2^{\circ}/\text{oo}$ respectively may be used to trace the inflows. Both the number and the strength of the inflows seem successively reduced by the thresholds. In 1963 the summer-autumn deep inflow was successively delayed from July at St. 18 to August-September at the inner stations. The strength of this inflow is demonstrated by salinities above $35.2^{\circ}/\text{oo}$ at St. 15 in August.

In 1964 an inflow at St. 18 in July seemed fairly strong, while only a relatively weak indication of the same inflow was found at St. 15, and at the two inner stations it was difficult to detect.

At the inner stations 6 and 1 a massive introduction of saline water started in May-June 1965 as indicated by salinities between 34.2 and $34.6^{\circ}/\text{oo}$. A separate inflow in August 1965 was indicated at all stations, but salinities of $35^{\circ}/\text{oo}$ were not recorded even at St. 18. At the two outer stations, particularly at St. 15, a very thorough change of the hydrographic development, perhaps a reversing of the current systems, seems to have taken place in July 1965.

During the sampling period the deep inflows did not coincide with any drastic change in temperature (Figs. 4-5) but an increase in oxygen content is clearly demonstrated (Figs. 10-11). Both the trend of the oxygen isopleths for 6 ml/l in the depths at St. 15, and the salinity isopleths for $34.4^{\circ}/\text{oo}$ closely following the $34.8^{\circ}/\text{oo}$ isopleth demonstrate that the deep inflows may at least influence the water from

bottom to about 100 m of depth.

The high salinity of the deep inflows in summer-autumn indicates an Atlantic origin, while the warm intermediate and subsurface water that enters the fjord is probably a mixture of Atlantic and coastal water.

COMPOSITION OF THE ZOOPLANKTON

The general composition of the zooplankton is demonstrated in Figs. 12-15, calculated in per cent of number of organisms. St. 15 is representative for the outer main fjord, St. 6 for the inner.

100-0 m, Figs. 12-13

The copepods form the main bulk of the zooplankton and in the period October-February they comprise more than 95% by number. The remaining 5% was composed to a great extent by bottom invertebrate larvae,

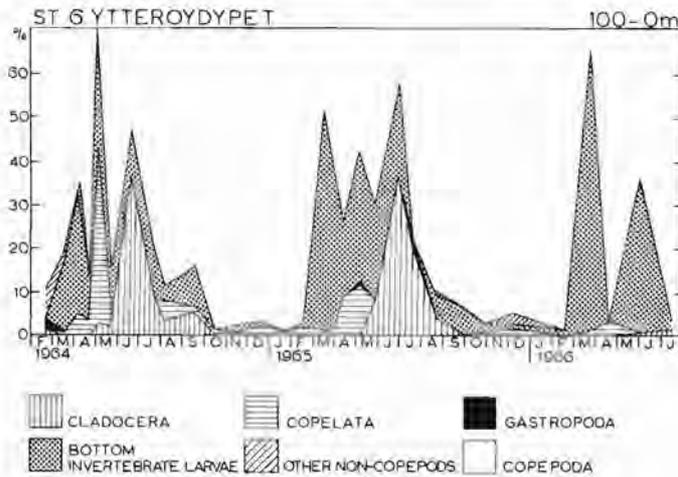


Fig. 12. Percentage composition of the zooplankton in 100-0 m at St. 6 during 1964-66.

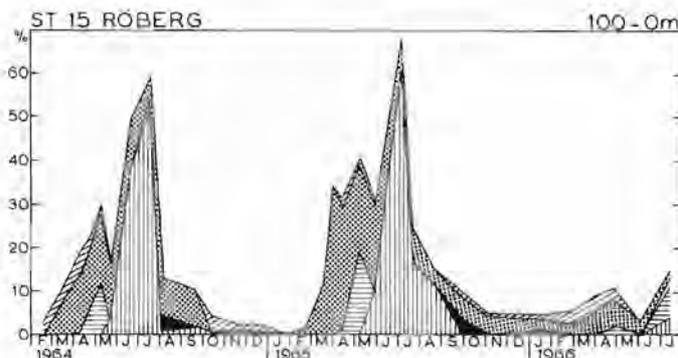


Fig. 13. Percentage composition of the zooplankton in 100-0 m at St. 15 during 1964-66. (Symbols as in Fig. 12).

mainly cirriped larvae. During spring the bottom invertebrate larvae increased in number, and this together with an increase in the Copelata stock reduced the copepod component to 60-70%. This percentage was further reduced to 30-40% in summer, mainly due to large numbers of Cladocera. In late summer the gastropod *Limacina retroversa* contributed with a small, but significant part mainly in the outer fjord.

Below 100 m, Figs. 14-15

In the layers below 100 m the variations throughout the year are smaller. As in the layer above, the copepods formed the bulk of the zooplankton with 90-95% in July-February, while the rest of the plankton was composed by Ostracoda, Chaetognata, Euphausiacea, and other noncopepods. During springtime the upward migration of important copepods with an increase in the stock of Ostracoda and Chaetognata reduced the copepod component to 50-70%.

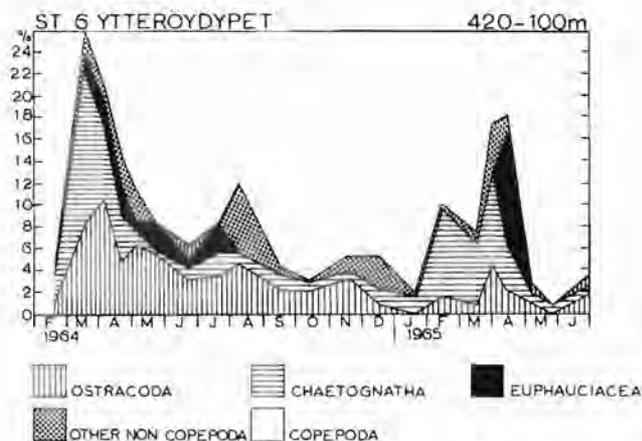


Fig. 14. Percentage composition of the zooplankton below 100 m at St. 6 during 1964-65.

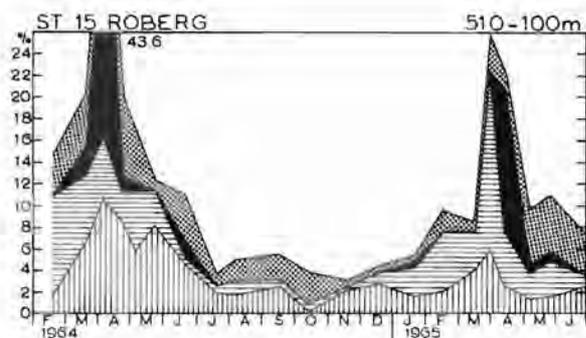


Fig. 15. Percentage composition of the zooplankton below 100 m at St. 15 during 1964-65. (Symbols as in Fig. 14).

From July to February the copepods formed the main bulk of the zooplankton, in average 70-80 per cent of numbers.

In spring the zooplankton was dominated by bottom invertebrate larvae, making in average 80 per cent of numbers in March-April.

Cladocera occurred in small numbers most of the year, but was significant only in summer from June to August-September. Copelata occurred regularly and seemed to be most important in spring. The gastropod *Limacina retroversa* was found in small numbers at all seasons, but was not important.

Comparison between the two layers

A general trend for both layers at all stations is a great and regular seasonal fluctuation each year, but a significant difference is found in the origin of the fluctuations. In the layer above 100 m maxima of noncopepods reflect a succession of species, while in the deeper layers the variations are due to fluctuations within the permanent members of the community.

The biological spring, indicated by larvae and young stages of holo- and meroplanktonic groups, occurs quite simultaneously in the whole water column. No significant differences either in time of maxima or in relative importance of the main groups are found from the outer to the inner fjord. The only major exception is the gastropod *Limacina retroversa* with reduced importance inwards in the fjord.

Comparison with other areas

Percentage composition of the zooplankton from the coast stations is given by Wiborg (1954) and refers to the whole water column. They are therefore not directly comparable to the results given here, but the upper 100 m in the fjord seems to correspond roughly to the total water column at the open coast stations.

The same general trend is found at all Norwegian localities, with the copepods dominating most of the year and the same succession

of different groups. Trondheimsfjorden seems to have a greater percentage of noncopepods during spring and early summer, the difference mainly caused by neritic and meroplanktonic components as Cladocera and bottom invertebrate larvae. Due to its position in the outer part of Vestfjorden, the coast station at Skrova has a significant percentage of deep water species such as Chaetognata and Ostracoda which mainly occur in the layers below 100 m in Trondheimsfjorden. In Oslofjorden (Wiborg 1940) the zooplankton community, Ostracoda excluded, was very similar to Trondheimsfjorden, both in composition and in seasonal succession. Wiborg found great differences between the outer and the inner Oslofjord, but a parallel to that was not observed in Trondheimsfjorden. In Hardangerfjorden the copepods dominated at all seasons in 100-0 m during 1955-56, while Cladocera and bottom invertebrate larvae were of little importance and Gastropoda was absent (Lie 1967).

COMPOSITION OF THE COPEPODA

The composition of the copepods is given in percentage of numbers and of relative volume units.

The percentage composition based on numbers in 100-0 m and below 100 m is shown in Fig. 16-19.

100-0 m, Figs. 16-17

Seasonal fluctuations occurred regularly each year. From October to May autochthonous species dominated. This period was characterized by low concentration of zooplankton in the 100-0 m layer.

In the beginning of this period, from October to February, *Microcalanus pusillus* plays an important role numerically, constituting up to 50% of the copepods. Its dominance increased inwards in the fjord. To some extent *Scolecithricella minor* followed the same pattern as *Microcalanus*, with percentages up to 50%, although it normally formed about 10% of the stock. These two copepods together with *Oncaea borealis* constituted nearly the entire copepod stock during this period. The rest of

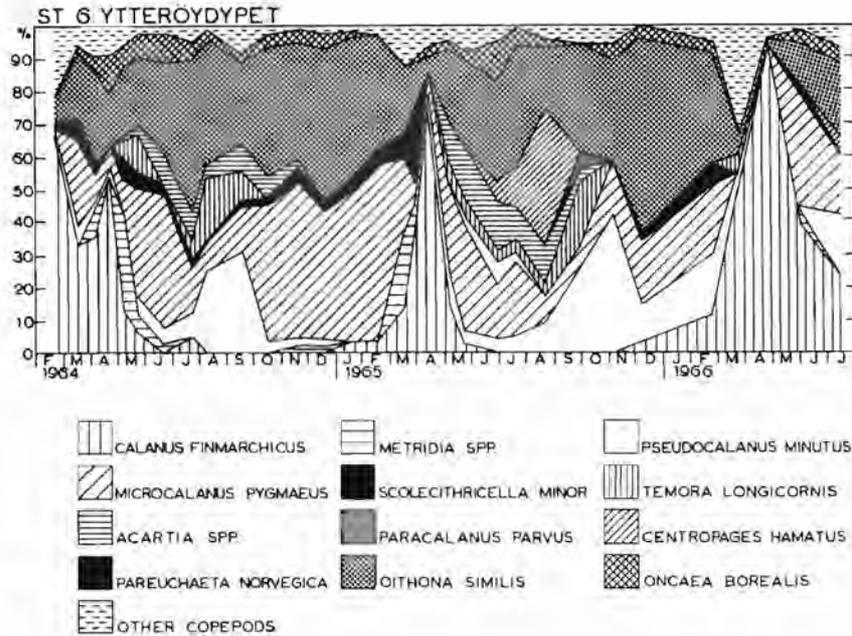


Fig. 16. Percentage composition of the copepods in 100-0 m at St. 6 during 1964-66

the winter period, from March to May, the importance of *Calanus finmarchicus* increased greatly, contributing up to 90% of the copepod stock. This rise coincided with the upward migration and spring spawning of *C. finmarchicus*.

From June to September *Temora longicornis*, *Acartia* spp., *Paracalanus parvus* and *Centropages hamatus* made up to 50% of the copepod stock. This component seemed partly dependent on influx and this pattern was reflected by reduced percentages at the inner stations. *O. borealis* was still of great numerical importance and formed together with *Oithona similis* 30-40% of the copepods.

In September-October the percentage of *Pseudocalanus elongatus* increased to 30-40%.

As shown in Figs. 16-17, 11 species of copepods were responsible for nearly 95% of the stock in the upper 100 m. The variation in percentage was partly due to a seasonal variation within the autochthonous species and partly to a regular succession of less autochthonous species.

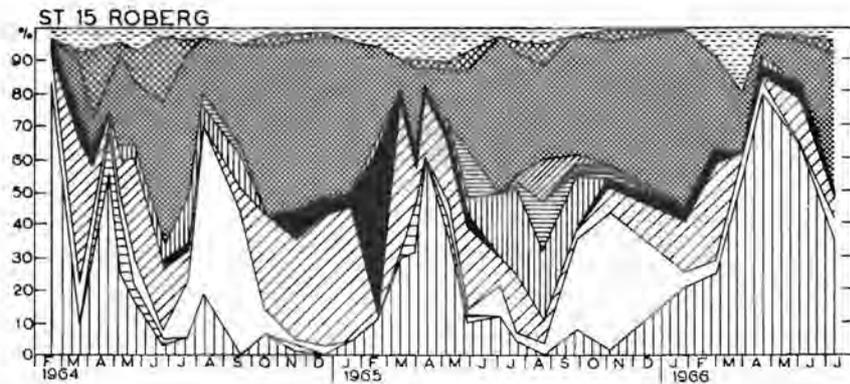


Fig. 17. Percentage composition of the copepods in 100-0 m at St. 15 during 1964-66. (Symbols as in Fig. 16).

Below 100 m, Figs. 18-19

In the layers below 100 m the number of important species is reduced to eight. These copepods constituted more than 95% of the copepod stock. Most of the summer and autumn species which occurred in the layer above were absent; they were replaced by two deep water autochthonous species, *Metridia longa* and *Pareuchaeta norvegica*.

The seasonal fluctuations were smaller than in the layer above, and the species composition was stable.

Calanus finmarchicus dominated in all parts of the fjord, but its importance was significantly reduced at the inner stations. The reduction of *C. finmarchicus*, which regularly occurs in April-May, was partly due to a migration of maturing *C. finmarchicus* to the layer above. Reduced importance of *C. finmarchicus* was followed by increasing percentages of *Microcalanus pusillus*, *Oithona similis*, *Oncaea borealis*, and *Metridia longa*. The percentage of *Scolecithricella minor* found during most of the year was unexpectedly large compared to that of *Pseudocalanus elongatus*.

Pareuchaeta norvegica contributed a small, but significant percentage in March-May at all stations. Due to its great size, this copepod has an importance far exceeding its numerical value.

In both layers the boreal and boreo-arctic species dominated. This is in accordance with the statement by Gran (1902) and Damas (1905)

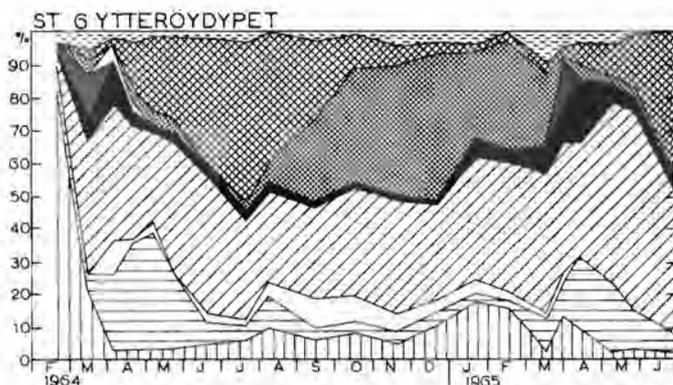


Fig. 18. Percentage composition of the copepods below 100 m at St. 6 during 1964-65. (Symbols as in Fig. 16).

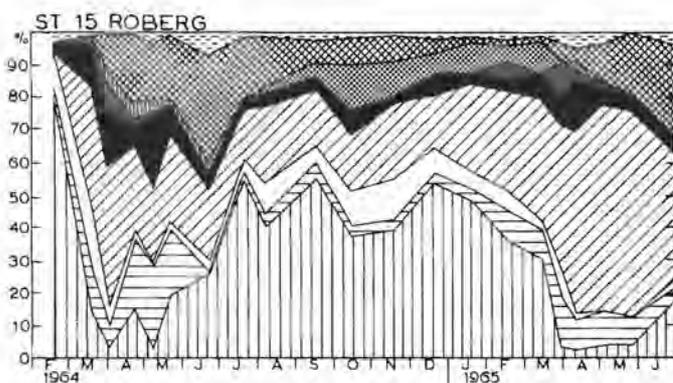


Fig. 19. Percentage composition of the copepods below 100 m at St. 15 during 1964-65. (Symbols as in Fig. 16).

that in the Norwegian Sea the main body of the zooplankton consists of autochthonous boreal species.

Comparison with other areas

The composition of the copepods in Trondheimsfjorden and at the coast stations also shows the same general trend with the autochthonous boreal species dominating. At the southernmost coastal station, Sognesjøen (Fig. 1), the importance of *C. finmarchicus* is significantly smaller than at the coastal stations further north. The reduction of the *Calanus* percentage at Sognesjøen corresponds to the composition in 100-0 m in Hardangerfjorden as shown in Table 2, calculated from Lie's

data (Lie 1967). Compared to the same layer in Trondheimsfjorden there is a significant reduction in the percentages of *Calanus* during the main spawning period. In both fjords there is a decrease inwards, but this is most marked in Hardangerfjorden. In Hardangerfjorden the percentage of *Calanus* ranges in spring from 34% in the outer part (H7) to 15% in the inner part (H5), while in Trondheimsfjorden the values are 80-90% and 45% respectively.

Table 2. Relative importance of *Calanus finmarchicus* in percentage of total number of copepods in Hardangerfjorden 1955-56.
(Calculated from Lie (1967))

	1955				1956								
	S	O	N	D	J	F	M	A	M	J	J	A	S
H7	1.0	6.0	19.5	10.0	11.5	28.0	29.0	34.0	31.5	44.0	44.5	29.0	3.0
H6	6.5	15.5	3.0	6.5	1.5	4.0	2.0	32.5	12.0	12.0	22.0	28.5	4.0
H5	8.5	9.0	2.0	2.5	2.0	26.0	5.0	15.0	1.0	3.5	12.5	7.5	2.0

During autumn the southern species *Paracalanus parvus* is important in Hardangerfjorden (from 30-60% in September 1955), while it is quite insignificant in Trondheimsfjorden.

Percentage composition of copepoda

based on relative volume

The percentage composition based on numbers greatly favours small and numerous species and stages, and may give a false impression of the relative importance of the members of the copepod stock.

The relative quantity of the various species and stages based on a common unit may be estimated either in absolute or relative values of volume or weight (Lohmann 1908), Bogorov & Preobrajenskaya 1934,

Bigelov & Sears 1939, Wiborg 1954 and others). The sources of error are numerous. Firstly, the values measured and calculated in one area cannot be directly transferred to another, since length, volume, and weight of different species and stages vary both in time and space according to environmental factors. Volume calculations by Wiborg (1954) give differences of more than 100% for several species and stages when the coastal stations Ona and Skrova are compared. In spite of the errors involved, several authors have found such methods useful, when interpreted with caution. The relative volume of the copepods was estimated by measuring length and diameter of the cephalothorax of each species and stage. If the cephalothorax is regarded as a cylinder, a volume may be calculated.

The relative volumes found in Trondheimsfjorden (Table 3) are in good accordance with those given by Wiborg (1954). It must be stressed that the calculations are based on means from different seasons for one year only, but will nevertheless give a rough picture of the relative importance of the different species.

As the absolute density of planktonic copepods in a living state might be supposed to be of the same order as the absolute density of the sea water, the diagrams based on relative volume may give a very rough picture of the relative biomass of the different species.

The composition of copepods in *Calanus* units in 100-0 m and below 100 m, shows a similar picture at all stations in the main fjord. Figs. 20-21 show the composition at St. 15. *Calanus finmarchicus* dominated in 100-0 m most of the year, and *Metridia longa* was of significant importance. Small species such as *Oithona similis* and *Oncaea borealis* represented a much smaller percentage than when the calculations were based directly on numbers, while summer and autumn species, *Temora longicornis*, *Acartia longiremis*, *Centropages hamatus*, and *Pseudocalanus elongatus* generally showed unchanged percentages. At the innermost station, St. 1, temperate species were of less importance.

Below 100 m *C. finmarchicus* dominated completely and together with *M. longa* averaged nearly 80% of the total stock. At the inner stations *M. longa* had a relatively greater importance. The large copepod *Pareuchaeta norvegica* was of significant percentage mainly in spring, and these three copepods together with the small percentage of *Scolecithriella minor* generally represented nearly 90% of the stock.

Table 3. Relative volume of the copepods in Trondheimsfjorden.

Calanus finmarchicus copepodite stage V = 100

	♂	♀	V	IV	III	II	I	N
<i>Calanus finmarchicus</i>	140	140	100	50	15	4	1.5	0.5
<i>Calanus hyperboreus</i>	700	700	500	200	40			
<i>Pareuchaeta norvegica</i>	600	1000	700	300	50	10	3	1
<i>Metridia longa</i>	100	100	60	30				
<i>Metridia lucens</i>	40	40	20	5				
<i>Metridia</i> spp.				10	4	1.5	0.5	0.5
<i>Heterohabdus norvegicus</i>	80	100	40	10	4	1.5	0.5	

	♂	♀	V-IV	III-II-I	N
<i>Pseudocalanus minutus</i>	7	9	7	2	0.1
<i>Microcalanus pygmaeus</i>	2	2	1	0.5	
<i>Scolecithricella minor</i>	9	13	8	2	
<i>Temora longicornis</i>	5	5	4	1	0.2
<i>Acartia</i> spp.	4	4	2.5	0.5	0.1
<i>Paracalanus parvus</i>	4	4	2.5	0.5	
<i>Centropages hamatus</i>	8	8	6		
<i>Centropages typicus</i>	16	16	10		
<i>Centropages</i> spp.				2	0.1
<i>Candacia norvegica</i>	50	50	20	5	
<i>Candacia armata</i>	15	15	8		
<i>Candacia</i> spp.			2	0.2	
<i>Chiridius armatus</i>	120	200	90	10	1

<i>Oithona</i> spp.				2	
<i>Oncaea borealis</i>				1	
Harpacticoida				1	

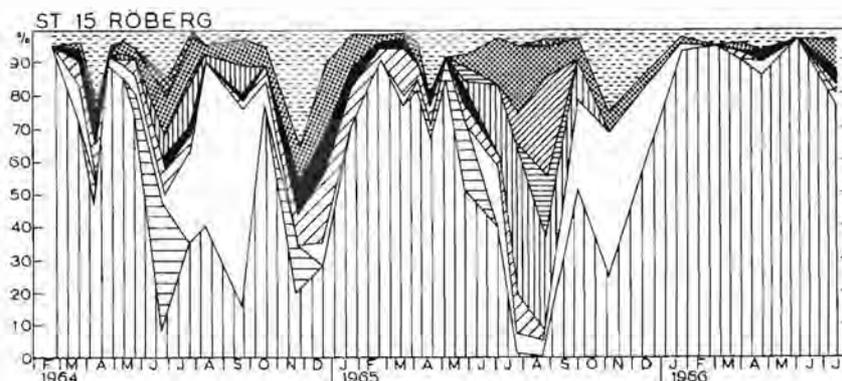


Fig. 20. Percentage composition in 100-0 m of the copepods in *Calanus* units at St. 15 during 1964-66. (Symbols as in Fig. 16).

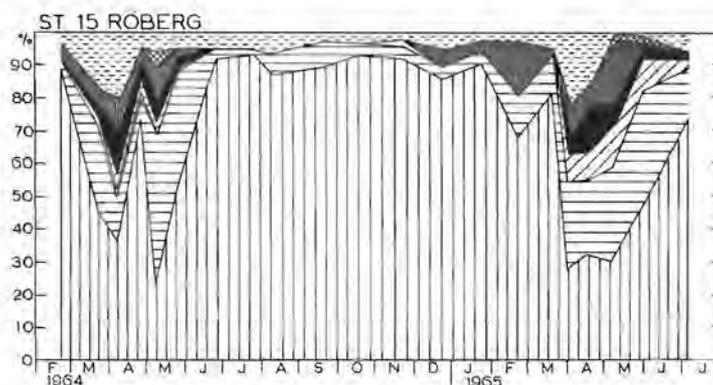


Fig. 21. Percentage composition below 100 m of the copepods in *Calanus* units at St. 15 during 1964-66. (Symbols as in Fig. 16).

VOLUME VARIATIONS

As a general rule the volume maximum of the year was found in summer and autumn, while the minimum was found in winter and early spring (Fig. 22). The plankton below 100 m dominated in both these periods. The fluctuations both from year to year and from station to station were large. In 1963 a distinct autumn maximum occurred at all stations i August-October. In 1964 the corresponding maximum was found in July-September at St. 18 and 15 only, while no significant maximum

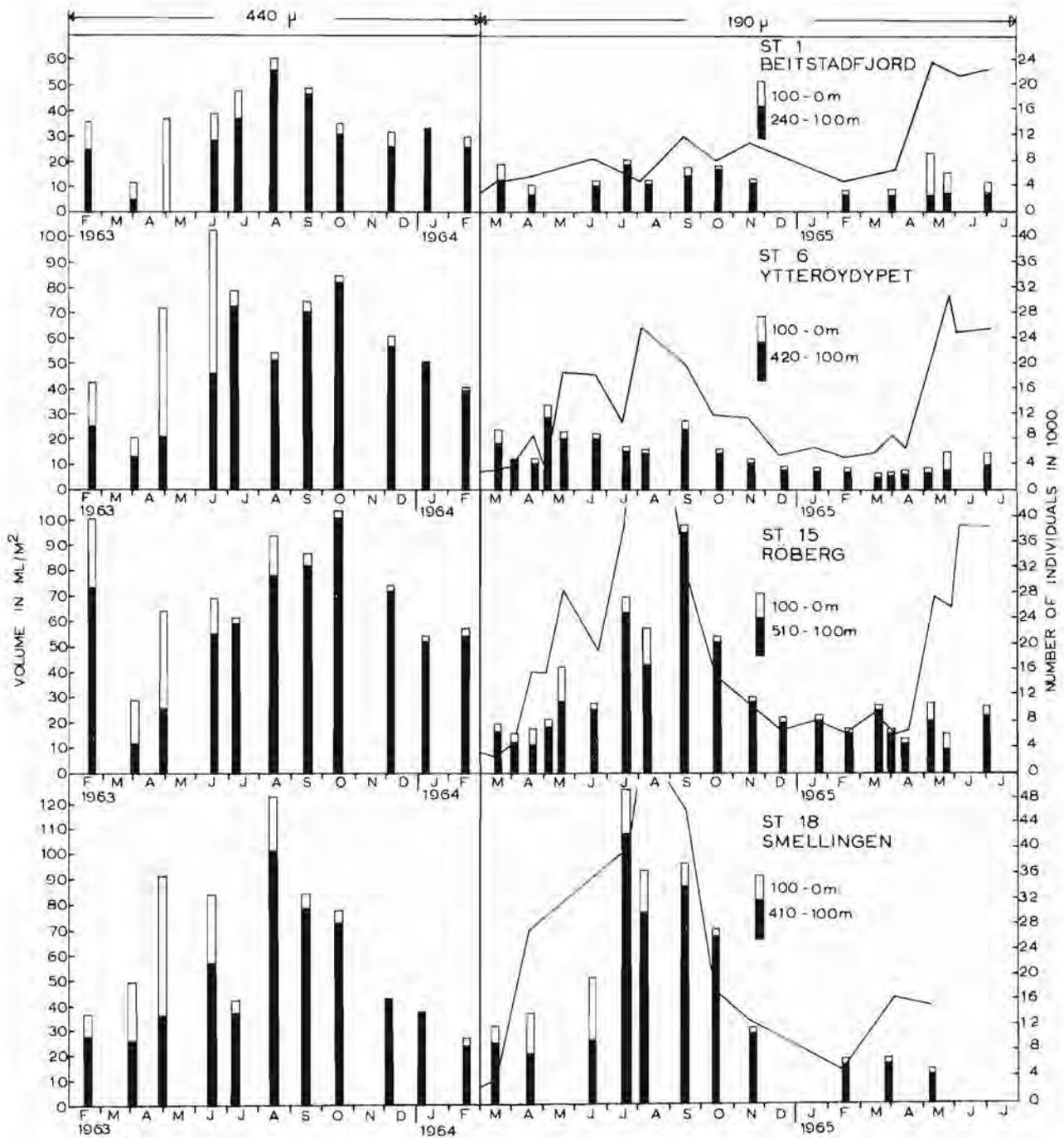


Fig. 22. Zooplankton volume below 1 m², 100-0 m and below 100 m separated (left scale), and total number of individuals in 1000s (right scale) at St. 18, 15, 6, and 1 during 1963-65. (From February 1963 to February 1964, mesh size 440 μ). The shadowed area of the histogram gives the volume below 100 m, the unshadowed, the upper 100 m.

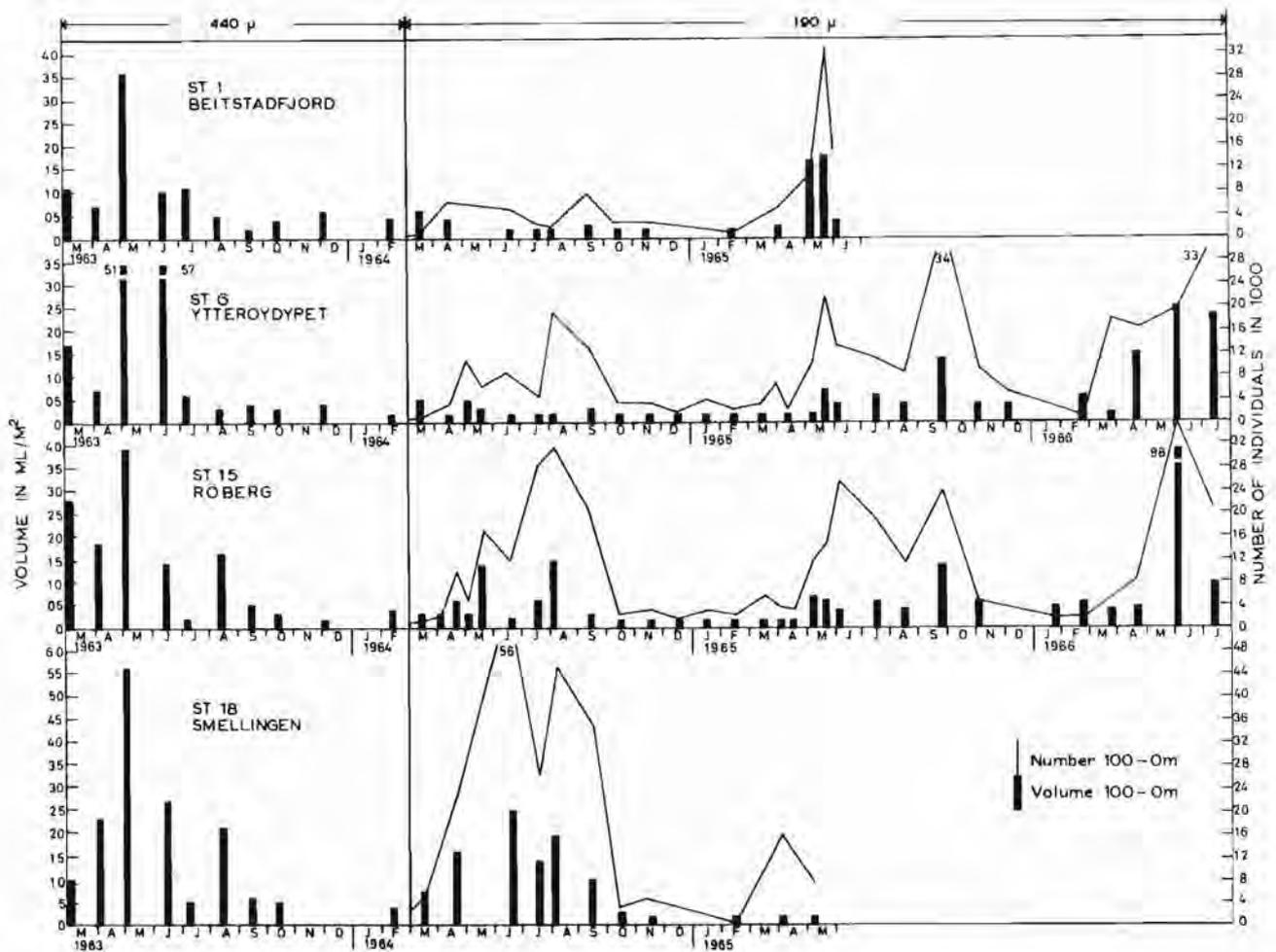


Fig. 23. Zooplankton volume in ml/m², and total number of individuals in 100s per haul in 100-0 m at all stations during 1963-66. (From February 1963 to February 1964, mesh size 440 μ).

was found at St. 6 and 1. In 1965 the small volumes at St. 15, 16, and 1 in July indicated less plankton than in 1963. Thus, on the basis of presence or absence of distinct maxima, gradients are found from year to year as well as from outer to the inner fjord.

The volume variations in the upper 100 m in the main fjord during 1963-66 are shown in Fig. 23, in ml below 1 m² of surface.

At St. 1 and 18 the sampling has been carried out from February 1963 to July 1965, and at St. 6 and 15 from February 1963 to July 1966. In 1963 a considerable stock was established in May at all stations, and at the two outer stations a second and smaller maximum occurred in August. A small stock persisted throughout the winter, mainly in

the inner fjord. In 1964 both spring and summer maxima were found in the outer fjord, but the spring maximum was much reduced compared to 1963. In the inner fjord the spring and summer stock did not exceed the winter population. The following winter 1964-65, the plankton volume was quite insignificant at all stations.

In May 1965 small spring maxima were observed at St. 1, 6, and 15, most pronounced at St. 1, while the volume was nearly zero at St. 18. An autumn maximum was found in September at both St. 15 and 6, while St. 18 and 1 were not sampled. In 1966 a very pronounced maximum was found in June at St. 15 and 6, with an extremely high volume at the outer station 15.

The number of organisms (Figs. 22-23) relatively closely follows the fluctuations in volume, but due to the change in mesh size the results from 1963 cannot be used for comparison. Generally the relation $\frac{\text{number}}{\text{volume}}$ was highest in spring and in the late summer and autumn maxima. This is due to vast numbers of nauplii and young stages from spring spawners, and to the adults and young stages of small species dominating the summer and autumn zooplankton.

Mean volume and percentage deviation from the mean

The mean volume for each month during 1963-66 in 100-0 m at St. 15 and 6 is given in Tables 4-5. Generally the greatest mean volumes were found in May-June at both stations, corresponding to the spring maxima. Another maximum was found at St. 15 only in August-September, related to the autumn maxima found at the outer stations.

An interesting record is the maximum found at both stations in February. Minima of the year are found from October to January.

The percentage deviations from the mean are also given in Tables 4-5. Generally the largest deviations seemed to occur in spring and early summer. Deviations exceeding 225% were found, and the average deviation from the mean was about 57% at St. 15 and 55% at St. 6. These deviations are remarkably great and demonstrate that single year cycle observations are of very restricted value in estimating average standing crop in the fjord. The average deviations from the mean at the coast

Table 4. Mean volume and percentage deviation from mean in 100-0 m at St. 6 during 1963-66

	J	F	M	A	M	J	J	A	S	O	N	D
Mean volume 1963-66	0.20	0.68	0.40	0.65	1.95	2.20	0.93	0.30	0.53	0.25	0.30	0.33
1963		+150.0		+7.7	+161.5	+159.1	-35.5	0	-24.5	+20		+21.2
1964	0	-70.6	+25	-69.2	-79.5	-90.9	-78.5	-33.3	-43.4	-20	-33.3	-39.4
1965	0	-70.6	-50	-69.2	-82.1	-81.8	-35.5	+33.3	+69.8		+33.3	+21.2
1966		-11.8	+25	+130.8		+13.6	+147.3					

Table 5. Mean volume and percentage deviation from mean in 100-0 m at St. 15 during 1963-66

	J	F	M	A	M	J	J	A	S	O	N	D
Mean volume 1963-66	0.30	1.00	0.30	0.74	1.80	2.70	0.60	1.17	0.73	0.25	0.40	0.20
1963		+180		+143.2	+116.7	-48.1	-66.7	+36.8	-31.5	+20		0
1964	-33.3	-60	0	-39.2	-52.8	-92.6	0	+28.2	-58.9	-20	-50	0
1965	-33.3	-80	-33.3	-73.0	-63.9	-85.2	0	-65.8	+91.8		+50	
1966	+66.7	-40	+33.3	-32.4		+225.9	+66.7					

stations calculated by Wiborg (1958) indicates that also at such localities long term investigations are necessary to get reliable information of the stock of zooplankton.

Volume variations in Trondheimsfjorden compared to other areas

The yearly fluctuations of zooplankton volume in Trondheimsfjorden, on the Norwegian west coast, and at St. M in the Norwegian Sea, are compared in Table 6.

Table 6. Zooplankton volumes in ml/m² from other localities in Norwegian waters compared to Trondheimsfjorden. (Calculated from Gundersen 1953, Wiborg 1954, and Lie 1966, 1967

	1963												1964												1965																							
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O														
Tr.heimsfjorden outer part	-	109	-	29	64	69	70	93	86	103	-	73	51	58	19	16	32	27	69	56	96	51	27	20	20	15	25	13	21	26	-	-	-	-														
Tr.heimsfjorden inner part	-	40	-	20	67	105	77	53	72	84	-	62	50	39	25	11	27	20	15	14	26	14	10	7	7	6	5	5	14	13	-	-	-	-														
St. M	-	-	-	-	54	57	41	36	29	32	18	20	18	20	20	30	28	44	53	-	-	-	-	10	7	33	35	35	94	107	70	33	25															
Eggum	-	-	9	18	175	147	114	45	25	10	9	-	-	-	-	230	75	85	27	71	125	1	-	-	-	1	45	60	-	64	30	47	30															
Skrova	17	13	14	17	41	49	116	65	42	35	33	43	33	8	9	17	40	30	20	18	45	42	15	14	23	14	5	38	52	53	49	26	17	45														
Hard.fjorden inner part	1950												1951												1955												1956											
	-	-	3	5	7	8	34	9	6	7	6	7	5	4	6	12	8	13	16	8	10	10	25	22	8	3	3	17	15	10	14	9	9															
Hard.fjorden outer part	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	5	9	5	8	7	7	5	3	2	6	5	7	4	5	6	15																
Sognesjøen	3	2	3	15	10	20	9	-	9	5	2	2	-	-	3	10	6	16	10	5	5																											

The quantity is given as monthly averages in ml/m². The whole water column was sampled except at St. M, where the volume refers to 600 m - surface. Except for Hardangerfjorden and Sognesjøen the years 1963-65 can be compared directly.

The southernmost coastal station, Sognesjøen, showed small volumes. This seems a general trend at this station (Lie 1965, 1966, Wiborg 1954). Also in Hardangerfjorden relatively small zooplankton concentrations occurred compared to Trondheimsfjorden (Gundersen 1953, Lie 1967).

The northern coast stations, Skrova and Eggum, generally showed a far greater standing stock, but a marked reduction occurred in 1965, and the same trend was found in Trondheimsfjorden, especially in the outer part.

On the contrary, St. M in the Norwegian Sea showed an opposite trend with a pronounced maximum in 1965 and smaller volumes in 1963 and 1964. In 1964 the sampling routine at St. M was interrupted from July, but the general trend at this stations since 1950 (Lie 1968, Wiborg 1958) indicates that the maximum of the year has normally occurred before that month.

The nature of the volume maxima

As shown by many workers (Ruud 1929, and others) the stock of *C. finmarchicus* is decisive for the size of the volume maxima. In Trondheimsfjorden this feature is evident for the summer-autumn maxima below

100 m and the spring maxima in 100-0 m.

The small zooplankton volumes recorded in Hardangerfjorden also seem related to a reduced importance of *C. finmarchicus*.

The summer-autumn maxima in 100-0 m in Trondheimsfjorden are of more complex composition than the *Calanus*-dominated spring maxima in the same layer. Beside *C. finmarchicus* a variety of small organisms take part in this maximum, especially the copepods *Temora longicornis*, *Centropages hamatus*, and *Acartia longiremis*. All these copepods are undoubtedly autochthonous in the area, but a significant immigration also seems to take place. This pattern may explain the reduced importance of the autumn maxima in 100-0 m in the inner parts of the fjord. Because variations in this summer-autumn maximum are mainly dependent on the group of variable species mentioned above, a specified discussion in terms of volume seems less relevant.

Because the summer-autumn maxima both in 100-0 and below 100 m to some degree seem dependent on supply from outside the fjord, the observed delay inwards in time for volume maxima may be explained as a transport effect. A similar trend may be assumed in Hardangerfjorden in 1956 (Lie 1967, Figs. 2 and 4).

In Hardangerfjorden both Gundersen (1953) and Lie (1967) found a tendency for the spring maximum to occur later in the inner part of the fjord, and Lie related this to an undefined "fjord effect." In Trondheimsfjorden the spring maximum at St. 18 seemed to occur a little earlier than in the inner fjord, but the material limits further interpretation. The phytoplankton bloom, however, simultaneously in all parts of the fjord (Sakshaug 1970), and the spring burst of *C. finmarchicus* should normally be timed to that, indicating a similar trend for the volume maxima in spring. The delay of maxima which is indicated from St. 18 to St. 6 in Fig. 39, is due to a successful local development and accumulation of older stages, and not a delayed initiation of the volume increase.

COPEPODA CALANOIDA

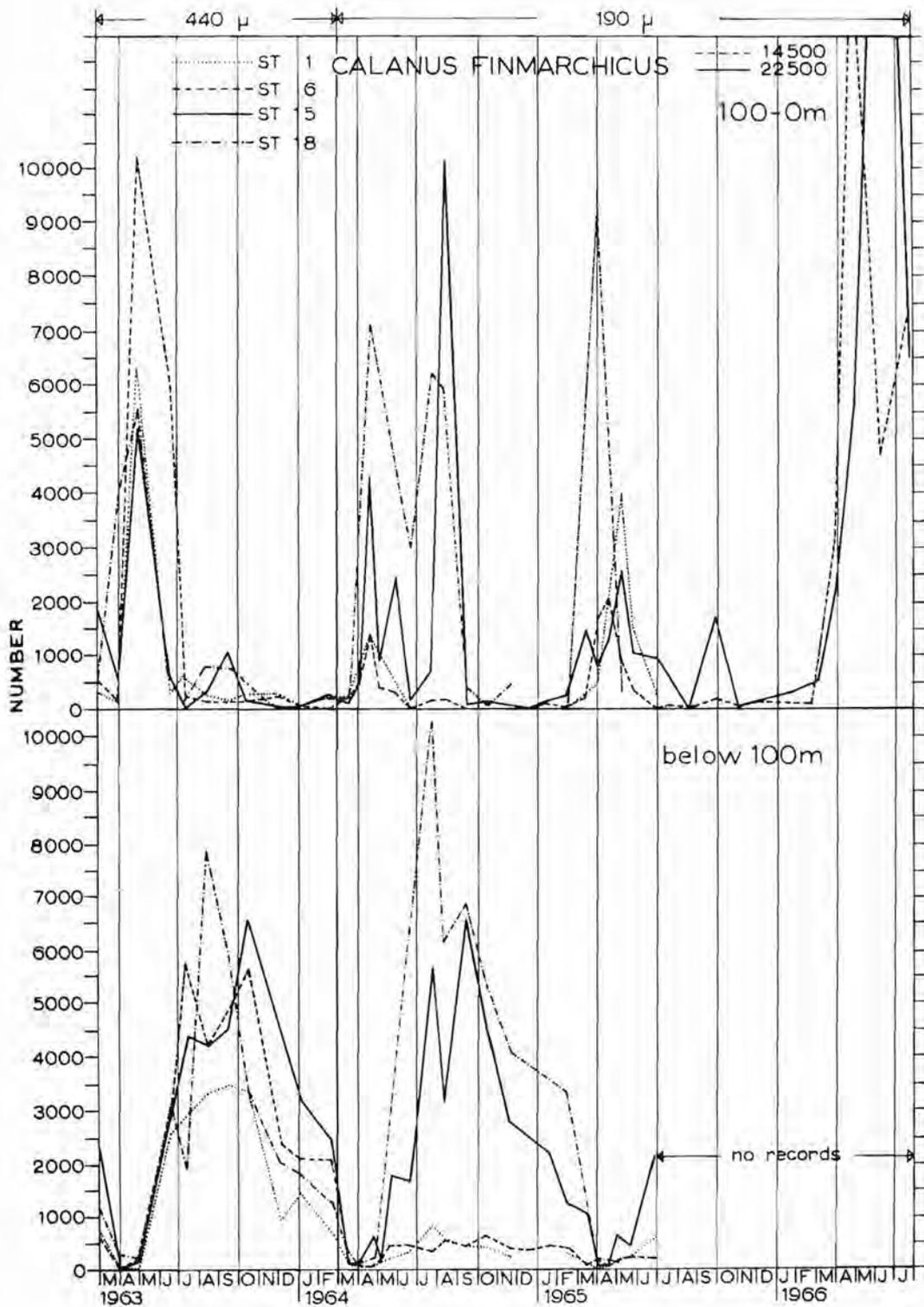
Calanus finmarchicus (Gunnerus)

Two nearstanding species are recorded in Norwegian waters, *C. finmarchicus* and *C. helgolandicus*. The latter has its centre of distribution in the North Sea, while *C. finmarchicus* has a more northern distribution. In Trondheimsfjorden only *C. finmarchicus* seems to be present.

Figs. 16-19 demonstrate clearly that *C. finmarchicus* is a very dominant component in the zooplankton in Trondheimsfjorden at all seasons. The species contributed by far the major part of the biomass, but the stock showed a very significant variation both in time and space. In coastal waters *C. finmarchicus* is a dominant member of the zooplankton, but in other fjords, especially the inner parts, its importance is normally significantly reduced and replaced by smaller neritic copepods (Wiborg 1940, 1954, Gundersen 1953, Lie 1967, Beyer, Dybwad & Versvik 1967), although accumulations in inner basins may occur (Wiborg 1940). In Oslofjorden, however, (Wiborg 1940) *C. helgolandicus* may have been taken as *C. finmarchicus*.

Variations in numbers

The numerical variations of *C. finmarchicus* at St. 18, 15, 6, and 1 during 1963-66 are shown in Fig. 24. In the hauls below 100 m, the numbers are not directly comparable due to different depths at different stations. When comparing 1963 with the other years, it must be remarked that due to the mesh size used before March 1964, sampling of lower stages was poor with significant consequences for the estimation of numbers. The stage distribution in the same periods is shown in Figs. 25-26.



Figs. 24. *Calanus finmarchicus*, total number per haul below 100 m and in 100-0 m at St. 1, 6, 15, and 18 during 1963-66. (From February 1963 to February 1964 mesh size 440 μ).

Variations in 100-0 m

In 100-0 m two main maxima were observed each year (Fig. 24). Normally the greatest maximum was found in April-May at all stations, while a much smaller maximum occurred in August-September at the outer stations only.

The spring maximum in 100-0 m was generally based on nauplii and lower copepodite stages, while in August-September all copepodite stages seemed to take part. The spring maximum occurred regularly each year in April-May at all stations, but the size of the maximum varied greatly. At the outer St. 18 the stock was rich every year, perhaps slightly reduced in 1964 and 1965. At the inner stations, 15, 6, and 1, there was a gradual and very significant reduction of the stock inwards in 1964 and 1965. In 1966 only St. 15 and 6 were sampled, but the abundance that year is clearly demonstrated at both stations.

In the rich years the stock in the April maximum was normally composed of nauplii and copepodite stages V-I, in comparable numbers, while in the poor years the copepodite stages IV-III were of much less importance. Obviously, the environmental conditions met during the first copepodite stages must be decisive for the success of the stock. The factors which are responsible for failure or success seem more accentuated in the inner fjord.

The August-September maxima of *C. finmarchicus* in 100-0 m were composed of nauplii and all copepodite stages, and occurred regularly at St. 18 and 15. They could be traced at St. 6, but were absent or nearly absent at St. 1. Presence of all stages indicate a local origin. The separate occurrence of copepodite stages II-III and V at St. 15 in August 1964 may be connected with a successful brood of young copepodite stages at St. 18.

In the summer-autumn maxima in 100-0 m all stages take part and are possibly derived from females of the spring generation. Accordingly, the reduced maxima in the inner part in the autumn only reflect the variable success of the spring generation, but immigration may also influence the distribution.

At the other localities along the coast a similar annual bimodal abundance is found. From Hardangerfjorden Lie (1967) reports maxima

in 100-0 m in April and July-August, while Gundersen (1953) at the same locality records the second maximum in September. In coastal waters south of Lofoten and at St. M in the Norwegian Sea, April and June-July seem to give the peaks of abundance (Wiborg 1954, Østvedt 1955). The spring maximum occurs simultaneously at all localities, while the second maximum is delayed a month or two in the fjords.

The size of the maxima shows interesting differences between the localities. In Table 7 the concentrations (ind./m³) of all stages of *C. finmarchicus* in 100-0 m or 50-0 m at different localities along the coast are compared.

Table 7. Concentration of *Calanus finmarchicus* in 100-0 m and 50-0 m at comparable localities along the Norwegian coast. Numbers in ind./m³

Locality	Depth	Spring conc.ind/m ³	Summer conc.ind/m ³	Reference
Trondheimsfjorden outer part	100-0	1.000-2.000	1.000	
Trondheimsfjorden inner part	100-0	100-1.500	100-1.000	
Hardangerfjorden inner part	50-0	100-1.000	300	Gundersen (1953) Lie (1967)
Lusterfjorden (inner part of Sognefjorden)	50-0	30	25	Gundersen (1953)
Ona	50-0	200	600	Wiborg (1954)
Eggum	50-0	1.600-10.000	1.000	Wiborg (1954)

The values obtained in Trondheimsfjorden, especially in the outer part, are quite high compared to other fjord localities. The inner part of Trondheimsfjorden shows great fluctuations, but in poor years the numbers are of the same size as in Hardangerfjorden. Lusterfjorden, in the innermost part of Sognefjorden, shows extremely low values.

The fluctuations in stock abundance in inner Trondheimsfjord

compared to the constant low stock recorded in the inner parts of other fjords raise a question as to whether the poor stocks in the inner fjords reflect the normal situation and indicate a fundamental difference in physical conditions or whether the occasional sampling has been made in poor years. This problem stresses the need for long term investigations of zooplankton in such localities.

Variations below 100 m

The variations below 100 m are shown in Fig. 24. The summer and the autumn maxima in this layer occurred in two main periods, in June-July and in September-October.

The June-July maxima of copepodite stages V-IV below 100 m are partly due to descendants from the spring generation migrating downwards, and the fluctuations partly reflect the success of these generations. This summer maximum seems delayed from yearly June at St. 18 to July at St. 15 and 6, and perhaps to August-September at St. 1. This delay in time for maximum and the reduced numbers inwards may indicate that immigrants are also present with the local stock.

The autumn maxima in August-October below 100 m are also dominated by copepodite stages V-IV and seem too large to be related back to local stocks. A supply from outside the fjord must take place, and the maxima seem correlated with the deep summer-autumn inflows (Figs. 6-9) both in time and strength.

In autumn the coastal stocks of *Calanus* migrate from the surface and may thus be brought into the fjord with the inflowing water. Within the fjord *Calanus* probably migrates further down and is trapped behind the thresholds. An accumulation of overwintering stages may thus take place in the fjord depths.

For the hauls below 100 m little information from comparable areas along the coast is available. Wiborg's data (1954) from the coastal stations indicate maxima in the layers below 50 m in July and August-September. In Hardangerfjorden (Gundersen 1953) small autumn maxima due to copepodite stage V were found in August-September and October-November in the fjord proper.

Propagation

The propagation of *C. finmarchicus* may be traced by the occurrence of nauplii and lower copepodite stages. In Figs. 25-26 the stage distribution is given in numbers per haul, and thus the strength of the different generations is demonstrated.

Nicholls (1933 a) has shown that the eggs of *C. finmarchicus* need at least 11 days to develop into copepodite stage I, while the development from one copepodite stage to the next requires at least three days. Low temperature retards the development (Hansen 1960). According to this scheme, the time for propagation may be traced back from the occurrence of nauplii and copepodite stage I. Further, the presence of adult males and females indicates spawning.

In 1963 males and females were absent at all stations in the end of February. The females probably spawned in February/March at St. 18 and in March/April at St. 15, 6, and 1. Peaks of copepodite stage V in June-July may be due to the spring generation. At all stations a summer generation seemed to be produced in July-August. The copepodite stage V of the August generation probably overwintered in deep waters, but the bulk of this stage below 100 m in autumn was obviously of other origin.

In 1964 maturing *C. finmarchicus* from the overwintering stock gave a February maximum of males at all stations, and a maximum of females in March. These females probably spawned at all stations in March/April, but development seemed to fail, partly in the young copepodite stages. The lack of success was accentuated inwards in the fjord. A small secondary peak of nauplii was found in May at St. 18, 15, and 6, indicating an April/May spawning. A July spawning succeeded at the outer station 18 and partly at St. 15, while it again seemed to fail at St. 6 and 1. At St. 18 a small spawning in November was due to an adult stock in October-November. This spawning may be traced also at St. 15. The overwintering stock of copepodite stage V is very small at the two inner stations 6 and 1.

In 1965 a maximum of males in February at all stations was followed by a maximum of females, and spawning probably took place in March at all stations. This generation had no success. A second

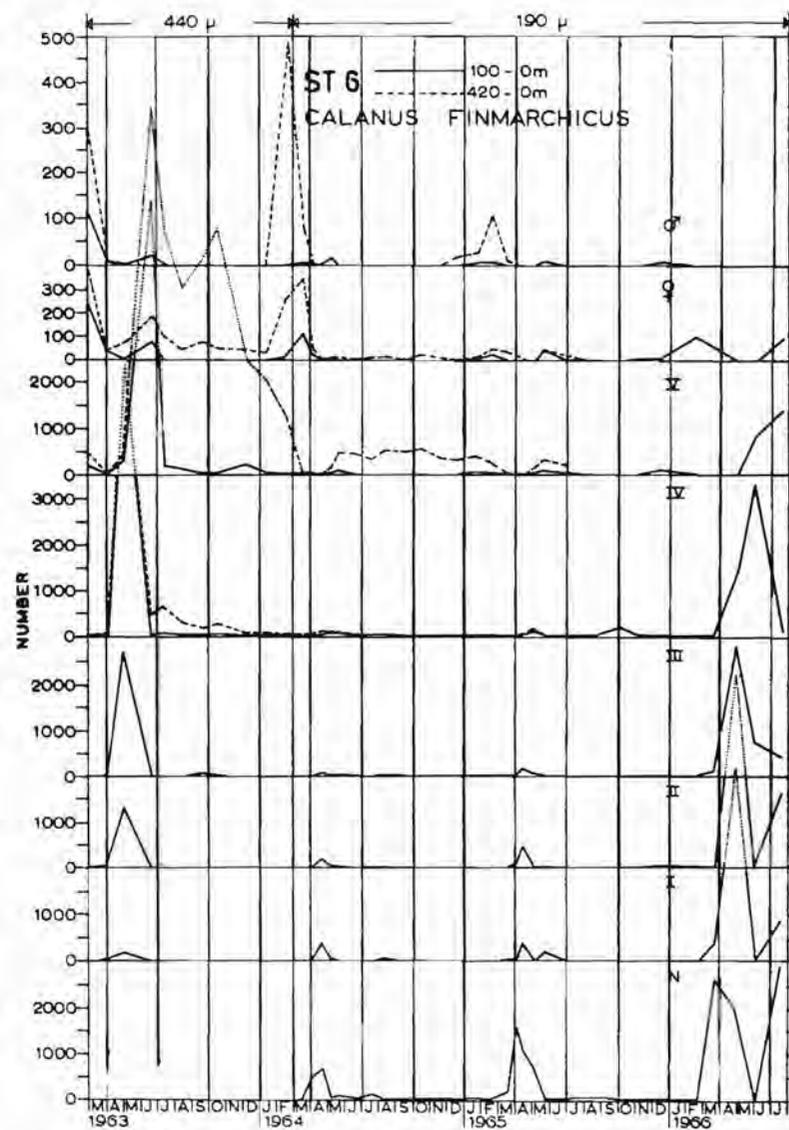
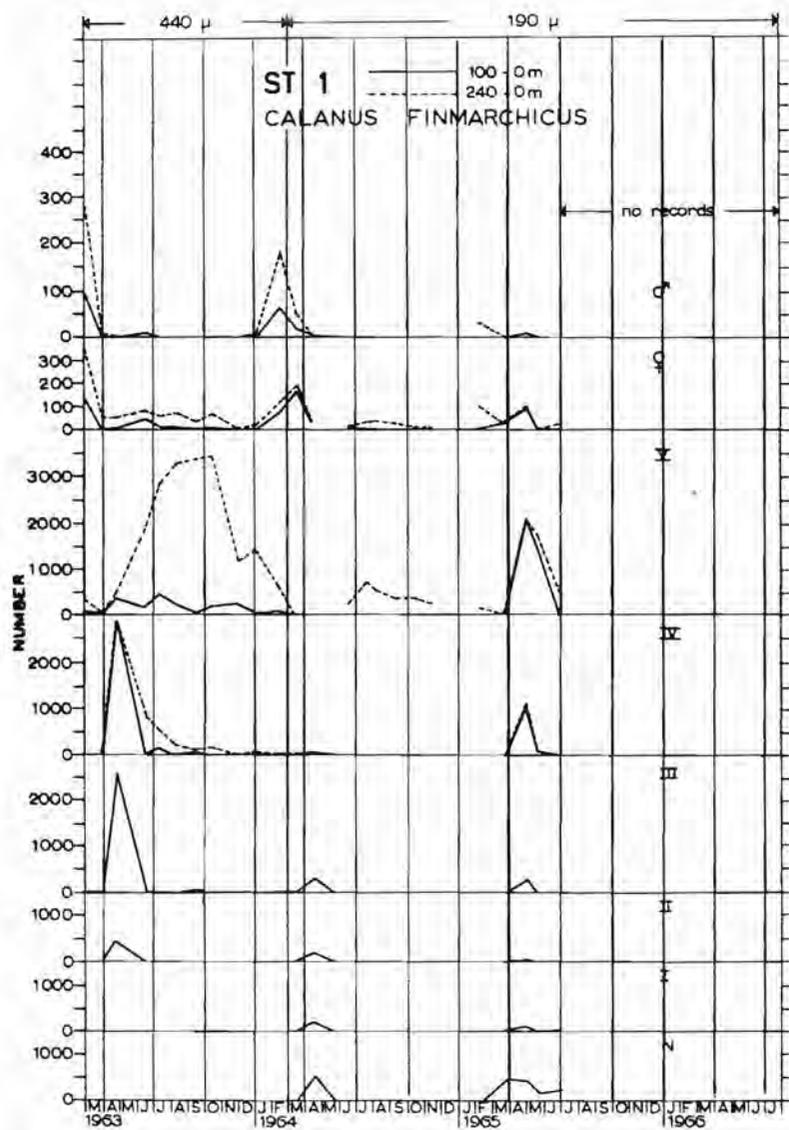


Fig. 25. *Calanus finmarchicus*, stage distribution in bottom - 0 m and 100-0 m at St. 1 and St. 6 during 1963-66. (From February 1963 to February 1964 mesh size 440 μ).

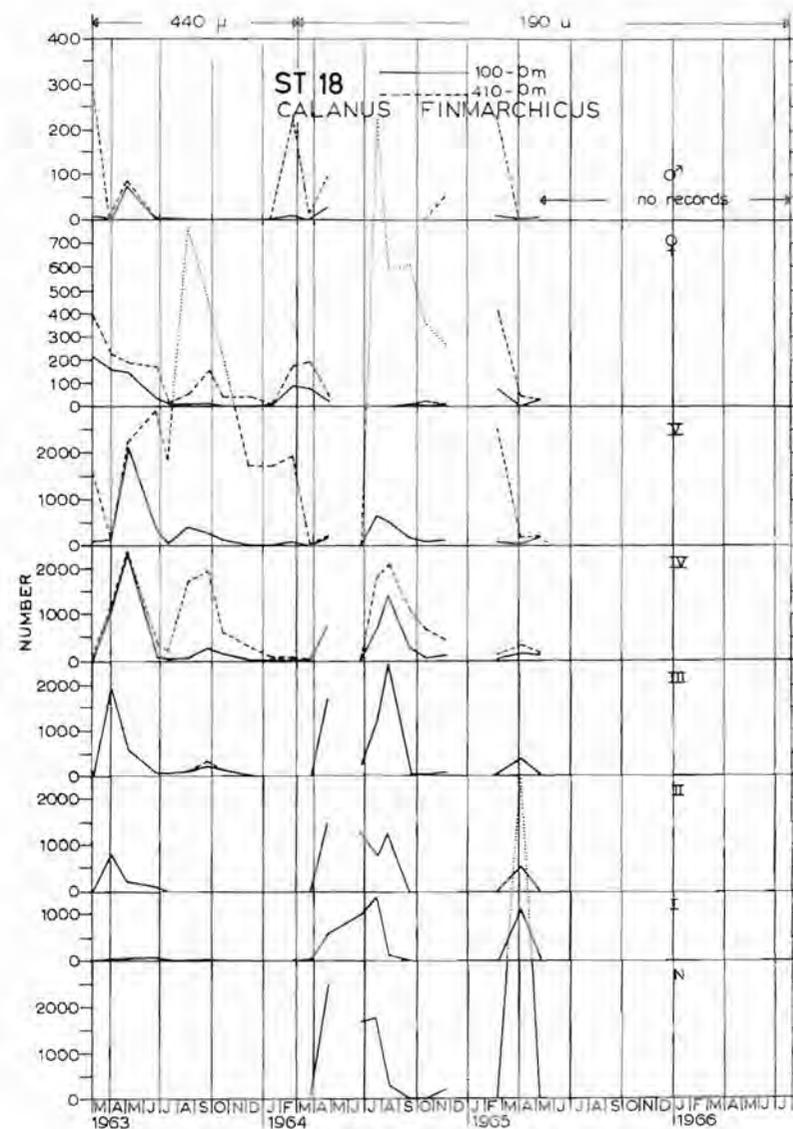
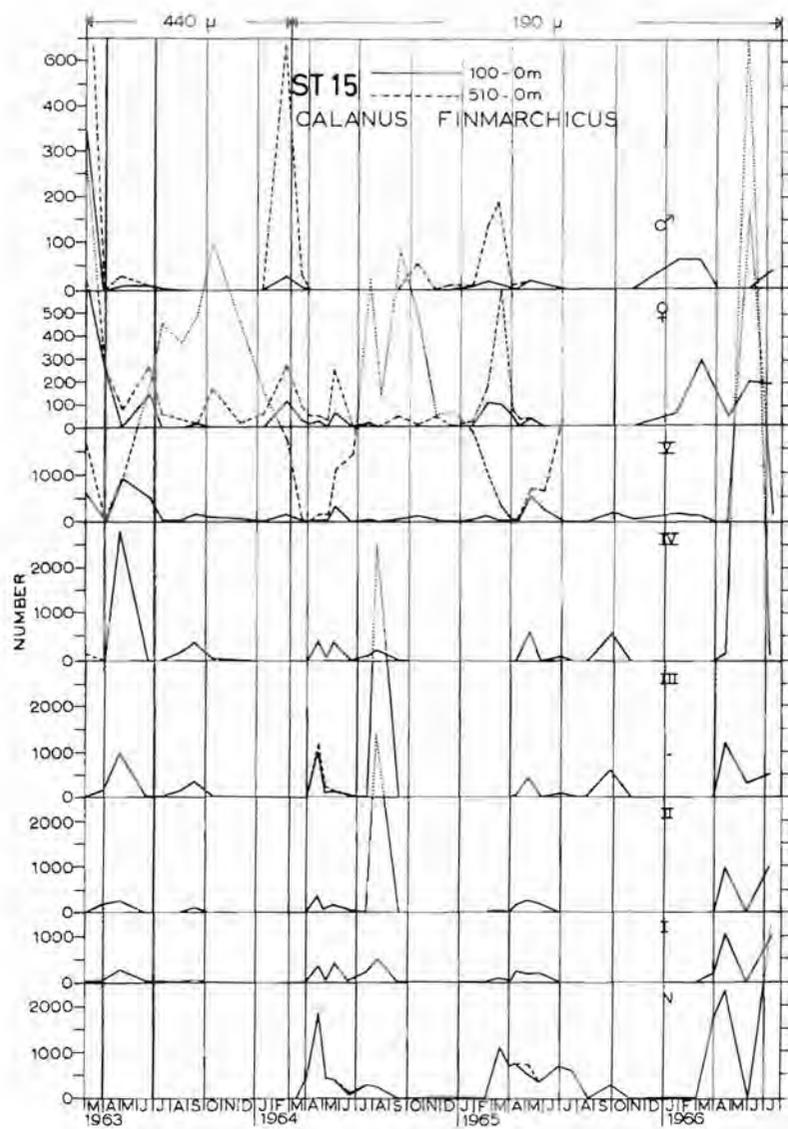


Fig. 26. *Calanus finmarchicus*, stage distribution in bottom - 0 m and 100-0 m at St. 15 and St. 18 during 1963-66. (From February 1963 to February 1964 mesh size 440 μ).

spawning, perhaps by the same stock, occurred in April at St. 15, 6, and 1, and a July spawning was recorded at the same stations. At St. 15 a small spawning was recorded in September. None of these spawnings resulted in a rich stock of overwintering stages.

In 1966 only St. 15 and 6 were sampled. The adult stock in February-March seems to have spawned in March, and produced a successful generation. Maxima of copepodite stage IV at both stations in June may be due to this generation. A second rich spawning is indicated in June at both stations.

The main spawnings in Trondheimsfjorden seem to take place in March, and at the outer stations two small secondary spawnings seem to occur regularly in April/May and in July. At the inner stations 6 and 1, the July spawning seems to be of less importance and may even be absent. Thus, there is a tendency of reduced numbers of spawnings inwards in the fjord. Besides these maxima, spawning later in autumn may occasionally take place at the outer stations.

In Hardangerfjorden Lie (1967) recorded spawnings in February, May-June and, possibly, in October-November. Gundersen (1953) found spawnings in February-March, May-June and in September in the same locality. These results are in good accordance with the observations from Trondheimsfjorden. A similar trend of maximal periods is also found at the coastal stations (Wiborg 1954, Lie 1965, 1966).

Lie (1967) mentioned that while the outer part of Hardangerfjorden follows the general pattern of the coastal stations with a major maximum in spring followed by minor spawnings later in the year, the inner part was characterized by small maxima of equal size all seasons. This pattern is also found in Trondheimsfjorden in the poor years, while in successful years the spring generation produced great numbers. As the investigation in Hardangerfjorden represents only one single year, it is impossible to know whether the comparatively small stock at all seasons reported by Lie is the permanent state, or if it was the result of an occasional lack of success of the spring generation.

In Oslofjorden Wiborg (1940) reported an inward delay in the time for spawning. In Ofotfjorden, in the inner part of Vestfjorden, spawning started 1-2 weeks later than in outer Vestfjord (Sømme 1934, Wiborg 1954). Fish & Johnson (1937) found that in the Bay of Fundy delay

inwards in vernal warming is reflected in breeding periods. In Trondheimsfjorden a significant delay inwards is not observed either for the spring spawning or for vernal warming, although at the outer station 18 the maximum of young stages seem to occur slightly earlier than at the stations in the fjord proper. On the other hand the intervals between the sampling dates may be too large to reveal if a small delay in time exists.

Marshall & Orr (1952) reported that individual females of *C. finmarchicus* might spawn in bursts for more than two months under laboratory conditions, depending on food supply. Accordingly, maxima of nauplii found within a span of one or two months might be spawned by the same females, and maxima of the nauplii recorded in March/April and April/May might belong to the same generation. Nevertheless, if significant peaks are found, the spawning activity reflects important variations in the environmental conditions stimulating spawning, and phenotypic changes may give broods of different quality.

In Trondheimsfjorden the nauplii spawned in spring seem to need approximately four weeks to reach copepodite stage V, and another four weeks to mature into ripe females. This estimation is in good accordance with the results obtained by Nicholls (1933 a) who found that in the laboratory a period of at least one month seemed necessary to develop from egg to copepodite stage V in the Clyde Sea. Fish (1936 a) observed a developmental period of 1-2 months in Fundy Bay, while in the Lofoten area Sømme (1934) found that only 42 days were needed for the same development.

Vertical distribution

The vertical distribution of *C. finmarchicus* at St. 15 is shown in Fig. 27. Black columns represent percentage distribution in the different depths of females, copepodite stages V-IV and copepodite stages III-I, including nauplii.

In 1963 and 1965 females migrated into the upper 50 m in February, and a considerable part of the female stock stayed in this layer until April. In 1964 the females were not found in the uppermost layer, although

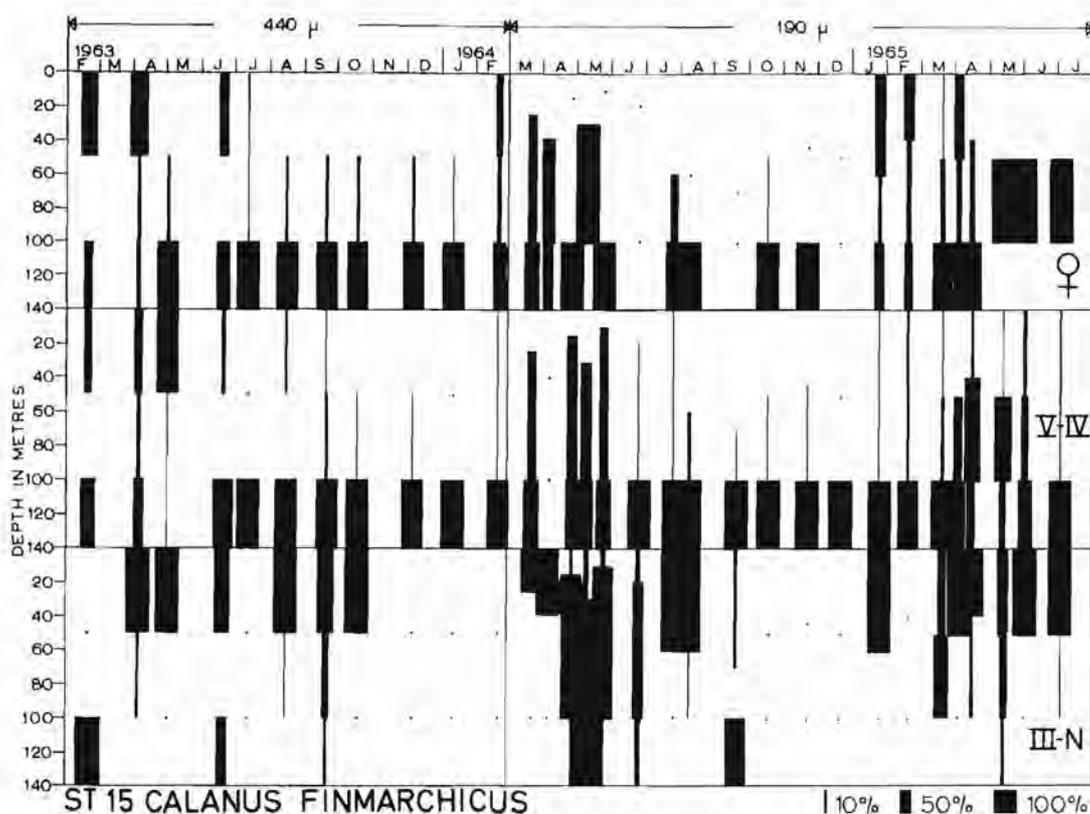


Fig. 27. *Calanus finmarchicus*, percentage vertical distribution of different stages at St. 15.

an upward migration above 100 m took place. In 1963 a significant percentage of females again invaded the upper layers in June, while in 1964 and 1965 this migration did not reach above 50 m. The rest of the year the bulk of females stayed below 100 m.

The copepodite stages V-IV had a vertical distribution similar to the females in the spring, but they generally showed small percentages in the upper layers. The greatest percentage above 100 m was found in April-May, which is when the female component in these layers diminished. In June-July a downward migration took place and the rest of the year copepodite stages V-IV seemed restricted to the layers below 100 m.

Copepodite stages III-I and nauplii had their main distribution in the upper 100 m during spring and summer. In 1963 the whole spring stock of these stages was found in the upper 50 m, while in 1964

a high percentage in the upper layers in March-April was followed by a deeper distribution of the main stock in April-May. While the March-April stock in 1964 was situated above the discontinuity layer, a very small percentage occurred in this layer in April-May. In 1965 the young stages were also less abundant in the uppermost layer than in 1963.

The general pattern of the seasonal migration and vertical distribution of *C. finmarchicus* in Trondheimsfjorden is in good accordance with observations from the coast and other fjords (Ruud 1929, Wiborg 1940, 1954, and Gundersen 1953). The outer and the inner Trondheimsfjord showed no differences in vertical distribution, but the vertical division used in the sampling may be too rough to reveal details. In spring 1965 a special sampling program was carried out at St. 15 to investigate the detailed vertical distribution of the nauplii and young copepodite stages of *C. finmarchicus*. The hauls were always taken in daytime, and were doubled in order to avoid extreme deviations. The percentage vertical distribution was calculated from the mean of the two hauls. The vertical distribution of copepodite stages III-I and nauplii is given in Table 8.

Table 8. *Calanus finmarchicus*, percentage vertical distribution of copepodite stages III-I and nauplii in the upper 50 m at St. 15 in spring 1965

Depth in m	March-April				April				May			
	III	II	I	N	III	II	I	N	III	II	I	N
0-10	9	31	51	64	18	32	13	51	16	16	25	38
10-20	17	32	20	21	25	25	48	42	13	43	42	43
20-30	32	12	14	9	12	11	18	1	35	24	12	5
30-40	25	15	6	3	33	21	12	5	11	5	8	11
40-50	17	10	9	3	12	11	9	1	25	12	13	3

The results strongly indicate that the younger stages, mainly copepodite stages II-I and nauplii, preferred the uppermost layers, particularly the upper 20 m. When copepodite stage III was reached, the distribution was more uniform, though the layer below 20 m seemed to have the greatest percentage. The same trend was found for all three months, but at the end of the period the youngest stages seemed to migrate from the 0-10 m layer and got their center of distribution at 10-20 m of depth.

Length distribution

The carapace length of 50 copepodites, stage V, was measured from nearly all samples taken below 100 m at both St. 15 and St. 1.

The fluctuation of mean length of *C. finmarchicus*, copepodite stage V, at these stations is shown in Fig. 28.

At St. 15 minima of mean size were each year found in March, preceded by small peaks in January. The largest mean length was found in April-May 1963 and June-July 1965, while in 1964 the mean size was less variable. The mean monthly length ranged from a minimum of 2.16 mm in March 1965 to a maximum of 2.54 mm in April-May 1963. At St. 1, the mean length was considerably more uniform, with total range 2.35 to 2.48 mm. This difference between St. 15 and St. 1 may indicate that the population at St. 1 is of local origin, while at St. 15 immigrants are of importance.

The size distribution of *C. finmarchicus*, copepodite stage V at St. 1 and 15, is shown in Fig. 29. At St. 15 the size distribution is quite irregular with a wide range and a pronounced bimodality. This

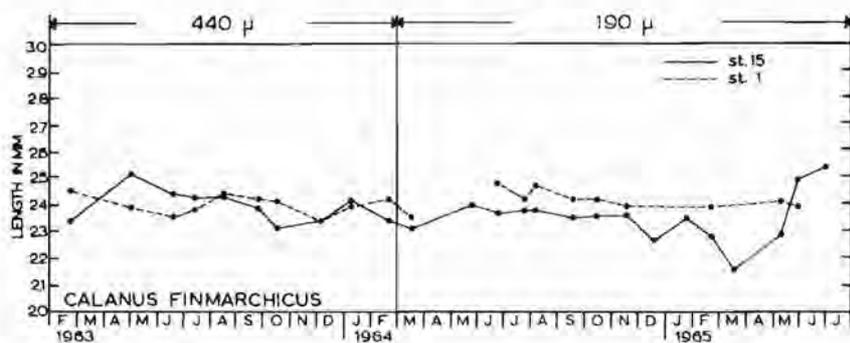


Fig. 28. *Calanus finmarchicus*, mean carapace length of copepodite stage V at St. 1 and 15 during 1963-65.

pattern may indicate that the stock of *C. finmarchicus* at St. 15 originates from several sources and that different generations live together. In 1963 a significant increase of larger individuals was found from February to May. During summer and autumn these were gradually replaced by smaller individuals. From December 1963 to January 1964 larger specimens increased in number. In February 1964 the size distribution was similar to February 1963 and throughout 1964 this distribution seemed to be fairly constant. In February 1965, the 1963 and 1964 situation seemed to be repeated, but with a greater proportion of smaller individuals, and in March 1965 a size group of about 2.2 mm dominated. In May 1965 these small specimens had nearly disappeared, and in late May a 2.5 mm group dominated. This increase continued and in July 1965 also a 2.7 mm group was found dominant.

The February-March size minima found at St. 15, probably resulted from the overwintering stock which was derived from the autumn generation the previous year. In this case, high temperature during the development may explain the size distribution. At Skrova Wiborg (1954) found a size minimum in February-March during three years, and he assumed that two generations had overwintered and that the large sized generation matured first, causing a drop in mean size of copepodite stage V. A similar explanation may be applied to the February-March minima in Trondheimsfjorden.

The increase in size found at St. 15 in May every year, especially in 1963 and 1965, may have been derived from the new spring generation which developed in cold water, but may also have been partly due to immigrants. Even abundant food supply may have improved the growth during spring.

During summer and autumn a gradual decrease in size occurred at St. 15, being most obvious in 1963 and 1965. It was, perhaps, related to summer and autumn generations which have developed in warm water. This smaller size coincided with a rapid increase in number of individuals, probably due to immigration.

The May maxima in size and the summer and autumn decline found at St. 15 are also recorded at the coastal localities, indicating similar conditions.

The variation in size distribution at St. 1 is significantly

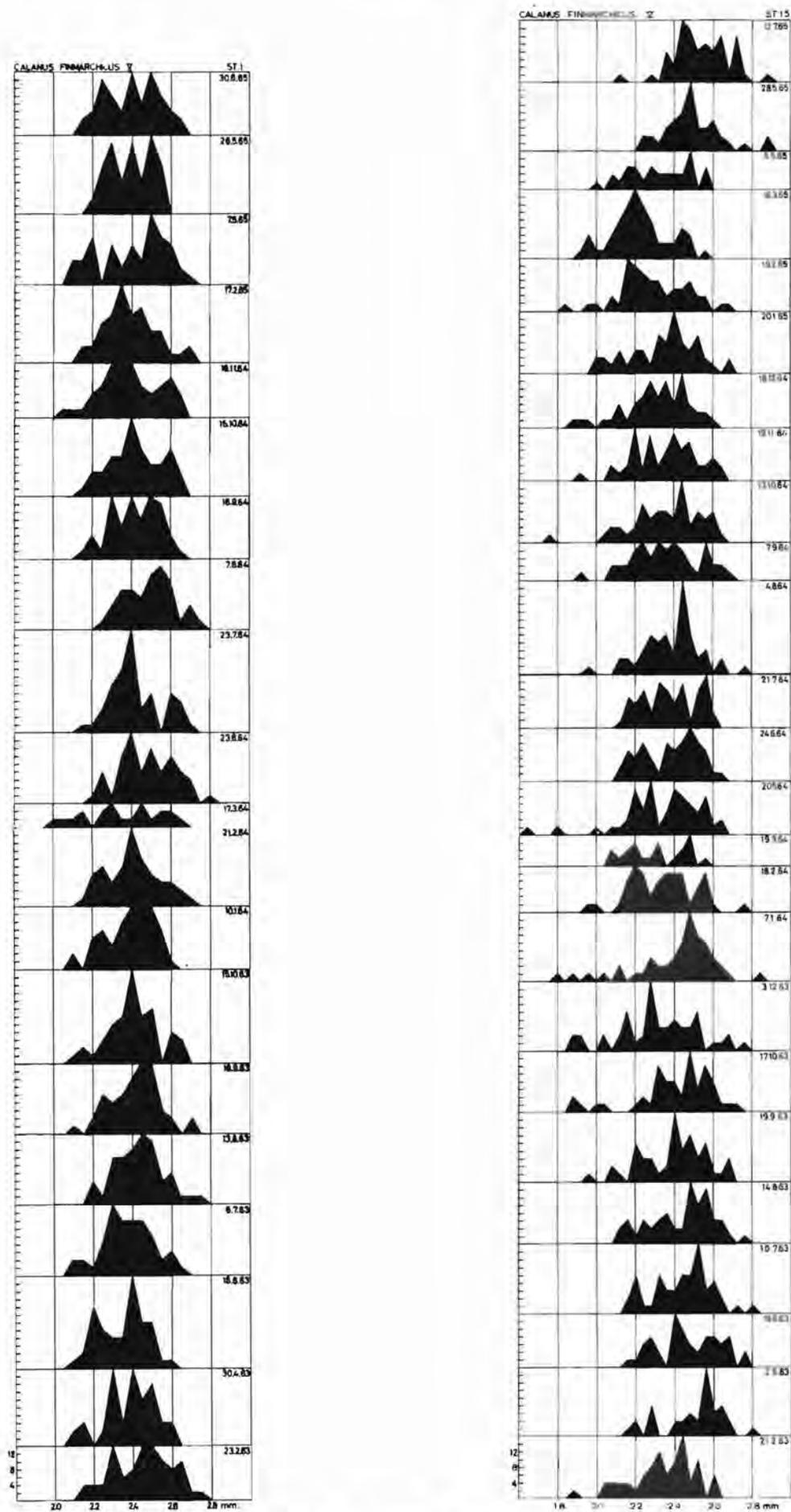


Fig. 29. *Calanus finmarchicus*, length frequency of copepodite stage V at st. 1 and 15 during 1963-1965 (left scale no of specimens counted).

smaller than at St. 15. A bimodality seems to occur, but the range of distribution is narrower, and one size group has a greater tendency to dominate. Individuals smaller than 20 mm were not recorded at St. 1. The distribution at St. 1 indicates more stable conditions than at St. 15 and in the coastal area.

Calanus hyperboreus Krøyer

C. hyperboreus is regarded as an arctic-oceanic species (Gran 1902) occurring in the North Atlantic and all Arctic seas (Brodskii 1950). It occurs in deep Norwegian fjords (Sars 1903, Runnstrøm 1932), sometimes in abundance (Sømme 1934). In Trondheimsfjorden very small numbers were found.

Length measurements by Ruud (1929) showed that stage V and females in the Møre fjords were significantly smaller than specimens from open water outside. In Trondheimsfjorden size differences between *C. hyperboreus* and *C. finmarchicus* were smaller than expected, and in the routine counting copepodite stages I-II of *C. hyperboreus* may easily have been taken for *C. finmarchicus*. Nauplii of *C. hyperboreus* and *C. finmarchicus* were not separated, but judging from the number of older stages, nauplii of *C. hyperboreus* were of minor importance compared to *C. finmarchicus*.

The numerical variations of *C. hyperboreus* in Trondheimsfjorden during 1963-66 are shown in Table 9, all stations combined.

Only one male was recorded in February 1964, but females and copepodite stages V-IV occurred at all seasons in small numbers. Copepodite stages III-I had a very restricted occurrence during February-April. The presence of copepodite stages II-I in Trondheimsfjorden indicates spawning in February-March, partly coinciding with the spawning of *C. finmarchicus*. According to Sømme (1934) *C. hyperboreus* propagates once a year in February-March in Vestfjorden, and this observation is confirmed by Wiborg (1954).

C. hyperboreus, females and copepodite stages V-IV, were recorded only once in the upper 50 m, and nearly the whole stock was caught

Table 9. *Calanus hyperboreus*, numerical variation in the main fjord during 1963-66, all stations combined. (From February 1963 to February 1964 mesh size 440 μ , numbers in paranthesis)

	J	F	M	A	M	J	J	A	S	O	N	D
1963 ♂-III	(0)	(5)	(0)	(16)	(10)	(36)	(23)	(10)	(43)	(20)	(0)	(0)
II-I	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
1964 ♂-III	(41)	(25)	25	3	9	0	20	13	14	19	17	11
II-I	(0)	(0)	10	20	10	0	0	0	5	0	0	10
1965 ♂-III	0	4	5	8	7	1	0	0	0	0	0	0
II-I	0	10	25	50	10	0	1	0	0	5	5	0
1966 ♂-III	0	0	35	50	1	0	0					
II-I	0	80	35	10	0	0	0					

below 100 m. Sømme (1934) assumed that spawning was connected with upward migration.

Paracalanus parvus (Claus)

P. parvus is regarded as a temperate form, and Wiborg (1955) lists it as neritic. It is reported as far north as the Barents Sea.

In Trondheimsfjorden adults and copepodite stages V-IV of *P. parvus* had a very restricted occurrence and were found only in autumn. The numerical variation of these stages is given in Table 10, which shows number per haul. Usually the maximal occurrence was found in September and October. Younger stages are difficult to distinguish from *Pseudocalanus* spp. and were not separated.

The distribution in time and space in Trondheimsfjorden indicates that *P. parvus* is not able to establish a local stock in the area. The species appears suddenly in September and declines in October, except in 1964 when it occurred as early as in July at St. 18, but was not found in the fjord proper. Both the number and the horizontal distribution of *P. parvus* seems correlated to the course of the warm water influxes into

Table 10. *Paracalanus parvus*, numerical variation of adults and copepodite stages V-IV at St. 1, 6, 15, and 18 during 1963-65. (From February 1963 to February 1964 mesh size 440 μ).

	1963		1964				1965	
	S	O	J	A	S	O	S	O/N
St. 1	(0)	(0)	0	0	0	0	-	-
St. 6	(0)	(67)	0	0	0	0	1.600	50
St. 15	(635)	(3)	0	0	0	0	500	100
St. 18	(370)	(90)	100	0	1	0	-	-

the fjord proper in autumn.

Both in Oslofjorden (Wiborg 1940) and Hardangerfjorden (Gundersen 1953, Lie 1967) the maxima occurred in September, but in both fjords small stocks persisted throughout the winter. In Oslofjorden the increase started in July, and in Hardangerfjorden not until August.

No spawning was recorded in Trondheimsfjorden, but possible copepodite stages III-I of *P. parvus* might have been taken as *Pseudocalanus elongatus* which occurred simultaneously in large numbers. The restricted occurrence, however, does not indicate that a possible new generation of *P. parvus* in autumn had any success.

All *P. parvus* were taken in the upper 50 m. This agrees with earlier observations, but Gundersen (1953) recorded that *P. parvus* kept below 50 m in Hardangerfjorden in July and August.

Pseudocalanus elongatus Boeck and

Pseudocalanus minutus (Krøyer)

G.O. Sars (1903) established three species of *Pseudocalanus* in Norwegian waters, *P. elongatus* Boeck, *P. major* G.O. Sars, and *P. gracilis* G.O. Sars. With (1915) classified these three species as forms of *P. minutus* (Krøyer).

Wiborg (1954) concluded that Sars' classification was correct, but, on the other hand, McLaren (1963) suggests that the separation of *P. minutus* (sensu lato) into three distinct species may have been done without proper consideration of **ecophenotypic variations**. *P. elongatus* is a dominating species in coastal waters, and one might assume that the major part of *Pseudocalanus* observed in Norwegian coastal waters belongs to this species (Wiborg 1954). In the Norwegian Sea at St. M, *P. minutus* (sensu strictu) dominated (Østvedt 1955).

In the present material a number of large size specimens of *Pseudocalanus* occurred in the deep hauls. The mean length of the females was a little under 1.20 mm, and they had a habitus typical of *P. minutus* (s.s.). Adults and copepodite stage V of *P. minutus* were found below 100 m in small numbers, but the material is too scanty to give background for conclusions. In the upper 100 m adults and copepodite stage V always showed a *P. elongatus* habitus.

P. minutus probably spawns in spring simultaneously with *P. elongatus* (Wiborg 1954), but young copepodite stages of the two species are difficult to separate. Younger copepodite stages were thus not separated, but the *elongatus/minutus* ratio in the material strongly indicated that the young copepodite stages without significant error might be classified as *P. elongatus*, at least in the upper 100 m. Even in the layers below 100 m *P. elongatus* dominated.

Pseudocalanus elongatus Boeck

Nauplii and the smallest copepodite stages of *P. elongatus* are only occasionally retained by the net, and the discussion is based upon adults and older copepodite stages. During February 1963 - February 1964, the mesh size used also reduced the catch.

Variation in numbers

The numerical variation of *P. elongatus* during 1963-66 is shown in Fig. 30. Two distinct maximal periods were found during the year in

coast Ruud (1929) also found a small spring maximum, while Wiborg (1954) recorded the main maxima of the year in this period.

The summer-autumn maxima in 100-0 m

In 1963 the summer-autumn maximum was found at St. 18 and 15 in July-August. At St. 6 it was much reduced and almost absent at St. 1. In 1964 the maxima were found in July-August at St. 18, 15, and 6, and in August-September at St. 1. At the outer stations the numbers were very large, nearly 300,000 ind/m² at St. 15. As in 1963 the maxima were significantly reduced at St. 6 and nearly absent at St. 1. In 1965 only St. 15 was sampled in late summer-autumn, and the maxima in September-October were significantly smaller than in 1964. In 1966 a significant increase was indicated at St. 6 in early July.

The summer-autumn maxima in 1963 and 1964 generally showed reduced numbers at the inner stations 6 and 1, and indicates that immigration may have taken place. In 1965 and 1966, however, no such gradient was found. In 1965 the total number was significantly reduced compared to 1964.

In the other Norwegian fjord localities the greatest summer and autumn maxima of *P. elongatus* were also found in the outer parts, but the numbers seem to be significantly smaller than in the outer part of Trondheimsfjorden.

From November to April the stock was very small in the upper 100 m.

Variations below 100 m

In the layers below 100 m, the *P. elongatus* population is mixed with *P. minutus* (s.s.). The latter was found mainly in the spring and made up nearly 20% of the females, but in summer and autumn it was outnumbered by *P. elongatus*. The stock was small with maxima in July-December.

Propagation

The stage distribution of *P. elongatus* is shown in Fig. 31. Males normally showed two maxima a year, corresponding to the maximal abundance of the total stock. In winter males were very scarce.

The main maxima of females followed the maxima of males, but small peaks were also found in early spring.

The females of the March-April maximum were probably responsible for the peak of copepodite stages III-I in April-May.

The summer-autumn maxima were composed of all stages, and a more or less continuous spawning is indicated.

If a period of 14 days is assumed for the development from egg to copepodite stage III, spawning took probably place in March, May, and several times in the summer and the autumn. A spring spawning in March was recorded by Ruud (1929), Runnstrøm (1932), and Wiborg (1940, 1944, 1954), and at Ona, Wiborg (1954) found maximal spawnings in May-June, August and October, in summer and autumn more or less continuously. Wiborg (1940) reported a delay in time for spawning inwards in Oslofjorden, but no such pattern has been observed in Trondheimsfjorden.

During spring the development from copepodite stages III-I to adults may be estimated to take 1.5-2 months in Trondheimsfjorden, indicating a total span of more than two months from egg to adult. Wiborg (1940) assumed a developmental period of two months in Oslofjorden, and in the Gulf of Maine Fish (1936 b) found a similar rate of development.

Vertical distribution

The majority of the stock was found in the upper 100 m (Fig. 32).

During spring the females had their main distribution above 100 m, but a significant part was also found below that layer. The summer stock, however, seemed more confined to the upper 100 m.

The copepodite stages V-IV generally showed the same distribution as the females, but had a greater preference for deeper waters. The copepodite stages III-I were mainly found above 100 m. The overwintering stages V-IV resided in deep waters, and a vertical upward migration of

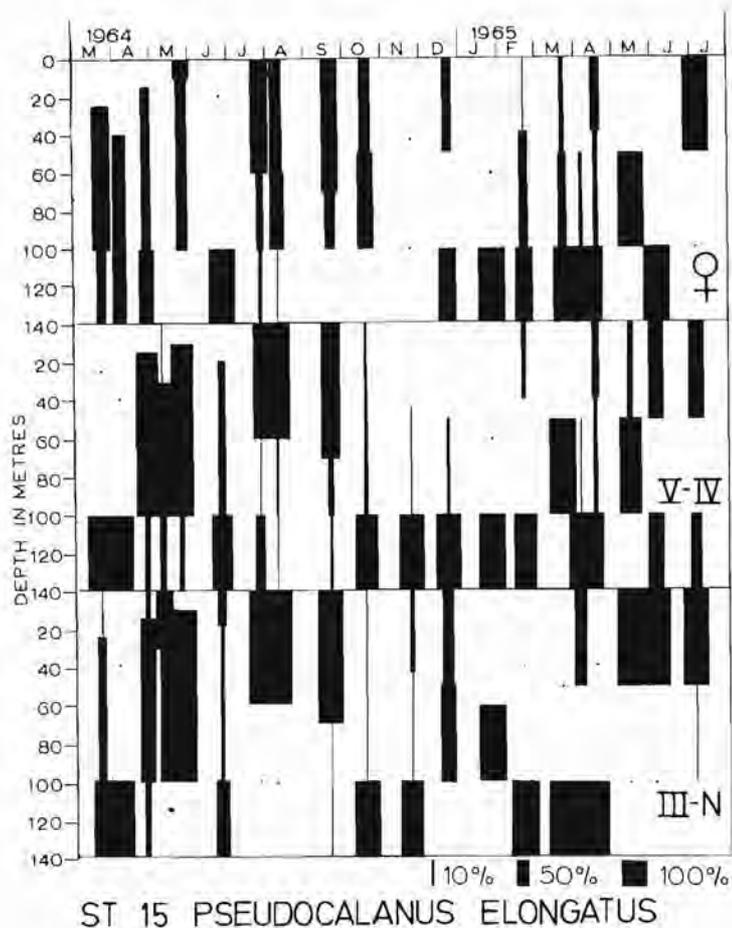


Fig. 32. *Pseudocalanus elongatus*, percentage vertical distribution of different stages at St. 15 during 1964-65.

females was indicated in February-March, followed by spawning.

The numerical variation below 100 m compared to 100-0 m indicates that in late autumn a downward vertical migration below 100 m takes place simultaneously with the vertical mixing of the water masses.

At other coast and fjord localities Ruud (1929) and Wiborg (1940, 1954) found most of the stock in the upper 50 m. This distribution agrees with the situation during summer and autumn in Trondheimsfjorden, but Wiborg (1954) observed that during certain periods adults and old copepodite stages were frequently found below 50 m.

Length distribution

The distribution of mean carapace length of females at St. 15 is shown in Fig. 33. There is a pronounced decrease in mean carapace length from the period February-May to August-October 1964, and a few

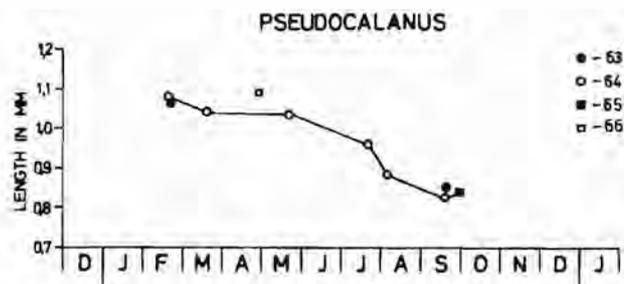


Fig. 33. *Pseudocalanus elongatus*, mean carapace length of females at St. 15 during 1963-1966.

observations from 1963, 1965, and 1966 support this observation. Obviously a large sized cold water generation dominated in spring, while in August-September a new generation brought up in warm water is of smaller size. The largest mean size was recorded in April 1966, and may be related to the very low water temperature that spring. The maximal range of mean length for all years was 1.10-0.80.

The size distribution (Fig. 34) is generally unimodal, but in September 1963 and in August 1964, there is a tendency towards bimodality. Obviously the spring generation is rather homogenous, while in autumn a mixing of local and immigrating populations may include slightly different size groups.

On the west coast (Wiborg 1954), the mean length increased in early spring with maximum in April-May and as in Trondheimsfjorden a decline in mean length took place throughout summer. In Trondheimsfjorden, however, the maximum length in February-May is of the same size as the minimum values found on the coast. Although a peak in April-May 1964 may have escaped attention, the observation in the end of April 1966 indicates that the mean length in Trondheimsfjorden rarely exceeds 1.10 mm, and individuals longer than 1.20 mm were never observed. During summer the mean length in Trondheimsfjorden also is much smaller than on the coast. Both variation in mean size and the total size range in Trondheimsfjorden, are quite similar to that found in Loch Striven (Marshall 1949) and near Plymouth (Digby 1950).

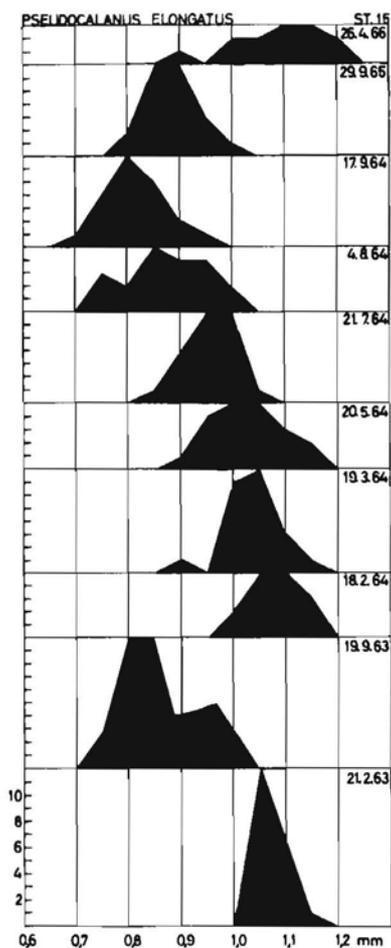


Fig. 34. *Pseudocalanus elongatus*, length frequencies of females at St. 15 during 1963-196 .

Pseudocalanus minutus (Krøyer)

Adults and copepodite stage V of *P. minutus* were found below 100 m in small numbers, but the material is too scanty to give background for conclusions. Spawning probably takes place in spring simultaneously with *P. elongatus* (Wiborg 1954), but young copepodite stages are easily overlooked.

Microcalanus pusillus G.O. Sars

Sars (1903) established 2 species of the genus *Microcalanus*, *M. pusillus* and *M. pygmaeus*, in Norwegian waters. With (1915) regarded both as varieties of *M. pygmaeus*, but Wiborg (1954) stated that Sars' opinion was correct.

M. pusillus dominates in Norwegian waters, but in the depths of the fjords *M. pygmaeus* (s.s.) is of some importance (Wiborg 1954).

In Trondheimsfjorden only *M. pusillus* was recorded, and the size distribution of females supports this observation. However, young stages of *M. pygmaeus* (s.s.) might have escaped attention.

Before March 1964, most of the stock passed the meshes of the net. During the rest of the period adults and copepodite stages V-IV were caught, while lower stages were found in very few numbers.

Variation in numbers

The variation of the stock during 1964-66 is shown in Fig. 35.

In 100-0 m a number of maxima were found throughout the year with main peaks in May-June. In 1964 the main maximum was found in May at St. 18, 15, and 6, but only indicated at St. 1. Smaller maxima were found at all stations in August and October-November. In 1965 the main maximum in total number was found in May at all stations, but with smaller maxima in February at St. 15. In July and September maxima occurred at all stations. In 1966 a large spring maximum occurred in May-June.

In the layers below 100 m a few maxima may be distinguished; the largest in April-May. In 1964 the major maximum seemed to occur in April-May at the outer stations, while no observations were made at St. 1. In October-November a second maximum occurred. In 1965 a rich April-May maximum was recorded at all stations.

Below 100 m the number of maxima were reduced compared to the layer above, and the main spring maximum in 100-0 m seemed to be delayed in time compared to the corresponding maximum below 100 m. A similar delay may be traced also in the later maxima.

In the fjords and at the coastal localities south of Trondheimsfjorden the major maxima were found in April-May, followed by a number of secondary maxima (Ruud 1929, Wiborg 1940, 1954). In Hardangerfjorden small numbers were found, especially in the outer part (Lie 1967). Generally, the maximal concentrations found in other fjord localities were small, while the values for Trondheimsfjorden during maxima were relatively high and comparable to the maximum concentrations found at Eggum (Wiborg 1954).

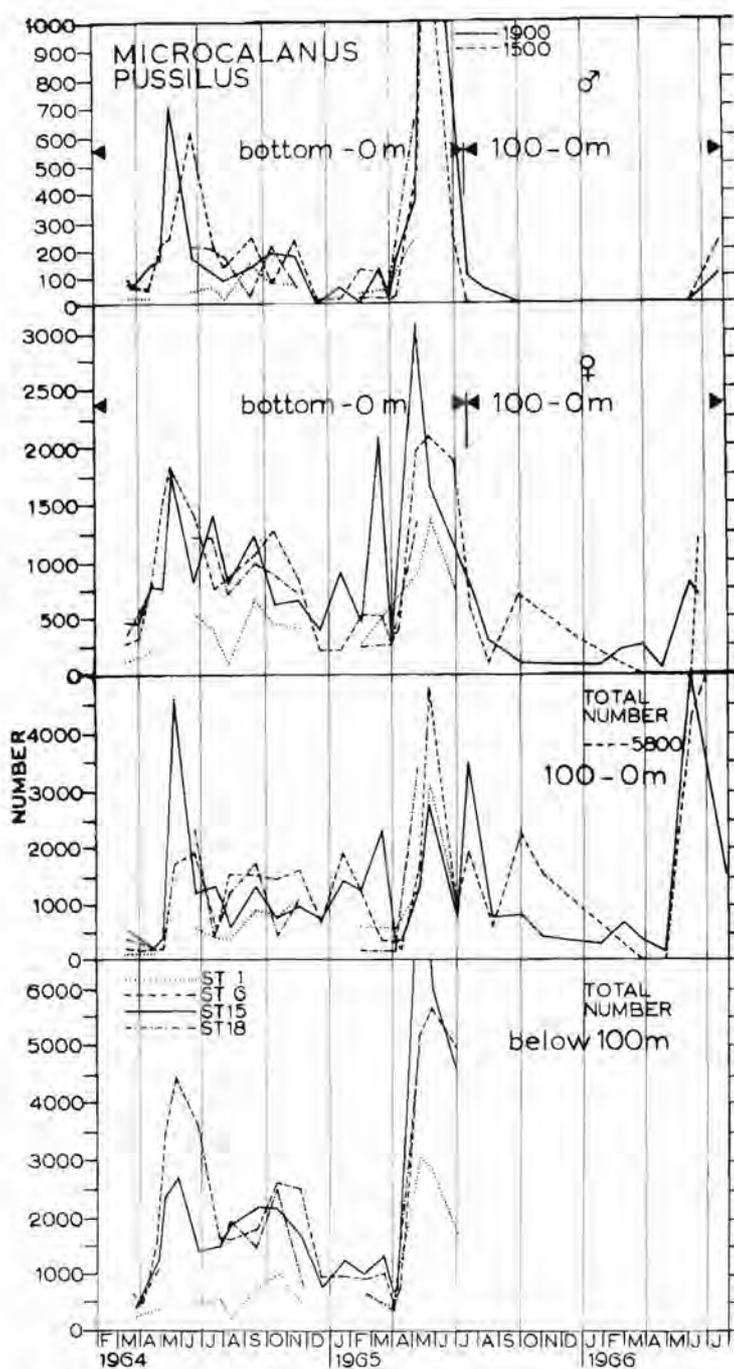


Fig. 35. *Microcalanus pusillus*, total number per haul below 100 m and in 100-0 m and total number of males and females at St. 18, 15, 6, and 1 during 1964-66.

Propagation

The number of adults is given in Fig. 35, males and females separated. The maxima of adults coincided with the maxima of total number in 100-0 m. Maxima of females were found in February-March, May-July and September, and the males partly showed a similar distribution. Small numbers of males and females were present outside these periods. The distribution of adults indicates that the main breeding periods are

probably found in February-March, April-May, June-July, and September. This pattern corresponds well with the spawning found at Ona in January, March-April, June-July, September, and November (Wiborg 1954).

Vertical distribution

The main stock occurred below 100 m (Fig. 36). Females and copepodite stages V-IV had an almost identical vertical distribution, while the males probably kept deeper. An upward migration in early spring seems probable, and was combined with an increase of the total stock, possibly related to spawning. Very few specimens were taken above the discontinuity layer. At Eggum Wiborg (1954) found that the main spring maximum in June was preceded by migration to the upper 50 m along with spawning.

Marshall (1949) found that *M. pusillus* did not show the same seasonal vertical distribution as the other copepods in Loch Striven, and that it always kept below 10 m.

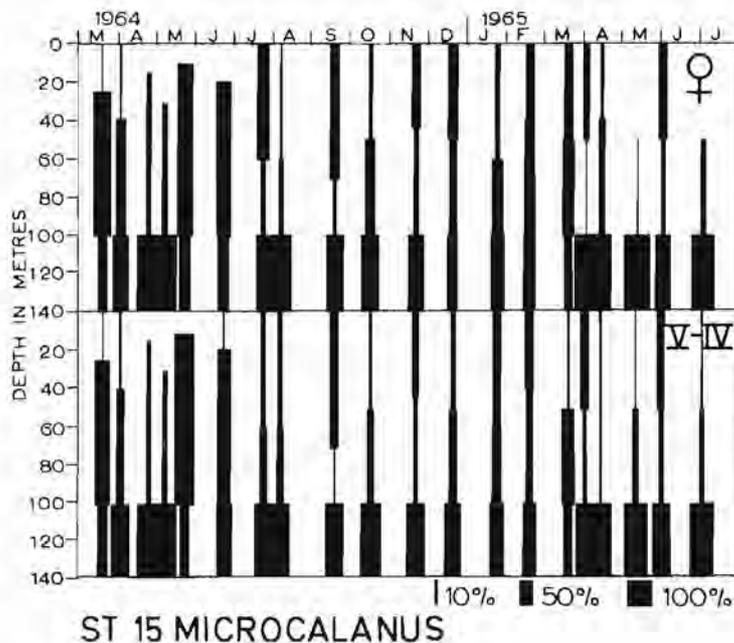


Fig. 36. *Microcalanus pusillus*, percentage vertical distribution of females and copepodite stages V-IV at St. 15 during 1964-65.

Size distribution

The length measurements of *M. pusillus* are based on (when possible) 50 females from 16 samples from the hauls below 100 m at St. 15 during 1964-65. The mean carapace length in different months is given in Fig. 37.

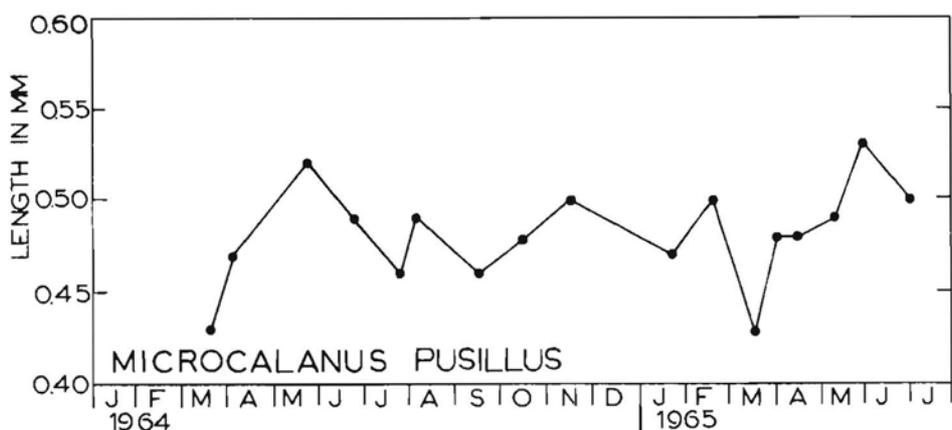


Fig. 37. *Microcalanus pusillus*, mean carapace length of females at St. 15 during 1964-65.

Minima seem to occur in March, followed by peaks in May-June. The maximal range of mean size is 0.43-0.53 mm. This distribution of mean size shows a very close parallel to that found at the coastal localities (Wiborg 1954).

The individual size distribution is demonstrated in Fig. 38. In March 1964 the distribution was bimodal with small individuals (0.43 mm) dominating, probably being derived from the autumn generation. The bimodality indicates several sources of supply, or that two generations were present. In April a larger size group was of equal importance, but in May both these size groups were replaced by large specimens (0.53 mm) and the distribution became unimodal. This increase in size was undoubtedly related to the new spring generation grown in cold water. From June to September smaller individuals again gradually took over, probably due to maturation of summer and autumn generations in warmer water. In October 1964 a bimodal distribution again occurred, due to large specimens, perhaps brought in by a simultaneous deep inflow. This size distribution persisted until February, but in March 1964 a new stock with smaller specimens was introduced, perhaps related to the deep spring inflow.

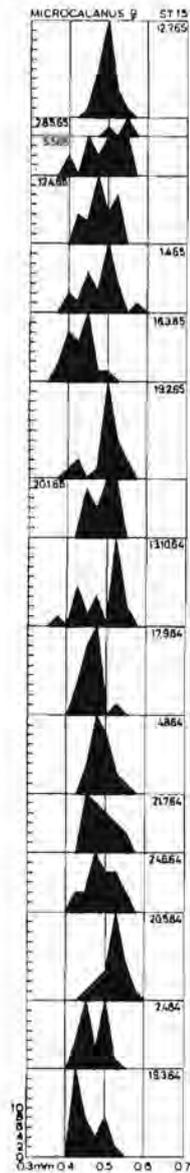


Fig. 38. *Microcalanus pusillus*, length frequencies of females at St. 15 during 1964-65.

In April, however, a large size fraction again appeared and a size bimodality persisted until July when the largest specimens dominated. The situation found in March-July 1965 showed a parallel to the same period in 1964, and the same explanation may be applied.

Chiridius armatus (Boeck)

C. armatus is an arctic species, distributed from the North Atlantic to the Arctic Ocean (Brodskii 1950). Sars (1903) mentions it

as being a pronounced deep water form off the coast of Norway and occurring in deep fjords. The sledge hauls compared to the ordinary vertical hauls indicate that adults and older copepodite stages of *C. armatus* live very near the bottom, and may thus escape the net. Similar observations are reported by Matthews (1964).

Young stages are probably less confined to the bottom and vertical hauls may accordingly give an impression of variations of the stock.

Variation in numbers

The variation in numbers, shown in Fig. 39, is mainly due to copepodite stages III-I. Periods of abundance seemed to occur in spring and summer-autumn with the main maximum in September-October. At St. 1 the stock seemed to be smaller than at the outer stations, probably due to the lesser depth at this station.

In Raunefjorden (Matthews 1964), total maximum was found in May, partly corresponding to the phytoplankton bloom in the upper layers and

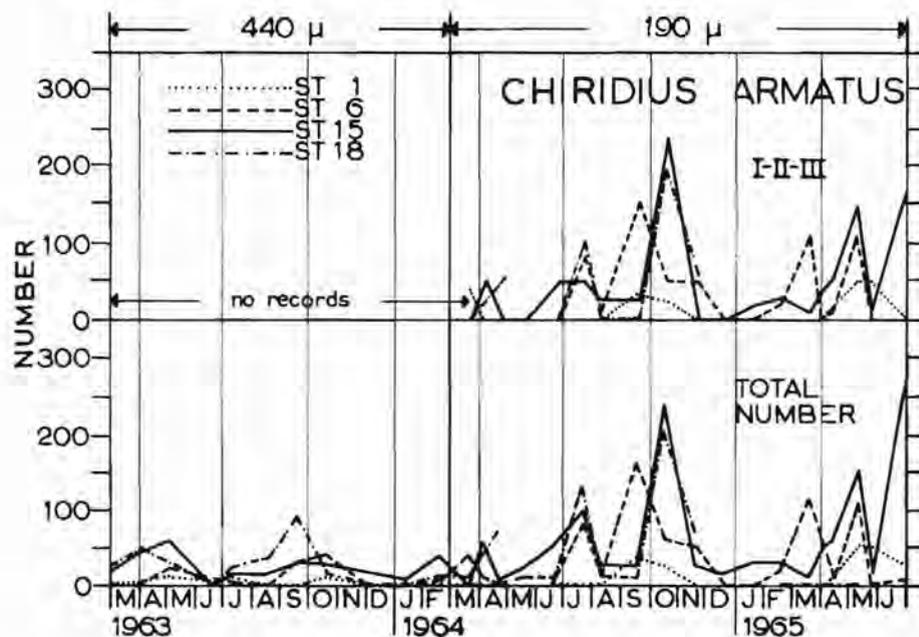


Fig. 39. *Chiridius armatus*, total number and number of the copepodite stages III-I in the total water column at St. 18, 15, 6, and 1 during 1963-65. (From February 1963 to February 1964 mesh size 440 μ).

partly to the temperature in deeper water. A small peak of adults occurred in August.

In Hardangerfjorden Gundersen (1953) found *C. armatus* to be sparse with peaks in February-March and May. In Oslofjorden *C. armatus* was found mostly in the inner fjord, with peaks in February, April-May, and December.

Propagation

In Trondheimsfjorden the occurrence of copepodite stages III-I indicates a more or less continuous spawning. In Oslofjorden Wiborg (1940) assumed that *C. armatus* propagated a greater part of the year with peaks in March-April and October-November. In Raunefjorden Matthews (1964) found the main breeding in May followed by a secondary spawning in June-July.

Vertical distribution

C. armatus was almost exclusively taken below 100 m, and the vertical distribution of copepodite stages III-I indicated that it spawned in deep water. No seasonal migration above 100 m was observed. Sars (1903) found this species mainly below 200 m in the fjords which is in agreement with observations by Gundersen (1953) and Wiborg (1940). At St. M, Østvedt (1955) recorded *C. armatus* nearly always below 600 m, and Jespersen (1939a) found this copepod exclusively in hauls below 600 m in Greenland waters.

Pareuchaeta norvegica (Boeck)

P. norvegica was reported by Gran (1902) to be a boreal-oceanic plankton element of the deep Atlantic water. In deep Norwegian fjords it occurs frequently (Sars 1903).

In Trondheimsfjorden specimens of *P. norvegica* are found in the

plankton during all seasons and usually in rather small numbers. However, due to its relatively large size it must be regarded as an important member of the plankton with respect to biomass.

Hauls with Beyers bottom sledge at different seasons always gave a considerable number of adults, mainly females, and copepodite stage V of *P. norvegica*, and indicate that these prefer near bottom habitats. Beyer (referred to by Wiborg 1954) has made the same observation in Oslofjorden. Thus the samples taken by vertical hauls are hardly representative for adults and old copepodite stages, but for the younger stages the numbers are probably more reliable.

Variation in numbers

The variation in numbers per haul of *P. norvegica* during 1963-66 (Fig. 40) is mainly due to copepodite stage I and nauplii. Main maxima are indicated in March-April at all stations, with smaller peaks in April-May and in July-August. During February 1963 to February 1964 copepodite stages were not separated.

In Oslofjorden peaks of abundance of young stages occurred in February-May (Wiborg 1940), and spring maxima of similar composition were found in Hardangerfjorden (Gundersen 1953), at the coastal stations (Ruud 1929, Wiborg 1954) and at St. M in the Norwegian Sea. Secondary maxima in autumn seemed to be the rule at all localities. The maximal periods found in Trondheimsfjorden agree well with these observations.

In Trondheimsfjorden the innermost St. 1 showed small numbers every year. In 1964 St. 18 apparently had a small stock, while in 1965 this station gave a rich yield of nauplii. In maximal periods an average abundance of $1,500 \text{ ind/m}^2$ was found, but extreme values in 1965 reached $11,000 \text{ ind/m}^2$, mainly nauplii, at the outer station 18. In Oslofjorden also the innermost stations were poor in *P. norvegica*, while the largest numbers were found in the outer part of the fjord.

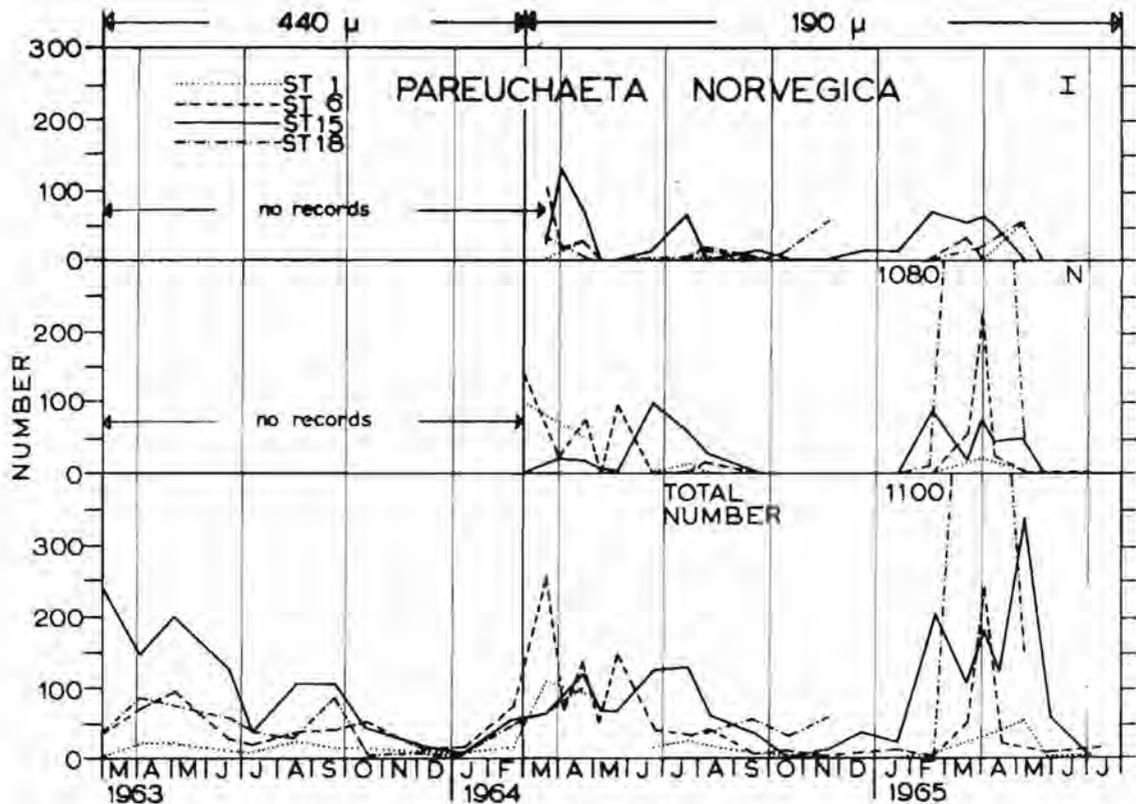


Fig. 40. *Pareuchaeta norvegica*, total number and number of copepodite stage I and nauplii in the total water column at St. 18, 15, 6 and 1 during 1963-65. (From February 1963 to February 1964 mesh size 440 μ).

Propagation

The maxima referred to above were mainly due to nauplii and young copepodite stages, and indicate two main breeding periods annually, in early spring and in late summer. The spring brood is the largest. Females carrying egg sacks and nauplii were found at all seasons, and *P. norvegica* obviously breeds more or less continuously in Trondheimsfjorden. The earlier records from Norwegian waters show similar breeding habits. The deep distribution of the bulk of the young stages indicates that *P. norvegica* spawns in deep water.

Vertical distribution

The vertical distribution of *P. norvegica* at St. 15 is shown in Fig. 41, with females, copepodite stages V-IV and copepodite stages III-I including nauplii, separated.

Females were exclusively found below 100 m. Males were uncommon in the hauls and they may have a deeper distribution, but Nicholls (1934) has shown that males have a significant shorter life than females, and smaller numbers must accordingly be expected. Copepodite stages V-IV occasionally occurred in the plankton above 100 m, but no regularity in vertical distribution at different seasons could be discovered. The copepodite stages III-I and nauplii are less confined to the layers below 100 m. In March-April small but significant percentages were found even above the discontinuity layer, but the major stock still kept below 100 m. This distribution coincided with the maximum of lower stages. In summer-autumn nearly the whole stock of these lower copepodite stages was observed

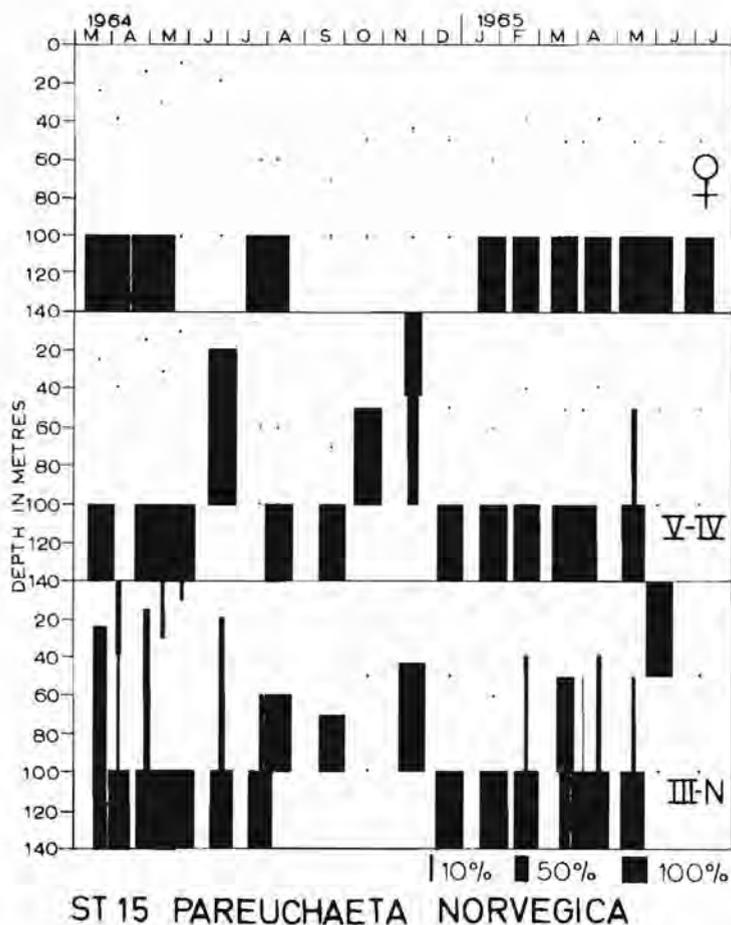


Fig. 41. *Pareuchaeta norvegica*, percentage vertical distribution of different stages at St. 15 during 1964-66.

above 100 m.

The vertical distribution of the larvae indicates that *P. norvegica* ascends to some degree during spawning. On the other hand, several workers state that the young copepodites **always** keep to deep water, (Ruud 1929, Størmer 1929 and others). Bigelow (1926) also made the same observation, but he found that individuals in breeding condition occasionally occurred at the surface.

It is a well known fact that adult *P. norvegica* prefers deep water down to 1,000 m in the Norwegian Sea (Wolfenden 1904), and at St. M, Østvedt (1955) found the maximal occurrence in 600-100 m.

Scolecithricella minor (Brady)

S. minor has a world-wide distribution, although probably different varieties are found in different parts of the worlds oceans (Brodskii 1950). It is very eurythermal and is said to be an arctic species (Fish & Johnson 1937) as well as a warm water indicator (Bigelow 1926). According to Jespersen (1939b) and Hansen (1960), *S. minor* must be regarded as an Atlantic species.

S. minor is normally an unimportant member of the zooplankton in Norwegian waters. In Trondheimsfjorden, however, it is of significance during certain periods.

Variation in numbers

The stock fluctuated rapidly, and several maxima occurred annually both above and below 100 m (Fig. 42).

In 100-0 m peaks were found in January-February 1965; March-April 1964 and 1965; May-June 1963, 1964, 1965, and 1966; September 1963, 1964, and 1965; and November-December 1963 and 1964. All stages took part in these maxima (Fig. 43). The stock was usually significantly reduced inwards in the fjord, particularly at St. 1.

Below 100 m peaks were found in March 1965; May 1963, 1964, and 1965; August 1963; October 1964; and December 1963 and 1964. As in

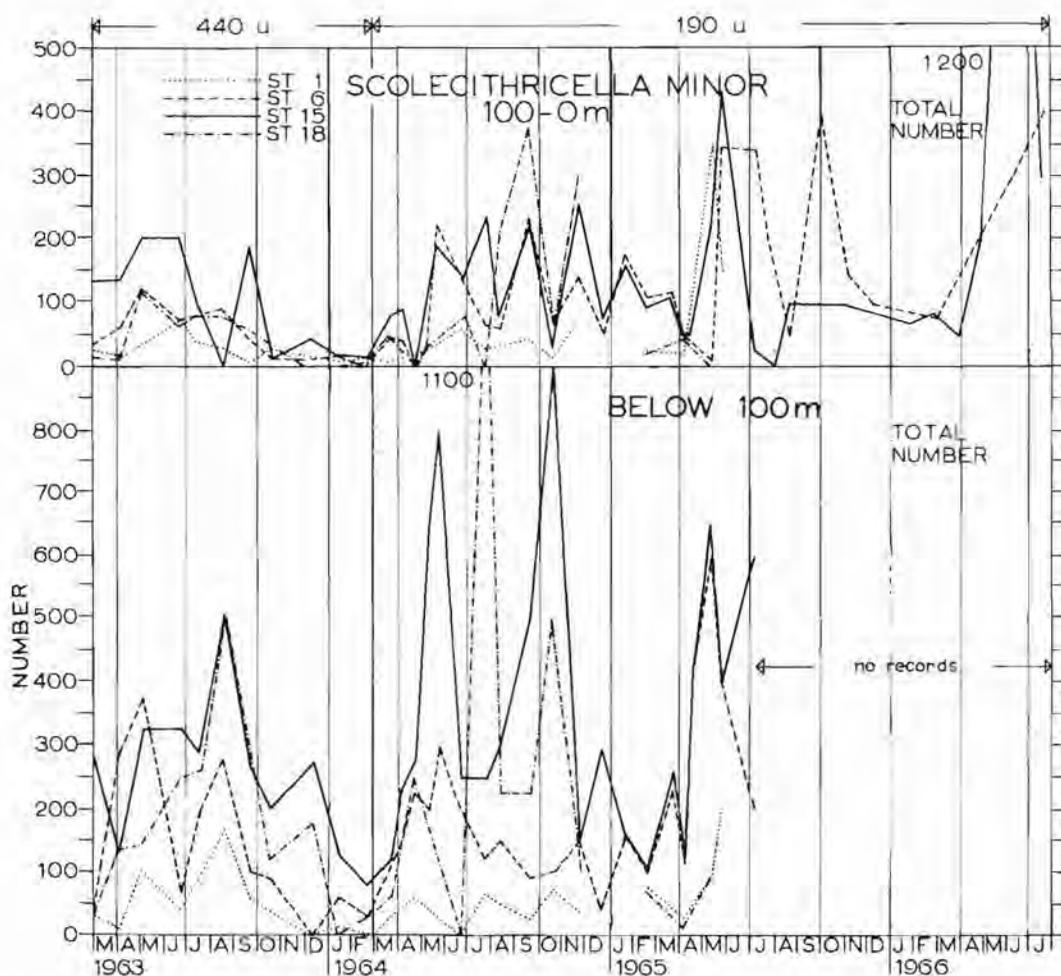


Fig. 42. *Scolecithricella minor*, total number per haul below 100 m and in 100-0 m at St. 18, 15, 6, and 1 during 1963-66. (Before March 1964 mesh size 440 μ).

the layer above all stages took part in the maxima and a similar stock reduction inwards was also evident.

The peaks in 100-0 m and below 100 m showed a tendency to alternate in time, most significant in 1964 and 1965. The alternation did not correspond to any significant change in stage distribution, and it seems as if the whole population undertook frequent vertical migrations. Spring and autumn seemed to be periods of maximal abundance, and the stock might exceed 10,000 ind/m².

At other localities in Norwegian waters only single specimens

occur (Gundersen 1953), or small numbers are found with peaks in different months (Runnstrøm 1932, Wiborg 1940, 1954, Østvedt 1955). This distribution with peaks scattered in time corresponds to the frequent maxima found in Trondheimsfjorden.

In Oslofjorden *S. minor* was mostly found in the outer part (Wiborg 1940).

Propagation

The stage distribution in 100-0 m is shown in Fig. 43. Small numbers of adults were present during almost all seasons, and the distribution of copepodite stages III-I indicates that spawning occurred more or less continuously. Below 100 m a similar pattern was observed, but males and females were more numerous. No females were observed in spring 1966, while copepodite stages V-IV were quite abundant. It is possible that the low sea temperature in 1966 was unfavourable to the maturing of *S. minor* and caused an accumulation of copepodite stages V-IV.

The main spawning seemed to occur in spring and autumn, both above and below 100 m. The development is probably rapid, going from copepodite stages III-I to females within four weeks, and a generation length of two-three months might be assumed. This corresponds well with the number of maxima of copepodite stages III-I. In the Labrador Sea Kielhorn (1952) suggested a breeding period from August to December, and in British Columbia Legare (1957) found young stages in numbers corresponding to the stock maximum in November distributed in the whole water column.

Vertical distribution

The vertical distribution of *S. minor* at St. 15 is shown in Fig. 44 with females, copepodite stages V-IV and copepodite stages III-I separated. The females have their main distribution below 100 m, but in spring a significant number visit the upper layers. Also the

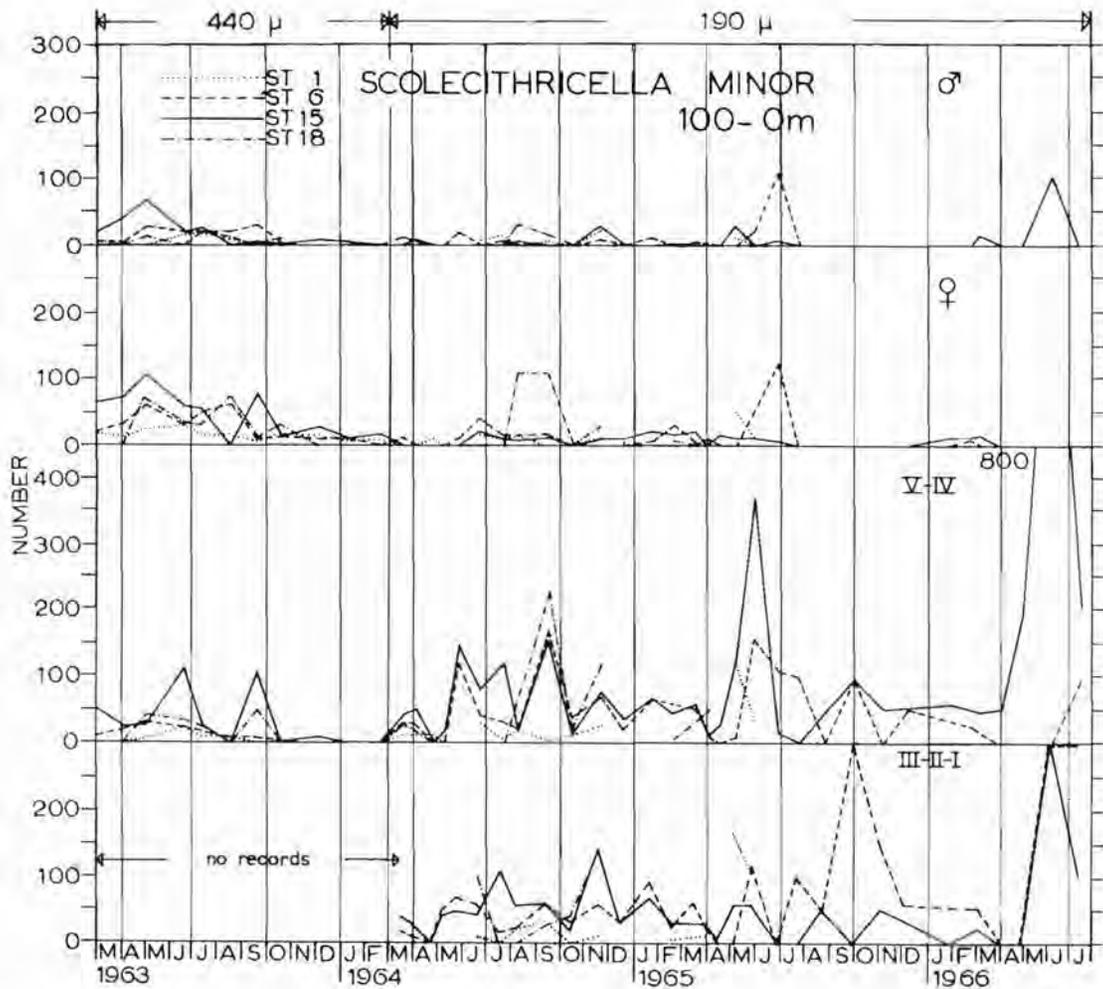


Fig. 43. *Scolecithricella minor*, stage distribution in 100-0 m at St. 18 15, 6, and 1 during 1963-66. (Before March 1964 mesh size 440 μ).

males showed the greatest numbers below 100 m. The copepodite stages V-IV had a vertical distribution similar to the females, but a slightly larger percentage was found above 100 m. The younger copepodite stages occurred more frequently above 100 m.

In Norwegian fjords and coastal waters *S. minor* is most frequent below 50 m (Wiborg 1940, Gundersen 1953) and in the Norwegian Sea Østvedt (1955) found its center of distribution in 600-100 m, corresponding to Atlantic water. In British Columbia Legare (1957) recorded both

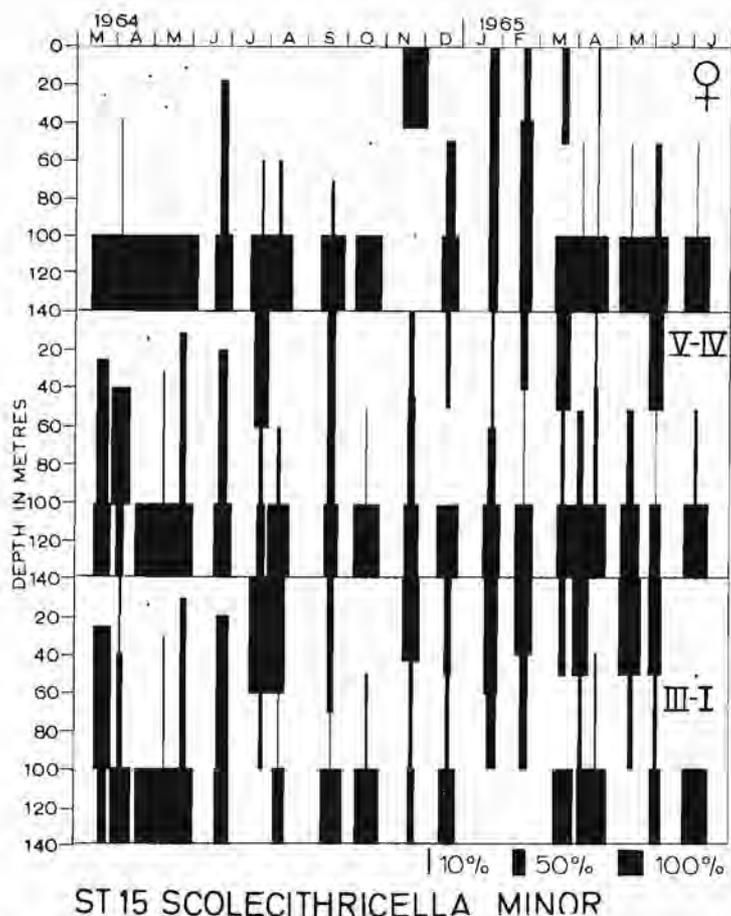


Fig. 44. *Scolecithricella minor*, percentage vertical distribution of different stages at St. 15 during 1963-65.

adults and young stages at all depths.

The variation in vertical distribution in Trondheimsfjorden may also indicate that all stages undertake frequent vertical migrations. Hansen (1960) assumed that *S. minor* submerged during summer, but no other records of seasonal migration are given in the literature.

Length distribution

The length measurements of *S. minor*, females and copepodite stage V are based upon 50 specimens for each date from the layers below 100 m at St. 15. The variation of mean carapace length of females and copepodite stage V is shown in Fig. 45. Minima were found in March-April both years, while the largest values occurred in May-June and August. The maximal range was 1.19-0.95 mm for the females and 1.02-0.88 mm for the copepodite stage V.

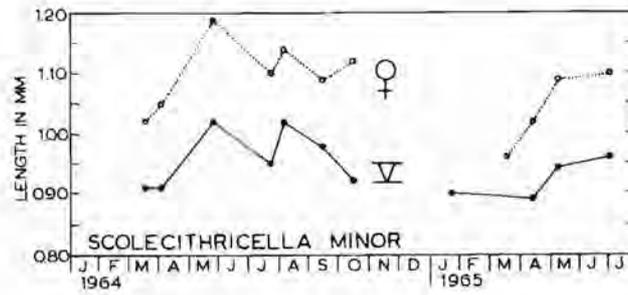


Fig. 45. *Scolecithricella minor*, mean carapace length of females and copepodite stage V at St. 15 during 1964-65.

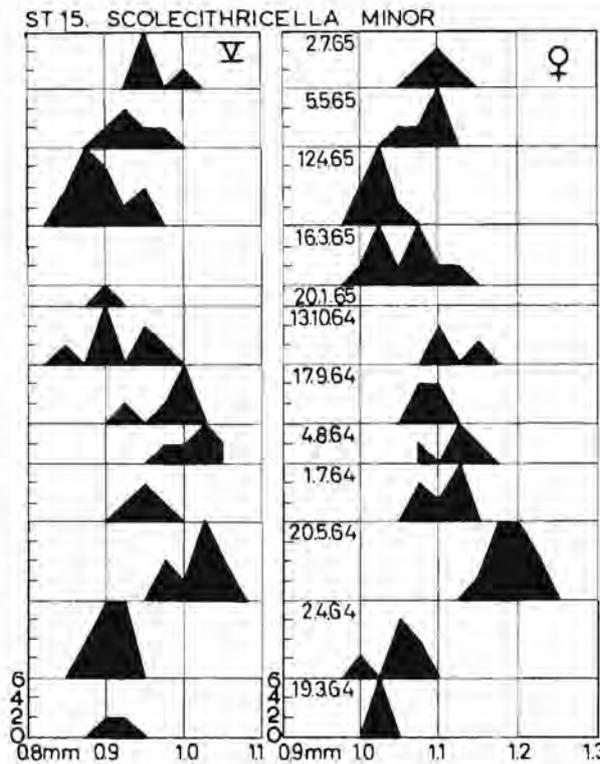


Fig. 46. *Scolecithricella minor*, length frequencies of females and copepodite stage V at St. 15 during 1964-65.

The length frequencies of *S. minor*, females and copepodite stage V are shown in Fig. 46. The minima in March-April of both years were probably due to an overwintering autumn generation, while the increase in size in May-June may reflect development in colder water during spring. The unimodal distribution indicates little mixing of stocks.

Temora longicornis Müller

T. longicornis is known to be a neritic species, but is also found in the open sea. It is common in the Skagerak, on the West Coast of Norway, and in the fjords (Sars 1903, Farran 1911).

According to Farran (1911) *T. longicornis* has a marked tendency to occur in patches. In Trondheimsfjorden, however, the general trend of the variations does not indicate an extremely clumped distribution.

During summer *T. longicornis* is numerically an important member of the zooplankton in Trondheimsfjorden. The smallest stages are unsatisfactorily retained by the net, especially during February 1963 - February 1964.

Variation in numbers

The variation in number of *T. longicornis* during 1963-1966 is shown in Fig. 47.

The main maxima are very distinct, and rapid variation of the stock is characteristic. The main maximum of the year was found in the period July-September, preceded by small maxima in March-May. During winter single specimens occurred occasionally in the hauls.

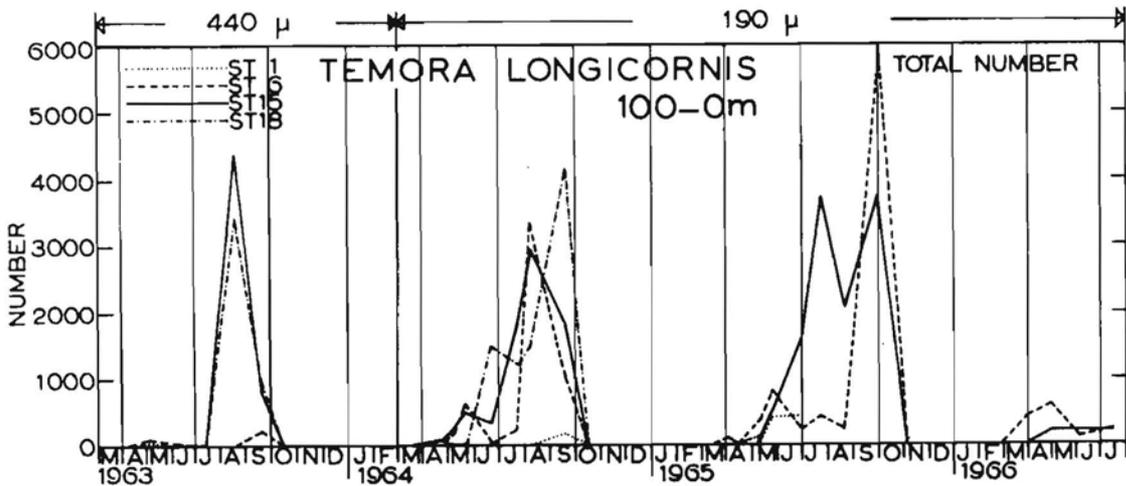


Fig. 47. *Temora longicornis*, total number per haul in 100-0 m at St. 18, 15, 6, and 1 during 1963-66. (Before March 1964 mesh size 440 μ).

Small numbers normally found in March were followed by a small maximum in April-May. The spring maximum seemed to occur simultaneously at all stations, being of the same size and composed of all stages (Fig. 48).

The summer-autumn maxima were generally very rich. In 1963 the maximum occurred at St. 18 and 15 in August. The corresponding maximum at St. 6 was much smaller, and was not found until September. These maxima were composed mainly of males and females. A few copepodites of stages V-IV were recorded, but due to the mesh size used before March 1964, lower stages passed easily through the net.

In 1964 a June maximum at St. 18 consisted mainly of adults and copepodite stages V-IV. In July 1964 a maximum due to copepodite stages III-I probably occurred at St. 18, but this maximum seemed to be overshadowed by the general rise in numbers. In August 1964 abundant maxima were found at St. 15 and 6. These maxima were composed of old and young copepodite stages. In September there was a third summer maximum at St. 18, composed of both adults and small copepodite stages. This maximum may also be traced at St. 15 and partly at St. 6. Even at St. 1 small numbers of copepodites were found.

From July 1965 only St. 15 and 6 were sampled. In July a summer maximum composed of all stages was found at St. 15, and in September a maximum occurred simultaneously at both stations. At St. 6 all stages took part in the maximum, while at St. 15 the copepodites dominated.

In 1966 small numbers were recorded in the middle of July, and a delayed maximum this year was obvious. The small numbers during June-July 1966 may not be related back to a lack of particular stages, but coincides with abnormally low temperatures during spring and early summer.

Large summer-autumn maxima seemed restricted to stations 18, 15, and 6. A gradient towards the inner part of the fjord both in respect to time of the maximum and partly to the number of specimens seems obvious.

In Hardangerfjorden Gundersen (1953) recorded maxima of medium size in May and July, while Lie (1967) in the same locality found very small numbers in spring and not until July was a small stock observed, mainly in the outer part. In Oslofjorden (Wiborg 1940) and at Møre (Ruud 1929) maxima were found in April-May and in June-July. As in Trondheimsfjorden the summer maxima were largest in the outer part with decreasing

values inwards, and in the Møre fjords they were absent even in August. In the landlocked Nordåsvann (Wiborg 1944) and in Lusterfjorden in the innermost part of Sognefjorden (Gundersen 1953) relatively large summer stocks of *T. longicornis* were found.

Propagation

The stage distribution of *T. longicornis* is shown in Fig. 48. The first males were found in April-May 1963, in the last week of May in 1964 and 1965, and in April 1966. Females were recorded simultaneously with the males in 1963, 1964, and 1965, but in 1966 they were not found until early June. Before these dates adults were not recorded in the plankton. Based on the presence of young copepodite stages, spring spawning probably occurred in April 1963, in early March and April 1964, 1965, and 1966.

In Hardangerfjorden Gundersen (1953) did not find the adults until late June, while copepodites and nauplii were recorded in abundance in April-May. In the Plymouth area Digby (1950) observed that while adults and copepodites were scarce early in the year, nauplii were found from February.

A winter stock probably existed in a low concentration in Trondheimsfjorden and was not caught by the ordinary vertical hauls, but in spring they were able to produce a new generation. On the other hand, Conover (1964, referring to Å. Berner pers.comm.) reports that *T. longicornis* has been found to have possible resting eggs, and freshwater copepods are also known to have resting eggs during unfavourable conditions (Elgmork 1955, Fryer & Smyly 1954).

The larvae which were spawned in Trondheimsfjorden in **March** did not seem to have any success. The April generation developed into stages V-IV in May and further to adults in July. The July females probably spawned in July-August, this generation reached stages V-IV in August-September and developed into adults in September. The September females spawned in September, but this generation did not seem to reach maturation. Spawning probably takes place rather continuously when temperature is favourable. Wiborg (1954) assumed that spawning occurred more or less

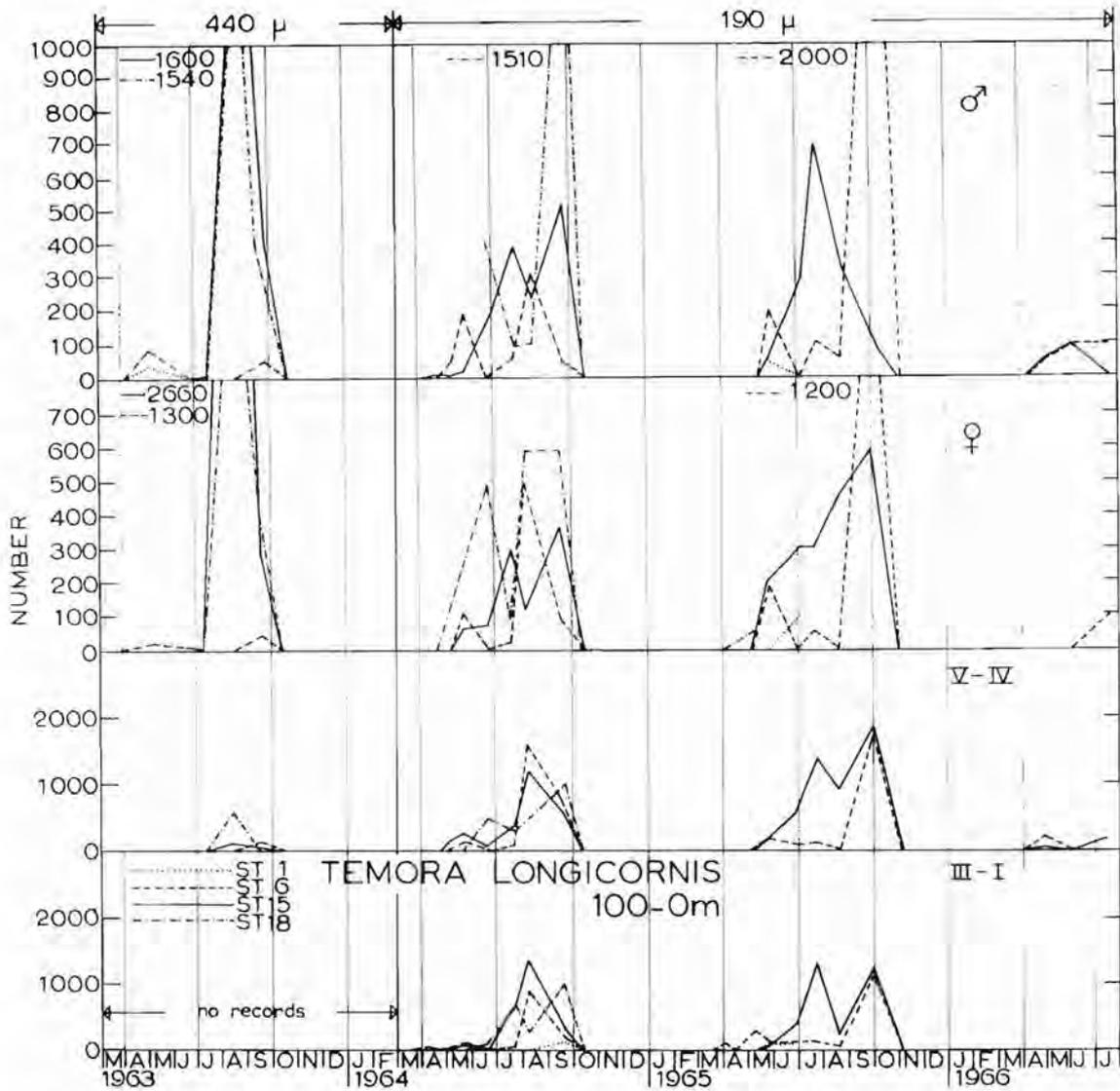


Fig. 48. *Temora longicornis*, stage distribution in 100-0 m at St. 18, 15, 6, and 1 during 1963-66. (Before March 1964 mesh size 440 μ).

continuously when *Temora* was present in numbers at the coast stations, and this assumption is supported by observations in the Norwegian Sea (Hansen 1960) and Long Island Sound (Deevey 1956). Wiborg found that on the coast the most intense propagation occurred in May, June-July, and August-September. In Oslofjorden Wiborg (1940) suggested spawning in April, and in Nordåsvannet Wiborg (1954) found three propagations periods; in May, July-August, and September-October. These main periods agree with the observations in Trondheimsfjorden. In Oslofjorden a

delayed spawning inwards was indicated in spring (Wiborg 1940), but in Trondheimsfjorden no such trend was found.

The spring generation seemed to require one month to reach stages V-IV, and two months more to mature into adults. This gives a total life span for the spring generation of two-three months. The summer generation seemed to develop rapidly into stages V-IV, and the adults were found less than two months later. In 1966, the April-May generation probably needed at least two months to reach stages V-IV. This delayed development may have been due to the extremely low temperature in spring 1966.

Vertical distribution

In Trondheimsfjorden the whole stock of *T. longicornis* was found in the upper 100 m, usually above 50 m (Fig. 49), and at the Borgenfjord

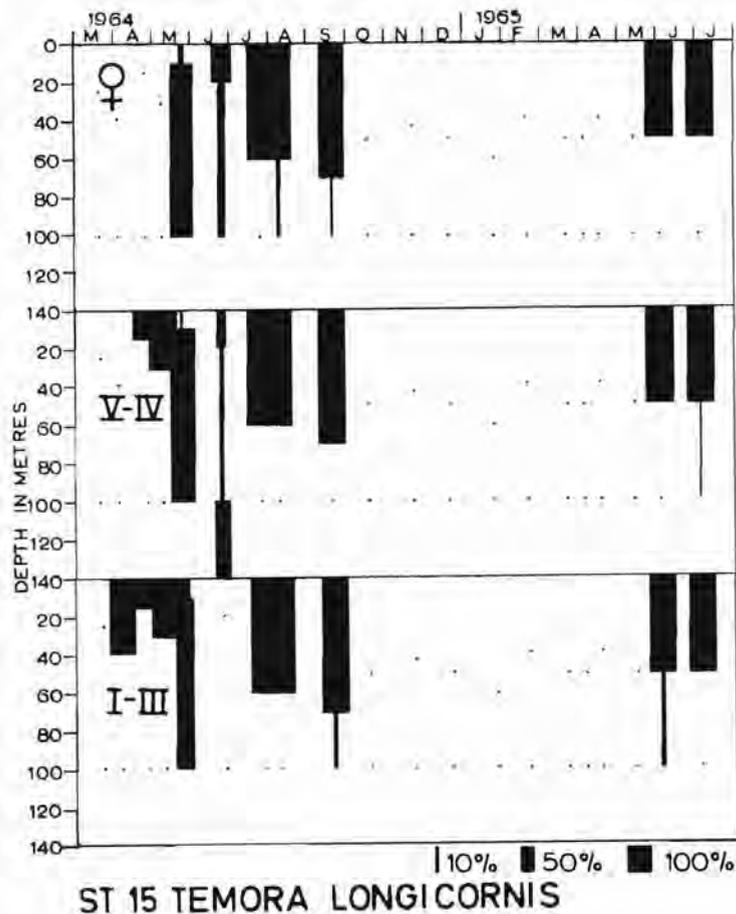


Fig. 49. *Temora longicornis*, percentage vertical distribution of different stages at St. 15 during 1964-65.

stations large stocks kept to the upper 15-20 m (Strømngren 1973). All stages had an identical vertical distribution. In Norwegian waters *T. longicornis* is known to be an inhabitant of the upper 50 m. In the Baltic it prefers the uppermost layers near the thermocline (Ackefors 1969).

Length distribution

The variation in mean carapace length of females of *T. longicornis* at St. 15 is shown in Fig. 50. In 1965 maxima occurred in July and in September, minima in May and August. Both in 1964 and 1965 there is a decrease from July to August-September, which may be due to a summer generation bred in warm water. The largest mean length, in April 1966, is perhaps related to low water temperature. Relatively rapid and large variations seem to be the general pattern and indicate that the population changes several times, partly due to new generations, and partly to immigrants. The total range in mean length in Trondheimsfjorden is 0.83 to 0.56. In British waters (Marshall 1949, Digby 1950), maximal mean size occurred in spring, while throughout summer, the individuals were significantly smaller. The autumn size maximum found in British waters is also indicated in Trondheimsfjorden.

The size distribution (Fig. 51) indicates a slight bimodality in July, while in autumn only one size group seems to dominate.

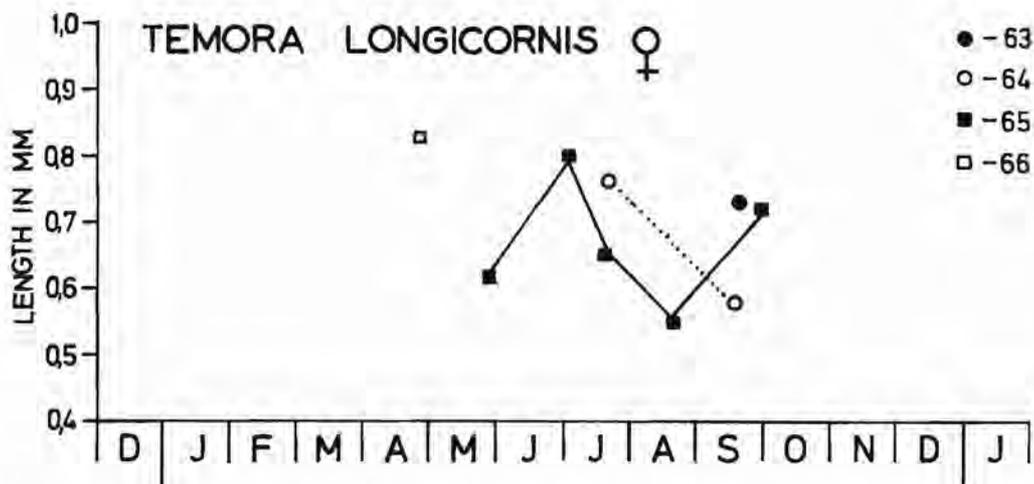


Fig. 50. *Temora longicornis*, mean carapace length of females at St. 15 during 1964-1966.

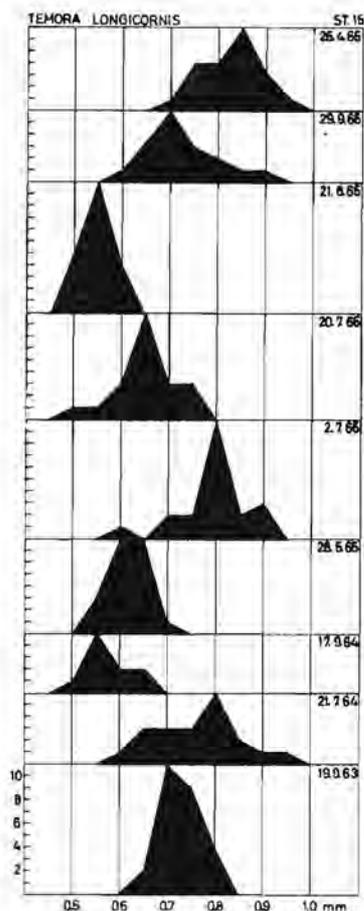


Fig. 51. *Temora longicornis*, length frequencies of females at St. 15 during 1964-1966.

Metridia longa (Lubbock)

Two species of the genus *Metridia*, *M. longa* and *M. lucens*, occur in the plankton in Norwegian waters.

Adults and copepodite stages V-IV were determined to species, while copepodite stages III-I and nauplii were classified as *Metridia* spp. As will be discussed later, *M. lucens* had an irregular and restricted occurrence in the fjord, and only single specimens were found at St. 6 and 1. Obviously, almost all of the young stages of *M. spp.* in the inner fjord and a great majority in the outer fjord belonged to *M. longa*. In the discussion *M. spp.* is taken as *M. longa* in all parts of the fjord.

M. longa is a distinctly northern form (Wolfenden 1904), and Bigelow (1926) regards it as a true arctic species. It is probably very common in the deeper layers all over the Norwegian Sea (Østvedt 1955, Wiborg 1955), and in deep Norwegian fjords (Sars 1903, Runnstrøm 1932,

Wiborg 1940, 1954, and Gundersen 1953).

Variation in numbers

The numerical variation of *M. longa* and *M. spp.* in the main fjord during 1963-65 is shown in Fig. 52. Two main maxima occurred during the year, a very significant one in April-May and a far smaller one in August-October.

In 1963 the spring maxima in May were composed of copepodite stages IV-I in the first part of May (Fig. 53), replaced by copepodite stage V in May-June. The maximum at St. 6 and 18 in August was due to adults and a few copepodites of different stages, and the October maximum at the three inner stations, 15, 6, and 1, had the same composition. In 1964 the spring maximum at St. 18, which started in the end of April,

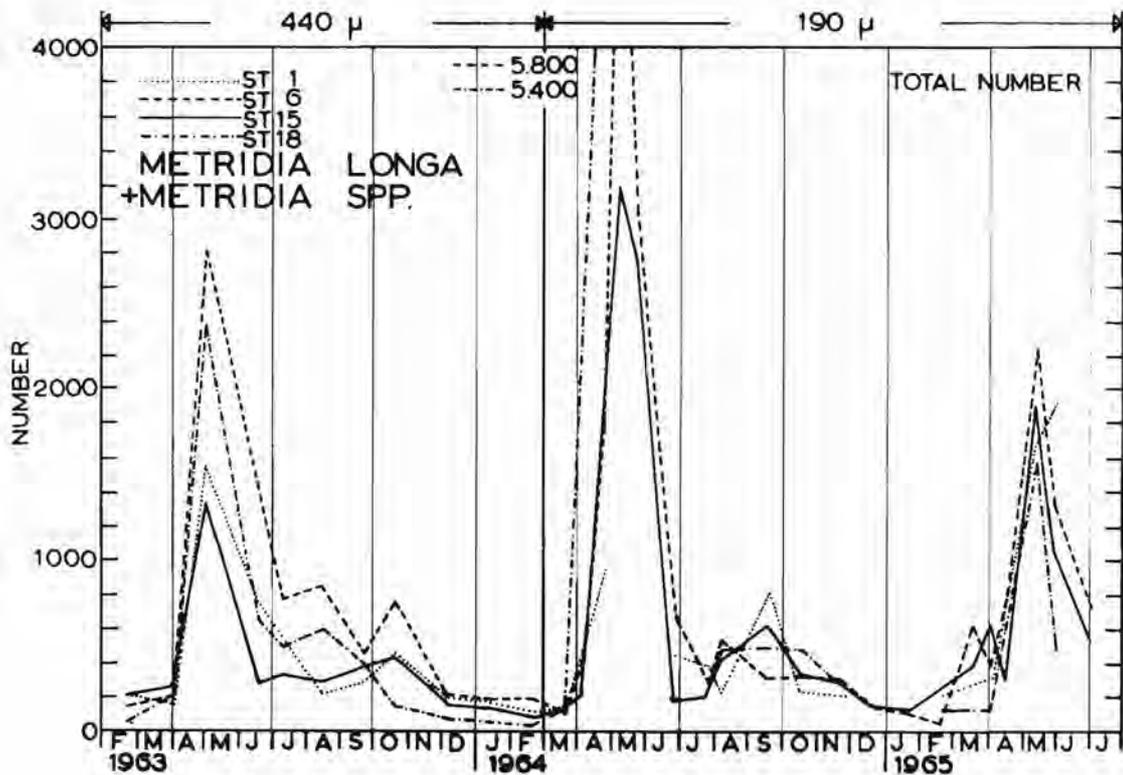


Fig. 52. *Metridia longa* and *Metridia spp.*, total number in the total water column at all stations during 1963-65. (Before March 1964 mesh size 440 μ).

was based on nauplii and copepodite stages III-I. At the other stations the maximum was not found until May, with nauplii and copepodite stages IV-I as the most important members. As in 1963 the stock composition shifted to copepodite stage V at the end of the period. The small maxima at St. 6 in August and October, at St. 15 in September and at St. 18 in August-September, were mainly due to females and copepodite stage V. Copepodite stages III-I dominated the September maximum at St. 1.

In 1965 an early maximum was found in March at St. 15 and 6, consisting of females and a small number of nauplii and copepodite stages II-I. The regular April/May maximum occurred simultaneously at all stations, but the peak at St. 1 was not reached until May-June. All stages took part in this maximum.

The general pattern of the yearly fluctuations of *M. longa* seems to be that large spring maxima in April-May occurred simultaneously and were of similar composition at all stations. When the inadequate sampling in 1963 is considered, the maxima in 1963 and 1964 probably were of the same magnitude, while in 1965 a significant reduction was found at St. 18, 15, and 6.

The autumn maxima were small and complex. Two main sub-periods may be distinguished, the first in August and the second in September-October.

In Oslofjorden Wiborg (1940) observed that *M. longa* had a maximum in June-July, followed by a larger one in October. From the fjords near Bergen Runnstrøm (1932) found maxima in March and September.

Propagation

The stage distribution of *Metridia* is shown in Fig. 53. In 1963 a number of females probably spawned in March-April at all stations, and this brood was recorded as copepodite stage I in April-May. They developed into copepodite stage V in June, males in July and females in August. A second spawning probably occurred in August-September at all stations. This trend was repeated in 1964. In 1965 an early spring spawning took place in February, probably at all stations, but this early brood did not succeed. It was followed by the usual spring spawning in April.

In inner Oslofjord (Wiborg 1940) and on the coast (Wiborg 1954) spawning was assumed in spring and in autumn. In Hardangerfjorden Gundersen (1953) supposed a spring spawning of *M. longa*.

Single specimens of young stages of *M. longa* were found in Trondheimsfjorden during all seasons, and indicate that occasional spawning may take place throughout the year. Digby (1954) considered the breeding season to be from April to September in Greenland waters and in the Labrador Sea a winter breeding was indicated (Kielhorn 1952).

If the maxima of copepodite stage V in May-June was due to a spawning in March, a developmental period of two to three months from egg to copepodite stage V is indicated. The development from copepodite stage V to male seems to take one month, and to female, two months. This gives a life span from egg to adult of four-five months. The autumn generation seems to show the same developmental rate. Females occurred in the hauls at all seasons, while males had a restricted occurrence. The males were found from June to December in 1963 and 1964, and from the last part of May in 1965. Maxima of males were found in the beginning of these periods, approximately a month earlier than the female maxima.

Vertical distribution

The vertical distribution of females and copepodite stages V-IV of *M. longa* and copepodite stages III-I including nauplii of *M. spp.* at St. 15 is shown in Fig. 54. The females were found below 100 m most of the year. Significant migrations to the layers above 100 m were indicated in March-April 1963 and in June 1964. An opposite migration

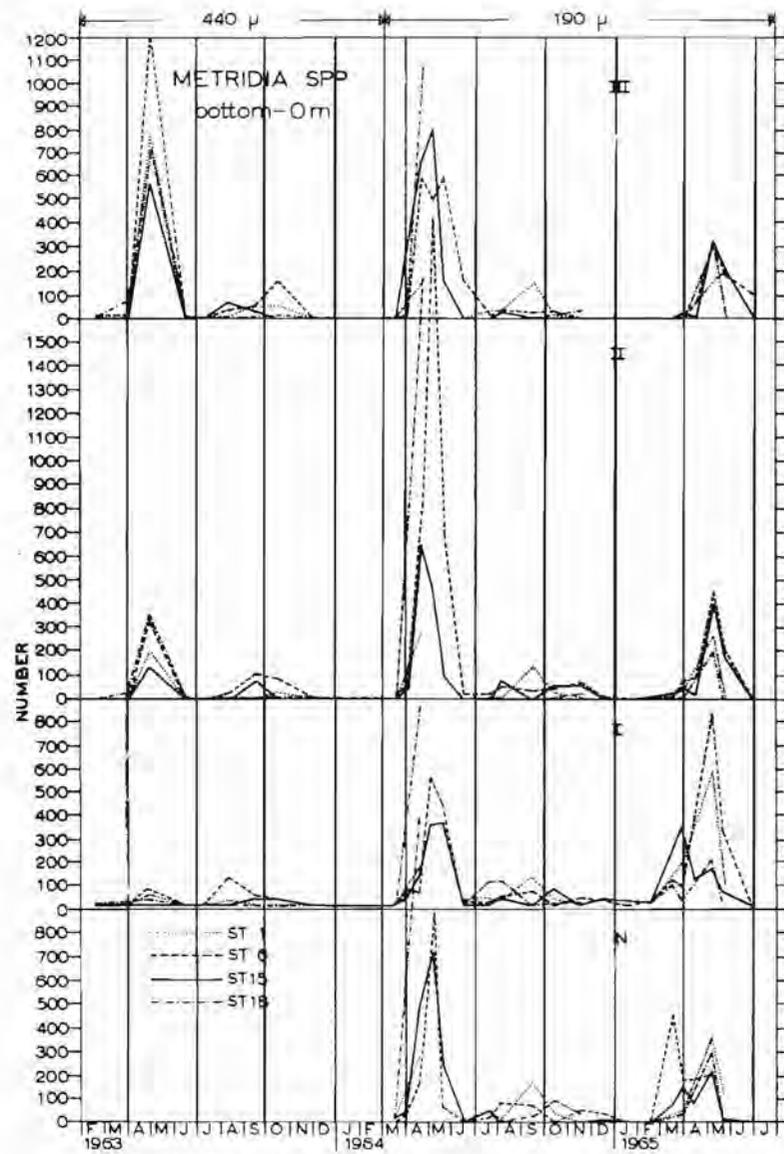
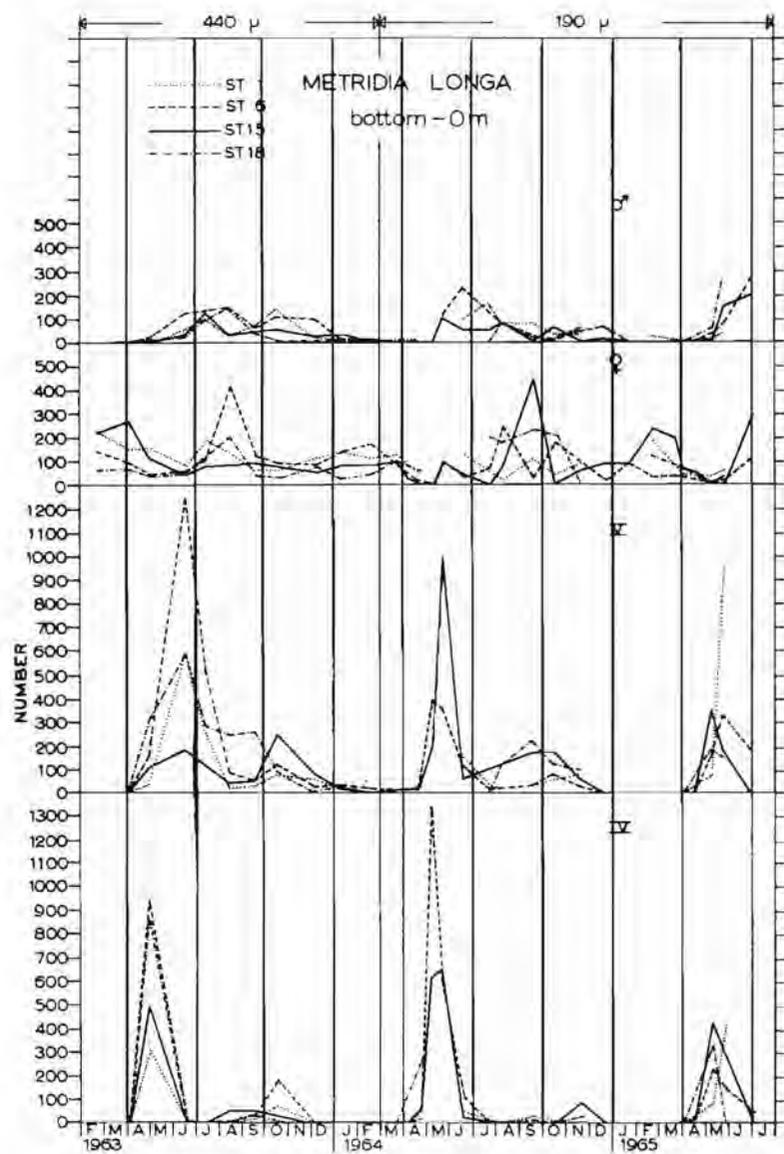


Fig. 53. *Metridia longa* and *Metridia* spp., stage distribution at all stations during 1963-65. (Before March 1964 mesh size 440 μ).

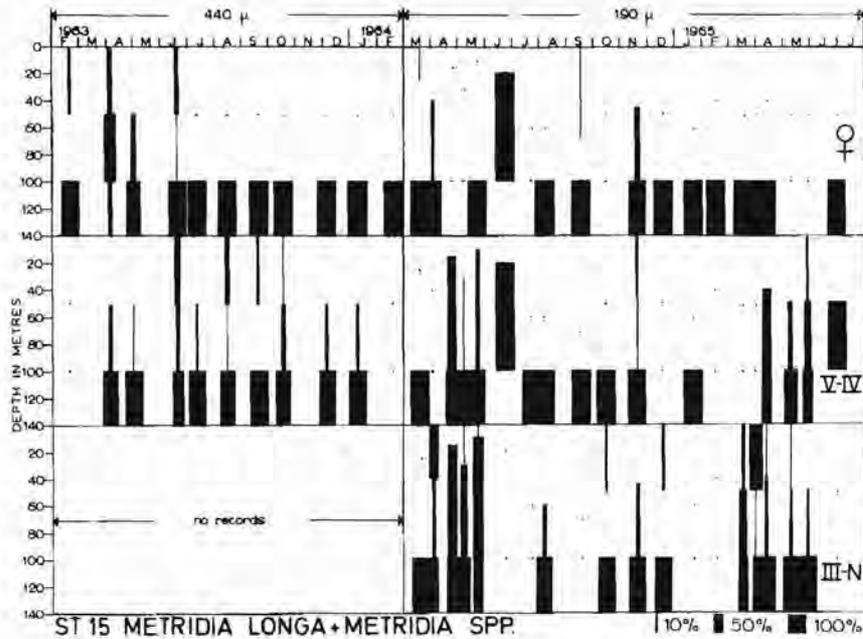


Fig. 54. *Metridia longa* and *Metridia* spp., percentage vertical distribution of different stages at St. 15 during 1963-65.

was observed by Digby (1954) in Greenland waters.

The copepodite stages V-IV were distributed like the females, but significant percentages were found above 100 m in April and June 1964. The young copepodite stages and nauplii were found in the upper layers in March-April all years, and in May 1964 and in August-September 1963, but the majority of these lower stages were found below 100 m. Moderate numbers of copepodite stages III-I inside the Borgenfjord thresholds indicate, however, that in spring the youngest stages may penetrate into the uppermost layers (Strømngren 1973).

The vertical distribution of *M. longa* in Trondheimsfjorden agrees with observations from other areas, but dissimilarities do occur. Bogorov (1946) suggests that *M. longa* has a different pattern of vertical migration dependent upon season and latitude. Perhaps there are changes in vertical distribution at different stages (Bogorov 1932, Digby 1954) as well as between various geographical areas (Jespersen 1934, Østvedt 1955, and Johnson 1963).

Length distribution

The carapace length measurements of *M. longa* females are based on 50 specimens per date from the layers below 100 m at St. 15.

The variation in mean size is shown in Table 11. Minima of mean size seemed to occur in April both years, while peaks were indicated in September 1964 and June-July 1965.

Table 11. *Metridia longa*, mean carapace length of females at St. 15 during 1964-65

1964										1965					
M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J
2.39	2.35	2.48	-	-	2.29	2.44	-	-	2.39	2.41	2.42	2.38	2.34	-	2.43

In Oslofjorden Wiborg (1954) recorded the smallest mean size in February and the largest in June. In both fjords this trend indicates two generations, which have developed at different temperatures.

The range of mean length in Trondheimsfjorden was 2.30-2.49 mm. From Skrova Wiborg (1954) reports an annual range of 2.50-2.60 mm, while in Oslofjorden the mean values in June and February were approximately 2.40 and 2.30 mm respectively. Wiborg (1954) suggested that the smaller mean size in Oslofjorden, compared to Skrova, might be related to reduced salinity. In Trondheimsfjorden, however, the mean size was the same as in Oslofjorden, although salinity conditions were similar to Skrova.

The individual size distribution is shown in Fig. 55. The size range was rather narrow, 2.20-2.64 mm. In spring a bimodal size distribution probably occurred both years, indicating two generations, perhaps the spring and autumn generation from the previous year. The minima of mean size were due to the occasional occurrence of a group of smaller individuals. The larger sized group was nearly constant during all seasons. A slight increase in length in summer-autumn may represent the spring generation developed in colder water. The size range of *M. longa* was quite narrow in comparison with *C. finmarchicus* (Fig. 29). This pattern

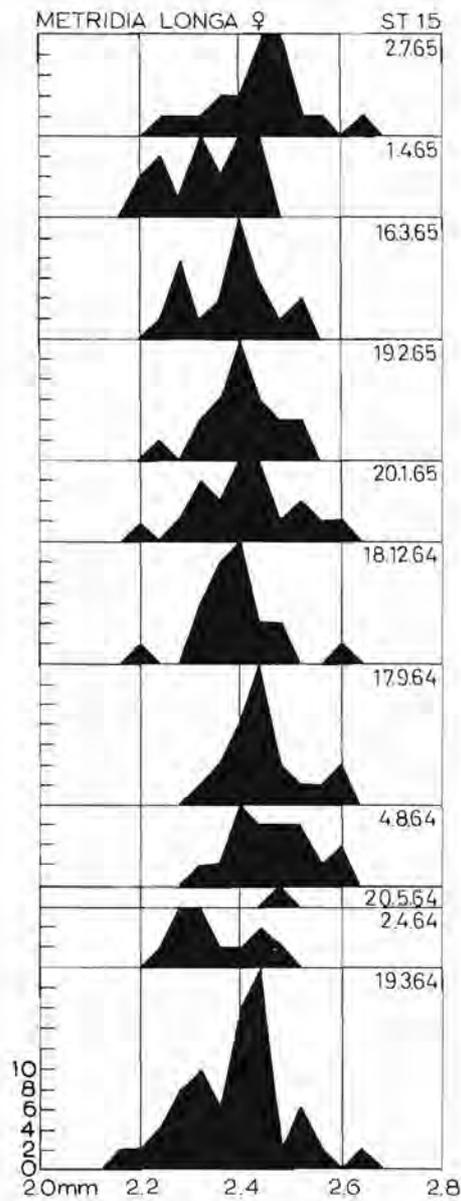


Fig. 55. *Metridia longa*, length frequencies of females at St. 15 during 1964-65.

obviously reflects a uniform population confined to water layers with relatively small fluctuations in temperature, and indicates that the population is local. Digby (1954) stated that *M. longa* was very uniform in size in Greenland waters.

M. longa prefers animal food (Haq 1967), and the uniformity of size may also reflect that food is available most of the year.

Metridia lucens Boeck

M. lucens is very common in the warm water of the Atlantic (Wolfenden 1904), and Gran (1902) regarded it as a temperate Atlantic-oceanic plankton element.

In Trondheimsfjorden *M. lucens* had a very restricted occurrence in time and space, and only small numbers were found (Fig. 56).

In 1963 *M. lucens* was observed only at the outer stations 18 and 15, with small numbers in spring followed by a maximum in July-August. Peaks were also found in September at St. 18 and in October-November at St. 15.

From December 1963 the stock declined, and *M. lucens* was not observed again until late 1964 when a small peak at St. 18 in November was followed by a slightly larger occurrence in January 1965 at St. 15. At St. 6 only stragglers were encountered. In March-April 1965 another few specimens were recorded at St. 18, a number were found at St. 15 in September-October, and at St. 6 a few individuals were found in November-December.

In spite of the scanty material, a few general trends may be distinguished. There is evidently a gradient inwards in the fjord both in time and space. The largest and the earliest occurrence was found at St. 18. At St. 6 and 1 it was recorded only twice and in very few numbers.

South of Trondheimsfjorden *M. lucens* occurs regularly on the

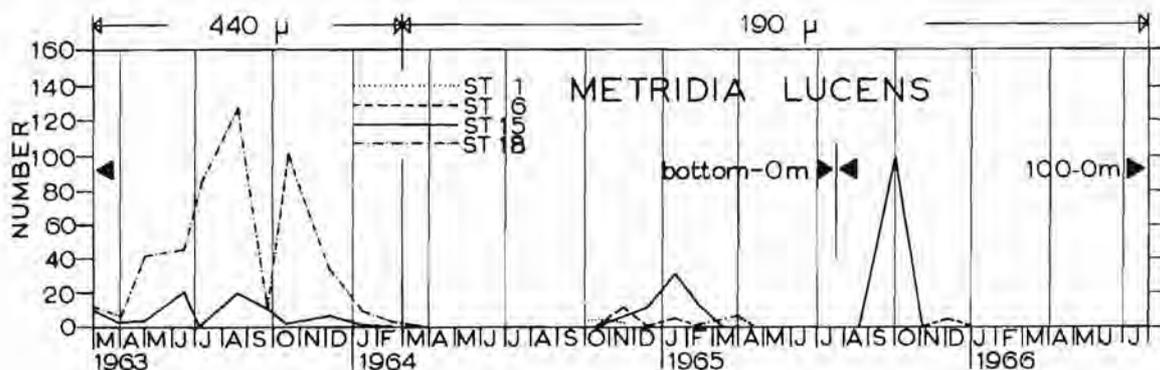


Fig. 56. *Metridia lucens*, total number of adults and copepodite stages V-IV in the whole water column during 1963-65, and in 100-0 m in 1965-66.

coast (Wiborg 1954, Ruud 1929), while it is more variable in the fjords where it is found almost exclusively in the outer parts (Ruud 1929, Wiborg 1940, Lie 1967).

This distribution indicates that it is an immigrant. Probably *M. lucens* may be used as an indicator of Atlantic water (Rae & Rees 1947, Rae 1950, 1957, Fraser 1952, and Rees 1957), and Østvedt (1955) found that deep registrations of *M. lucens* were correlated with deep Atlantic water. Thus, occurrences of *M. lucens* in the fjord may indicate inflows of Atlantic water. Wiborg (1954), however, supposed that local stocks existed on the coast, and in that case coastal water may also be a source of supply.

The small numbers in spring, which are also found in other fjords, are probably remnants from the autumn stock. Rae (1951) stated that a winter population found in the Norwegian Sea between Bergen and St. M belonged to a stock which arrived in the previous autumn. At St. M Østvedt (1955) found that the autumn increase was dependent on inflow, while the local stock died out during winter.

Winter stocks in Trondheimsfjorden may benefit from the relatively high temperature in the deep layers. In the Bay of Fundy warm winters tended to give a large occurrence of *M. lucens* inshore, and high temperature seemed to improve the survival rate (Bigelow & Sears 1939).

Haq (1967) reported that *M. lucens* preferred animal food and independence of phytoplankton may be favourable for surviving during winter in the deep fjord basins.

Propagation

Due to mixing with *M. longa* a possible propagation of *M. lucens* was not detected, but even if spawning did occur, a local stock was not established in the fjord. At St. M Østvedt (1955) assumed that if spawning took place in early summer, the brood might not survive. Wiborg (1954), however, suggested five main spawnings at Sognesjøen.

Vertical distribution

The few winter records in Trondheimsfjorden were from below 100 m, but in periods of relative abundance it was distributed mainly below 50 m.

M. lucens is mainly found below 50 m in the fjords and along the coast (Wiborg 1940, 1954). Similar vertical distributions are observed in other localities (Cameron 1957, Legare 1957). Marked vertical diurnal migrations are recorded (Farran 1947).

Centropages hamatus (Lilljeborg)

C. hamatus is considered to be a neritic species. In Trondheimsfjorden this species has a marked seasonal occurrence.

Variation in numbers

The variation in numbers of *C. hamatus* during 1963-66 is given in Fig. 57.

In the main fjord two maxima were indicated annually, a very small one in spring and a large one in summer-autumn.

C. hamatus occurred in April-May at St. 6 and 1 in 1963, and at St. 15 and 18 in 1964. In April-May 1965 and 1966 *C. hamatus* was not observed.

All stages normally seemed to be present during the spring maxima.

During summer-autumn 1963 smaller stages were inadequately sampled, but the number of adults indicates a significant maximum in August at St. 18 and 15. At St. 6 a small peak occurred in September, while no *C. hamatus* were observed at St. 1.

In 1964 maxima occurred at St. 18 in July, and at St. 15 in August. As in 1963 a smaller peak was found at St. 6 in September, while it was absent at St. 1. The 1964 maxima were significantly reduced compared to 1963. In 1965 maxima were observed at St. 15 and 6 in August,

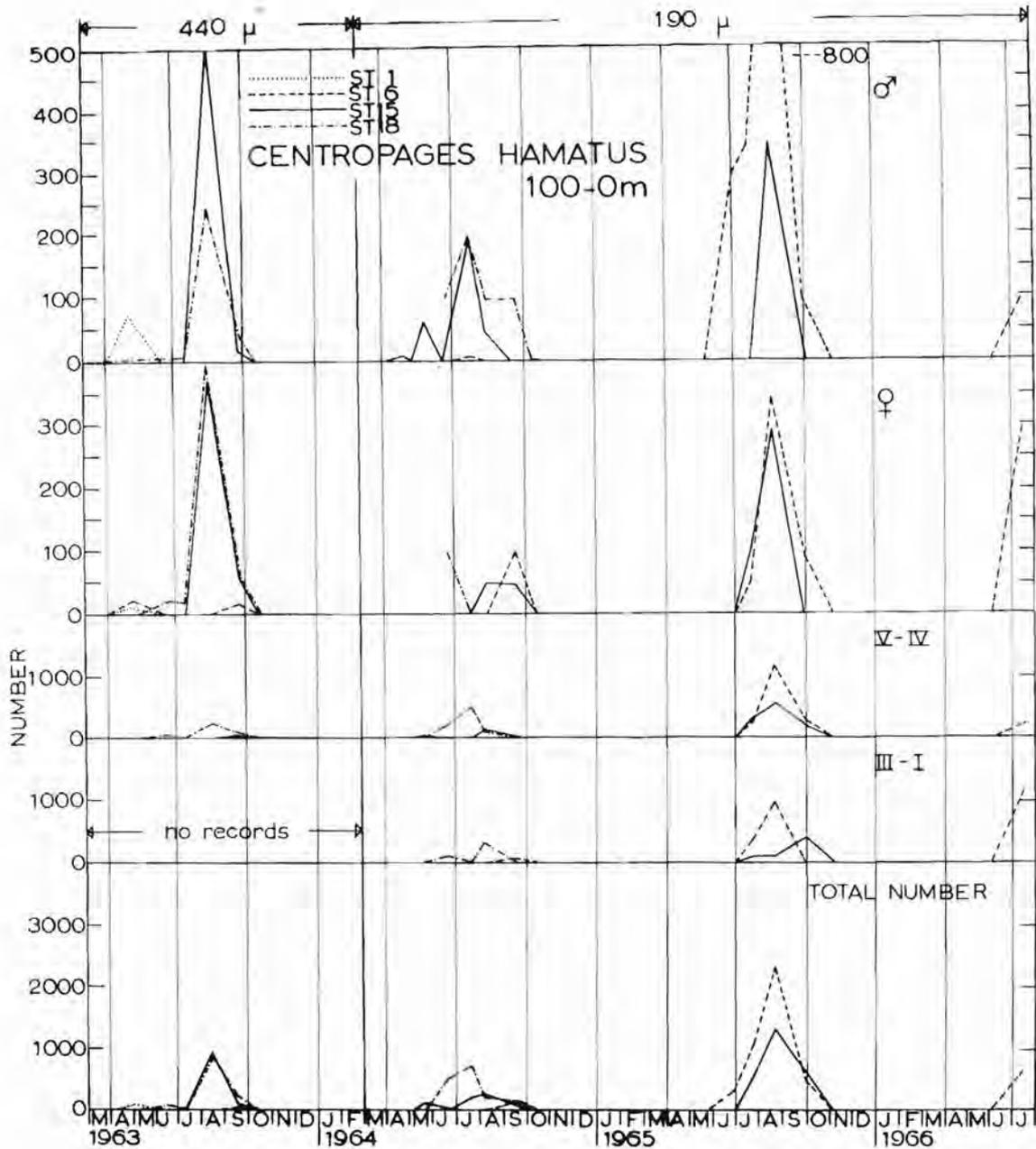


Fig. 57. *Centropages hamatus*, total number per haul and stage distribution in 100-0 m at St. 18, 15, 6, and 1 during 1963-66. (Before March 1964 mesh size 440 μ).

and were significantly larger than in 1964.

In 1966 an increase had started when the sampling stopped in July at St. 6, while no *C. hamatus* was recorded at St. 15.

The summer-autumn maxima were composed of all stages. In the

main fjord a gradient inwards both in number of specimens and in time for maxima was found in 1963 and 1964 indicating immigrants in the local stock. No such trend, however, was observed in 1965.

In Oslofjorden Wiborg (1940) found the largest numbers in the inner fjord, with maxima in May-August, exceeding 5,000 ind/m² in June. In Hardangerfjorden, however, *C. hamatus* was recorded neither by Gundersen (1953) nor by Lie (1967). In the landlocked Nordåsvann, *C. hamatus* was not very abundant with maxima in June-August. On the coast immediately outside it was common from May to October (Runnstrøm 1932), while at the coastal stations investigated by Wiborg (1954) *C. hamatus* occurred rather scarcely.

Propagation

The stage distribution of *C. hamatus* is shown in Fig. 57 with males, females, copepodite stages V-IV and copepodite stages III-I separated.

Although very few adults occur, they may have produced the small spring generation.

The summer-autumn generations spawn in Trondheimsfjorden, and young copepodite stages are abundant. A more or less continuous spawning may be assumed when conditions are favourable. In Nordåsvannet spawning probably occurred from May to September, and Marshall (1949) assumed a continuous breeding during July and August in Loch Striven. In Oslofjorden, however, Wiborg (1940) found that spawning was less in summer than in spring.

During maximal periods the percentage of males was larger than females. A similar sex ratio in *C. hamatus* was observed in Nordåsvannet (Wiborg 1944), and in Loch Striven (Marshall 1949).

Vertical distribution

In Trondheimsfjorden all stages of *C. hamatus* were always found in the upper 100 m, and mostly above 50 m. In spring it occurred both above and below the thermocline.

Centropages typicus Krøyer

C. typicus is a true Atlantic form (Scott 1911). It is brought into the Norwegian coastal waters by the North Atlantic or the coastal current, and no local stocks exist (Wiborg 1954). In Trondheimsfjorden *C. typicus* was recorded only twice; in October 1963 in small numbers at St. 1, 2, 3, 6, 7, 15, 16, 17, and 18, and once in July-August 1964 at St. 18, outside the fjord proper. Lysholm (1912) reported 5 adults taken in September from the outer fjord, while two adults were found in October in the innermost basin another year.

The percentages of *C. typicus* in all parts of the fjord in October 1963, and the simultaneous occurrence of other rare warm water species in autumn 1963, proved that water of Atlantic origin had been introduced. Strong westerly winds and minimal brackish water runoff may have improved the immigration. The single specimen of *C. typicus* at the outermost St. 18 in July-August 1964 may be explained in the same way. This late occurrence of *C. typicus* in Trondheimsfjorden agrees with the seasonal distribution observed in coastal areas. In Hardangerfjorden it was recorded in autumn by both Gundersen (1953) and Lie (1967). Gundersen recorded a small but continuous occurrence from June to September 1950, and stray specimens were also observed in early spring. Lie, on the other hand, recorded *C. typicus* only in September 1956 in the fjord proper.

All specimens of *C. typicus* were taken in the upper 50 m.

Heterohabdus norvegicus (Boeck)

H. norvegicus is an oceanic-bathypelagic species, but small numbers of *H. norvegicus* are found in the depths of Norwegian fjords. This species probably prefers the near bottom layers and is thus insufficiently sampled by ordinary vertical hauls.

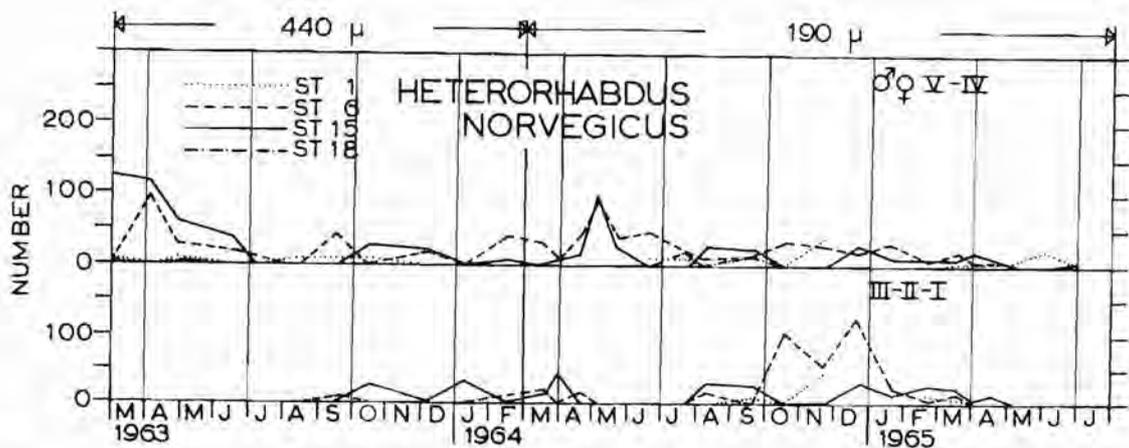


Fig. 58. *Heterohabdus norvegicus*, stage distribution at St. 18, 15, 6, and 1 during 1963-65. (Before March 1964 mesh size 440 μ).

Variations in numbers and propagation

In Trondheimsfjorden *H. norvegicus* was found in moderate numbers at St. 15 and 6 (Fig. 58). At the shallower station 1, the stock was smaller, and at St. 18 it was very rarely caught. This distribution indicates that *H. norvegicus* has its main distribution in the deep basins in the fjord proper. A few numbers were found at all seasons and a small maximum of adults and copepodite stages V-IV seemed to occur in March-May 1963 and 1964. Numbers exceeding 500 ind/m² occurred frequently and in maximal periods more than 1,000 ind/m² were recorded. Because *H. norvegicus* probably lives near the bottom, it may be of some importance to the plankton community near the seabed.

In the outer Oslofjord maximal periods seem to occur in February and April-May (Wiborg 1954), while Gundersen (1953) found only single specimens in August and November in Hardangerfjorden.

In Trondheimsfjorden copepodite stages III-I seem restricted to the period August-April, and indicate that propagation takes place then, perhaps with main periods in October-November, December-January, and March-April. In inner Oslofjord Wiborg (1940) found copepodite stage I in December and copepodite stages IV-III in February. *H. norvegicus* probably spawns during a long period in autumn and winter in Norwegian waters. Jespersen (1939) has reported spawning in July and August in Greenland waters.

Vertical distribution

The vertical distribution of *H. norvegicus* in Trondheimsfjorden indicates that a small portion of the stock migrated above 100 m in March-April. The rest of the year it was confined to greater depths. At St. M in the Norwegian Sea *H. norvegicus* occurred mainly in the 600-100 m hauls (Østvedt 1955), and near Iceland it was found in deeper water (Størmer 1929).

The vertical and horizontal distribution of *H. norvegicus* in Trondheimsfjorden indicates that the local population has little exchange with stocks outside the fjord.

Candacia armata (Boeck)

C. armata is a surface form belonging to Atlantic water (Scott 1911, Russel 1939, and Rae 1951). A few specimens have been recorded occasionally in October-November in Norwegian waters, but local stocks are not established.

Very few specimens were recorded in Trondheimsfjorden. In September 1963 five individuals occurred at St. 15, and in October 1963 the records were: St. 18 - 5 ind., St. 15 - 3 ind., St. 6 - 1 ind., and none at the innermost station 1. In 1966 one specimens was encountered at St. 15 in July. At the Borgenfjord stations *C. armata* was not observed. Lysholm (1912) reports one male of *C. armata* in the outer fjord in December, simultaneous to *C. typicus* and *Acartia clausi*.

The occurrence of *C. armata* in September-October 1963 shows a parallel to *C. typicus* and was probably related to special hydrographic conditions that probably favoured the immigration of the epiplanktonic *C. armata*. In Hardangerfjorden it is not recorded by Gundersen (1953) and Lie (1967).

C. armata probably may be used as an indicator of surface drift into Trondheimsfjorden in autumn.

Candacia norvegica (Boeck)

C. norvegica is a deep water species (Farran 1948). A few specimens of this species and *Candacia* spp., probably belonging to *C. norvegica*, were encountered in Trondheimsfjorden at all seasons. It was always taken below 100 m and was most frequent in the fjord proper. Wiborg (1954) recorded *C. norvegica* only at Skrova and Gundersen (1953) found it twice during October and December in Hardangerfjorden, while Østvedt (1955) did not report it at St. M.

Acartia longiremis Lilljeborg

In Norwegian waters three species of *Acartia* occur, *A. longiremis*, *A. clausi*, and *A. discaudata*. The latter was not found in the fjord, but an occasional sampling at a large tide pool outside the fjord proper showed an abundance of adult *A. discaudata* in June 1966. *A. discaudata* has earlier been reported from a few localities in the Bergen area, and also Runnstrøm (1932) recorded it in a landlocked basin.

A. longiremis and *A. clausi* were both found in the fjord, and in some periods they occurred simultaneously. Nauplii and young copepodite stages of these species are difficult to separate, and nauplii and copepodite stages III-I were taken together as *Acartia* spp.

A. longiremis is a widespread neritic surface species more northern than *A. clausi* (Brodskii 1950). In our waters its neritic character is stated by several workers (Farran 1911, Jespersen 1940, Wiborg 1954, 1955, and others).

In Trondheimsfjorden *A. longiremis* is numerous.

Variation in numbers

The fluctuations of the *A. longiremis* stock during 1963-66 is shown in Fig. 59. Two main maxima seem to occur annually, in May-June and in late summer-autumn.

In 1963 *A. longiremis* was inadequately sampled, but the absence

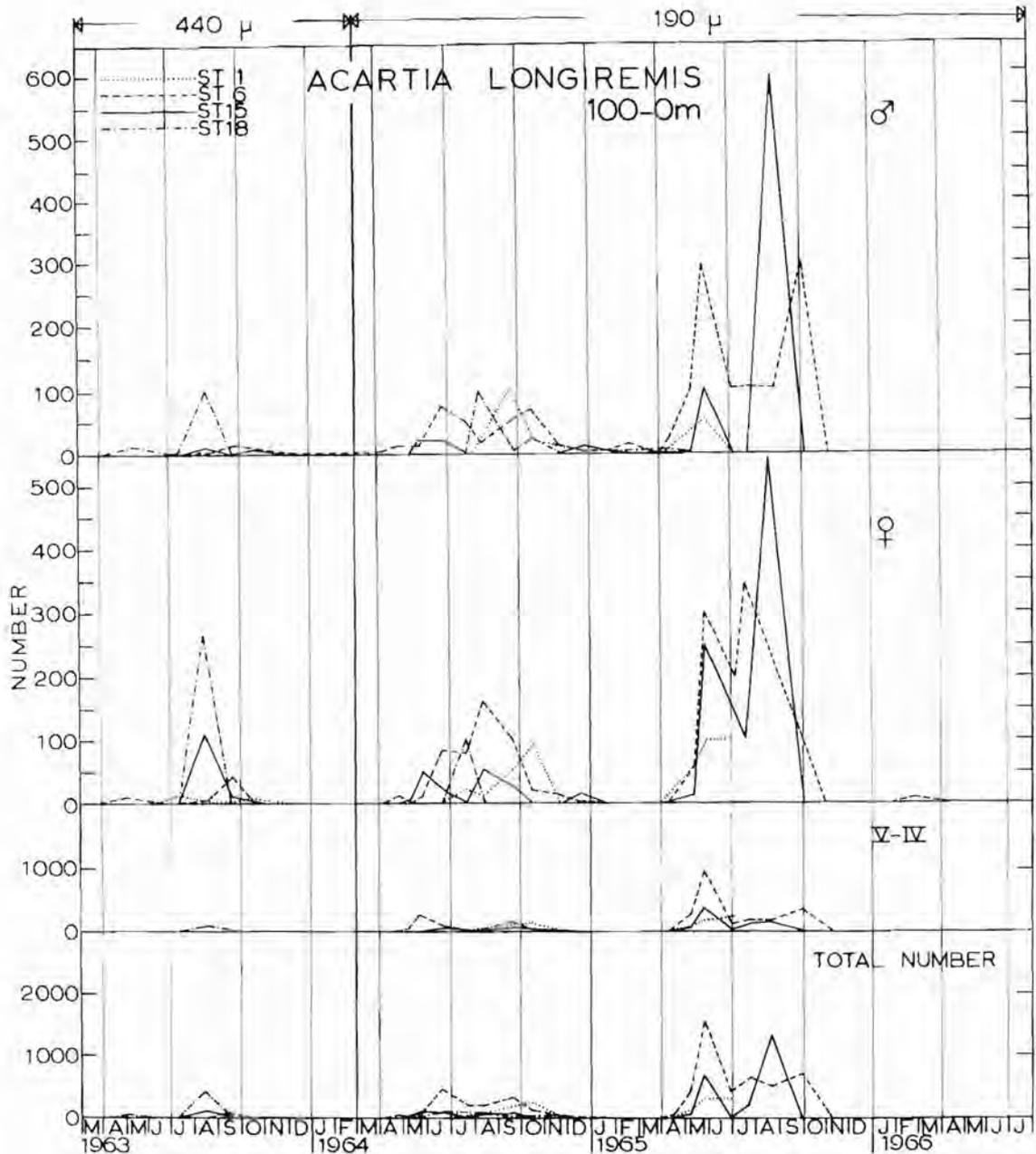


Fig. 59. *Acartia longiremis* (copepodite stages III-I excluded), total number per haul and stage distribution in 100-0 m at all stations during 1963-66. (Before March 1964 mesh size 440 μ).

of adults indicates that no maximum took place in May-June. The May-June maxima in the main fjord were quite small in 1964, relatively large in 1965 and absent in 1966.

Late summer-autumn maxima occurred in the main fjord in August 1963 and in August-October 1964 and 1965. The number of adults indicates a maximum of moderate size in 1963, smaller in 1964 and quite large in 1965.

During the May-June maxima the largest numbers seemed to occur at St. 6, while *A. longiremis* was almost absent at St. 18. During late summer and autumn a delay in time for the maxima toward the inner part of the fjord is perhaps indicated in 1963, 1964, and 1965.

Lysholm (1912) found *A. longiremis* in numbers in Trondheimsfjorden, while it was scarce or lacking in offshore waters.

The general trend of the fluctuations of *A. longiremis* on the west coast from Bergen and northwards, shows that two peaks of abundance occur, in spring and in summer-autumn, just as in Trondheimsfjorden. In Hardangerfjorden *A. longiremis* was practically absent in 1950-51 (Gundersen 1953), while in 1955-56 Lie (1967) found significant numbers in May and July. At the coastal stations visited by Wiborg (1954) *A. longiremis* was relatively scarce, while more sheltered coastal areas generally seem to be favourable to *A. longiremis*, and Hansen (1960) reports it to constitute 30-60% of the copepods in such localities.

The May-June maxima occurred in a period with maximal freshwater supply. In the Straits of Georgia, Legare (1957) also found that the main peaks of *A. longiremis* in June corresponded with maximum increase of river discharge. This pattern may be connected with the preference of *A. longiremis* to the fjord proper in May-June.

The maxima later in summer seemed also to be dominated by the local stocks, but in August-September 1963 and in August-October 1965, the general trend of the maxima indicates a supply from other areas.

In Trondheimsfjorden the abundance of *A. longiremis* in May-June seemed to be inversely correlated to the number of *C. finmarchicus* in the same period. In 1966 and probably in 1963, the May-June maxima of *A. longiremis* failed, coinciding with a very large stock of copepodite stages V-IV of *C. finmarchicus*. Also in May-June 1965 the importance of *C. finmarchicus* was inverse to *A. longiremis*, and in 1964 a similar trend was partly indicated. This negative relation between *A. longiremis* and *C. finmarchicus* may be due to a different response to freshwater discharge. On the other hand, Conover (1964) found that *C. finmarchicus* fed readily on *Artemia nauplii*, and although *C. finmarchicus* is regarded to be an herbivorous copepod in natural habitats, smaller stages of *A. longiremis* might be taken.

Propagation

If spawning in *Acartia* takes place when females and males occur simultaneously in numbers, both *A. longiremis* and *A. clausi* may spawn in the fjord, and the young stages which were found, may belong to both. The temporal and spatial distribution of the two species, however, may point out periods when copepodite stages III-I and nauplii of *Acartia* spp. probably were *A. longiremis*. *A. clausi* was not observed in the fjord before July, and the spring stock of younger stages was obviously due to *A. longiremis*. In the inner fjord *A. clausi* was of little or no importance, and at St. 1 the summer-autumn stock in 1964 was evidently *A. longiremis*.

The stage distribution of *A. longiremis* during 1963-66 is shown in Fig. 59; of *Acartia* spp. during 1964-66 in Fig. 60.

In 1963 no records of small stages were obtained due to the mesh size used. In 1964 the nauplii at St. 1 in August indicate a spawning of *A. longiremis*. This generation probably developed in the copepodite stages III-I found in September, while the corresponding peaks of copepodite stages V-IV and adults occurred in September-October. This indicates a developmental period of less than two months for the August generation of *A. longiremis*. A period of 6-8 weeks is indicated for the May generation in 1965. In Nordåsvännet Wiborg (1944) assumed an interval of 6-8 weeks between two generations of *A. longiremis*.

During spring 1964-65 spawning was indicated in the main fjord before the females were observed. This pattern shows a parallel to

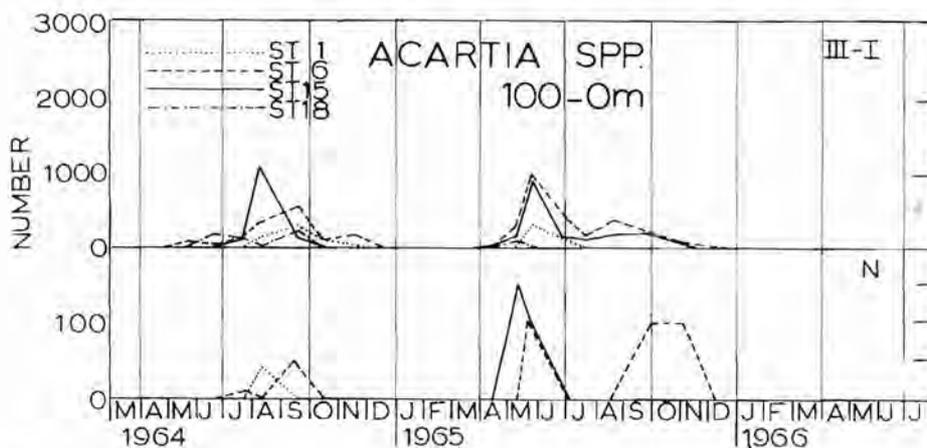


Fig. 60. *Acartia* spp., number per haul of copepodite stages III-I and nauplii in 100-0 m at all stations during 1964-66.

T. longicornis and may be due to a very low concentration of adults, but the existence of resting stages or eggs may be possible. Conover (1956) mentions that some form of resting stages might explain the seasonal fluctuation of *Acartia* spp. in the Long Island Sound.

During maximal periods the males normally seem to be more abundant than the females. A similar sex ratio was observed also for *C. hamatus*.

In Trondheimsfjorden adults and copepodite stages V-IV of *A. longiremis* are confined to the 100-0 m layer with the main bulk in the upper 50 m. Seasonal vertical migrations into deeper layers were not observed. In Nordåsvannet Wiborg (1944) found that *A. longiremis* kept mainly in the upper 15 m.

Acartia clausi Giesbrecht

Wiborg (1955) regards *A. clausi* as a neritic species, but on the other hand, it is typical to Atlantic water (Hansen 1960), and is obviously less neritic than *A. longiremis*. Colebrook et al. (1961) stated that in the Atlantic *A. clausi* fits into the oceanic grouping of zooplankton, while in the North Sea it has a distribution which places it with the neritic species, and separate populations may occur. In Trondheimsfjorden *A. clausi* has a very restricted seasonal distribution.

Variation in numbers

The numerical variation in the main fjord during 1963-66 is demonstrated in Fig. 61.

There seems to be one maximal period each year. In 1963 a maximum in August at St. 18 was followed by corresponding maxima at St. 15 in September and at St. 6 in September-October, but very few specimens at St. 1 in October. There was a successive reduction of numbers inwards in the fjord. When the abundance in 1963 is compared to the other years, the inadequate sampling in 1963 must be remembered. In 1964 maxima occurred in August at St. 18, 15, and 6 with significantly

reduced numbers at St. 6. In 1965 maxima were found in August at St. 6, and at St. 15 in October-November. This late autumn maximum was also indicated in 1963 and 1964.

The general pattern of the maxima of *A. clausi* in the fjord is reduced and delayed inwards, but the small numbers recorded prevent a detailed interpretation. The occurrence was restricted to summer-autumn, and although a small number may survive until midwinter, a spring generation was not found.

The temporal and spatial distribution of *A. clausi* indicates that the species is dependent on immigration.

The numbers of *A. longiremis* and *A. clausi* seem to be negatively correlated. Also in Hardangerfjorden a similar relation seems to occur.

In Norwegian waters *A. clausi* generally seems to have its main maximum in summer-autumn, but small spring peaks are also found (Runnstrøm 1932, Wiborg 1940, 1954, and Gundersen 1953).

Propagation

The stage distribution of *A. clausi* is shown in Fig. 61, with males, females and copepodite stages V-IV separated. All stages took part in the summer maximum, and the relatively large maximum in 1965 was mainly due to copepodite stages V-IV. As with *A. longiremis* adults made a significant percentage of the stock, and in 1964 and 1965 the males were more numerous than the females. A similar trend was observed in Loch Striven by Marshall (1949).

Due to the mixing with *A. longiremis* no conclusions on spawning can be drawn from the material. If spawning takes place when males and females are present in numbers, one might assume spawning in summer-autumn. On the coastal stations Wiborg (1954) assumed that spawning took place 4-5 times from March to October at the localities south of Trondheimsfjorden, while at Skrova a single spawning occurred in October.

Vertical distribution

The whole stock in Trondheimsfjorden is found in the upper layers, nearly always above 50 m. In the Baltic, Ackefors (1969) recorded the bulk of the stock above the thermocline, i.e. in the upper 15 m.

Rhincaianus nasutus Giesbrecht

Two specimens of this Atlantic species were recorded at St. 15 in December 1963 and in February 1964. Both specimens were taken in the 100-50 m hauls. *R. nasutus* is considered to be bathypelagic (Brodskii 1950) and it always kept below 100 m at St. M (Østvedt 1955). The two specimens of *R. nasutus* may have been introduced into the fjord by deep inflows of Atlantic water. Another indicator of Atlantic water, *Metridia lucens*, occurred in the same samples.

Aetideus armatus (Boeck)

A. armatus is a deep water form, but may undertake daily migrations to the upper layers (Verwoort 1952). In Trondheimsfjorden it was taken four times in the deepest hauls in April in the inner fjord, and in April, May, and October in the outer fjord. At St. M *A. armatus* is mainly found in water of Atlantic origin (Østvedt 1955).

Xanthocalanus borealis G.O. Sars

X. borealis was caught once in the outer fjord in October 1963 in the deepest haul. Sars (1903) regarded this species as Arctic.

Dialixis hibernica (A. Scott)

According to Sars (1903) *D. hibernica* lives very near the bottom. It was recorded once in August 1963 below 100 m in inner Trondheimsfjord.

Tharybdis macrophthalma G.O. Sars

One specimens was taken in May 1965 at St. 1. Sars (1903) recorded this Calanoid in Oslofjorden, Trondheimsfjorden, and off the west coast of Norway.

Isias clavipes Boeck

One male and one female were found at St. 6 in August 1969.

Anomalcera patersoni Templeton

This copepod is a surface form, typical to the North Sea and Skagerak (Farran 1911, Rae & Rees 1947, and Østvedt 1955). It was found once in Trondheimsfjorden, in September 1963 at the outermost station 18. This occurrence agreed well with the assumed inflow of surface water bringing in *Centropages typicus* and *Candacea armata* in autumn 1963. Lysholm (1912) reported *A. patersoni* in May and June in the outer fjord. In Oslofjorden it occurs from July to October (Wiborg 1940), but in Hardangerfjorden it was not recorded (Gundersen 1953, Lie 1967), showing a parallel to *Candacea armata*.

COPEPODA CYCLOPOIDA

Oithona similis Claus

O. similis is accepted as a typical epiplanktonic copepod (Farran 1911), and is known to be very abundant in our waters. Due to its small size nauplii and small copepodite stages, *O. similis* easily pass the meshes of the net, and only adults are retained satisfactorily.

Variation in numbers

The numerical variation of *O. similis* during 1964-66 is given in Fig. 62.

In 100-0 m *O. similis* had its main maximum in July-September. In 1964 an August maximum was recorded at all stations, prolonged until September at St. 18 and 15. Possibly this prolongation was due to separate maxima in September. At St. 1 a small July maximum was followed by

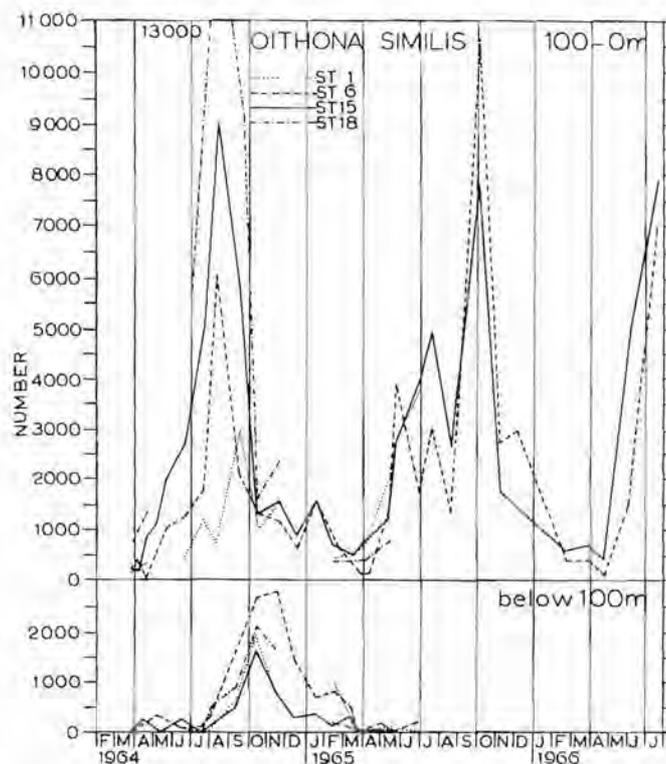


Fig. 62. *Oithona similis*, total number per haul below 100 m and in 100-0 m at all stations during 1964-66.

a larger one in September.

In 1965 a July maximum was found at all stations sampled, but for this year the greatest maximum occurred in September-October. Small but significant spring maxima were found at all stations in May-June 1965.

In 1966 a July maximum was indicated at St. 15 and 6.

Below 100 m a maximum in October 1964 was recorded simultaneously at all stations, and prolonged at St. 6 until November.

Small numbers of *O. similis* were always present during winter.

On the West Coast (Wiborg 1954) and in the Norwegian Sea at St. M (Østvedt 1955) the stock of *O. similis* reached maximum in the 50-0 m layer in the periods May-June and August-September. The late June maximum at St. M and the August maximum at Ona were very pronounced.

In fjord localities main maxima are observed in the periods April-May and July-September (Ruud 1929, Wiborg 1940, 1944, Gundersen 1953, and Lie 1967).

These results are in accordance with the observations from Trondheimsfjorden, but the numbers of *O. similis* in the upper layers were quite a bit larger in Trondheimsfjorden than in the other fjord localities. In Hardangerfjorden proper, both Gundersen (1953) and Lie (1967) recorded less than 20,000 ind/m², while Trondheimsfjorden yielded more than 70,000 ind/m² several times.

In 1964 the greatest numbers in summer-autumn were found at the outermost station 18, and there was a significant reduction in the size of the maximum inwards in the fjord. A simultaneous gradual delay in time for the maximum was found from St. 18 to St. 1. In 1966 the summer maximum also seemed to occur first in the outer fjord, while in 1965 no gradient in time or size of maxima was detected. This distributional pattern indicates that immigrants may be of importance for the summer-autumn stock.

In Oslofjorden Wiborg (1940) stated that the spring increase started earlier in the outer fjord, and the autumn increase in Hardangerfjorden, reported by Lie (1967) seemed to start at the outermost station and was gradually delayed inwards in the fjord. This delay seemed to be combined with small numbers at the innermost stations and higher numbers at the outermost station. These patterns show a parallel to the general trend in Trondheimsfjorden.

Propagation

Most of the specimens caught were adults, and no attempt was made to separate different stages in order to find propagation periods. The phytoplankton net, however, retained nauplii of *O. similis* in great numbers. No quantitative estimation could be made because clogging influenced the catch very significantly, but the net samples shows an abundance of nauplii of *Oithona* spp., probably *O. similis*, at all seasons. Based on male and female percentage Wiborg (1954) assumed that propagation took place during all seasons in coastal waters, with 3-5 maximal spawnings during the year, and in the Plymouth area Digby (1950) recorded five generations a year.

Vertical distribution

The vertical distribution of *O. similis* is shown in Fig. 63.

From May to September the main stock kept in the upper 100 m, while in late autumn and winter a significant part was found below 100 m. This pattern indicates a downward migration in autumn, corresponding to the maxima found below 100 m, followed by a rise in May. A deeper distribution of *O. similis* during certain periods in summer and especially in autumn is reported from Norwegian waters (Ruud 1929, Gundersen 1953, Wiborg 1954, Østvedt 1955), and Bigelow (1926) suggested that in the Gulf of Maine *O. similis* migrated to deeper water in autumn. On the other hand, Hansen (1960) reported that in the Norwegian Sea *O. similis* was a surface form in all its stages.

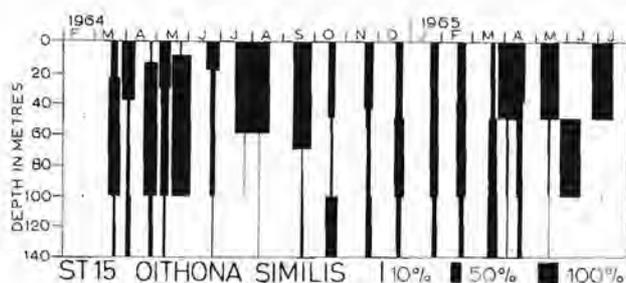


Fig. 63. *Oithona similis*, percentage vertical distribution at St. 15 during 1964-65.

Oithona spirostris Claus

During the present investigation small stages of *O. spirostris* and *O. similis* were not separated, and only specimens which could be determined with certainty were classified as *O. spirostris*. Accordingly, young stages of this species were taken together with *O. similis*, but the ratio of adult *O. similis*/*O. spirostris* indicates that the error introduced does not make the interpretation unreasonable.

Variation in numbers

The variation of adult *O. spirostris* in Trondheimsfjorden during 1964-66 is demonstrated in Fig. 94.

In 100-0 m the variations were irregular, but the main maxima seemed to occur in April-May and August-September at St. 15, 6, and 1 in 1964 and 1965. At St. 6 a winter maximum in November-December was indicated.

Below 100 m the stock was smaller. Increased numbers in April-May were probably related to the corresponding maximum in 100-0 m.

O. spirostris showed a significant preference for the fjord proper, and very few specimens were found at the outer station 18, thus showing a similarity to *H. norvegicus* and *Oncaea borealis*. This distribution indicates that the stock of *O. spirostris* is rather local.

Also in other fjord localities and on the coast, small peaks

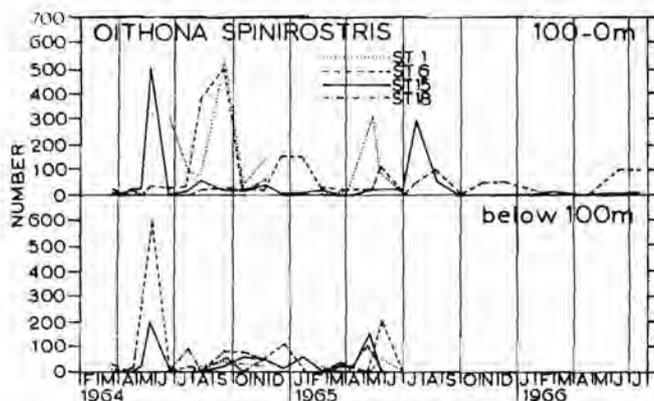


Fig. 64. *Oithona spirostris*, total number per haul below 100 m and in 100-0 m at all stations during 1964-66.

are found in spring and in autumn (Ruud 1929, Wiborg 1940, 1954, Gundersen 1953, and Lie 1967).

Propagation

No indications of spawning were recorded, but *O. spirostris* undoubtedly spawns in Norwegian waters, perhaps twice a year. In Icelandic waters Jespersen (1940) assumed that breeding coincided with the warming of the water, while in the Labrador Sea an abundance of nauplii occurred in December-February (Kielhorn 1952).

Vertical distribution

The vertical distribution of *O. spirostris* is shown in Fig. 65.

The main bulk was found above 100 m in spring and summer, but the uppermost layers were avoided. In autumn a downward migration seemed to take place into deeper layers, tending to give a more even vertical distribution. In the Norwegian Sea, Østvedt (1955) found 55% of the stock in the 600-100 m layer. On the Norwegian west coast Wiborg (1954) found that the main stock inhabited the layers below 50 m. In fjords, however, a significant part of the stock is found above 50 m.

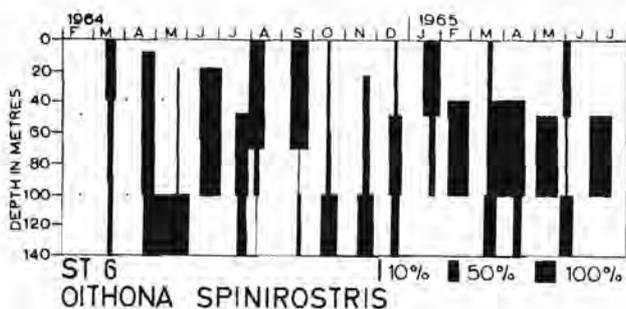


Fig. 65. *Oithona spirostris*, percentage vertical distribution at St. 15 during 1964-65.

Oncaea borealis G.O. Sars

O. borealis is small in size, and even in periods of abundance it is of little importance to the biomass. Smaller stages pass the meshes of the net, and in 1963 very few *O. borealis* were found, due to the mesh size used then. Most of the catch consisted of adults with females dominating.

Variation in numbers

The variation in total number of *O. borealis* during 1964-1966 is shown in Fig. 66.

In 100-0 m small maxima were found in April, May-June, and August-September in 1964, in May-June, July, August-October in 1965, and in July 1966.

In Hardangerfjorden Lie (1967) observed peaks in April and September in 100-0 m. At Sognesjøen Wiborg (1954) recorded a maximum in June, and at St. M, Østvedt (1955) found relatively many individuals above 100 m in May and June.

Below 100 m maxima were found in April/May, July and September-

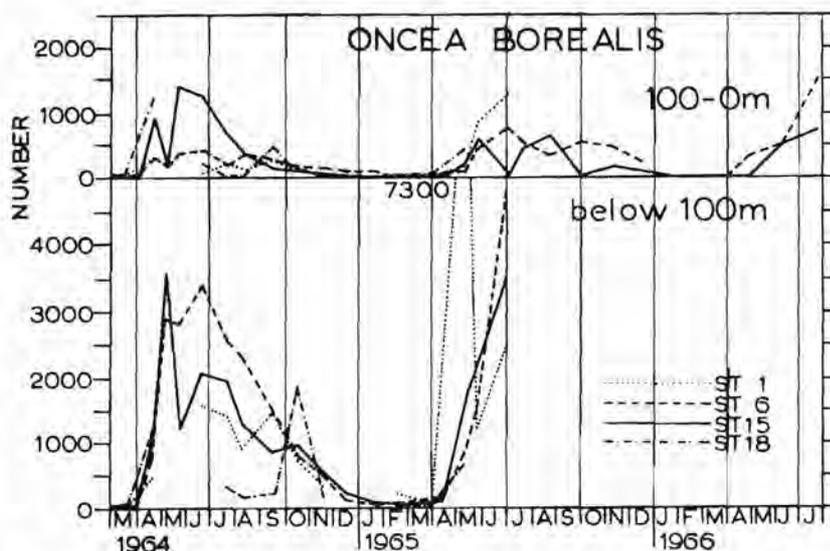


Fig. 66. *Oncaea borealis*, total number per haul below 100 m and in 100-0 m at all stations during 1964-66.

October in 1964, and in April-May and July in 1965. The greatest numbers were found in April-May with 30,000-70,000 ind/m². Gundersen (1953) found maxima below 50 m in May in Hardangerfjorden, and in Oslofjorden (inside Drøbak) maxima with 20,000-50,000 ind/m² were found in May-June (Wiborg 1940).

In Trondheimsfjorden *O. borealis* was almost absent at the outermost St. 18, while the maximal numbers were found at the innermost stations. *O. borealis* seems to prefer fjord localities, and also in Oslofjorden (Wiborg 1940) and Hardangerfjorden (Lie 1967), the greatest numbers were found in the inner parts.

Propagation

Propagation periods were not determined directly, as lower stages were not retained by the net. The bulk of the stock was made up by females, while males seem to occur in the plankton from April to August, with peaks in June-July (Table 12). Adults in copulation were observed in May 1964 at St. 15.

Wiborg (1940) found egg-sacks, females and individuals in copulation at all seasons, but in very small numbers in winter from October to February, and he suggested spawning from January to May and perhaps in August. Runnstrøm (1932) found that in Hjeltefjorden near Bergen, propagation took place most of the year, except in winter from December to February.

Table 12. *Oncaea borealis*, total number of males at St. 18, 15, 6, and 1 from bottom to surface during 1964-65

	1964				1965							
	A	May	J	J	A	S	May	J	J	A		
1	15	-	-	50	0	20	20	50	50	10	-	-
6	0	0	0	60	20	0	0	0	0	0	100	0
15	0	50	50	10	110	0	0	0	0	0	0	50
18	0	-	-	0	0	0	0	0	-	-	-	-

Vertical distribution

During 1963-1966 the main stock of *O. borealis* was found below 100 m at all stations, but an upward migration was indicated in March-May 1964. Similar behaviour was also observed in April-May 1963 (Figs. 66 and 67). Wiborg (1940) stated that in inner Oslofjord *O. borealis* preferred the upper 50 m, while it had a deeper distribution in the outer part. At Møre, however, Ruud (1929) observed the opposite trend. Østvedt (1955) recorded a seasonal difference with large numbers above 100 m in May and June, but with a deeper distribution in autumn.

The majority of the males were taken in the upper 100 m, and in Oslofjorden Wiborg (1940) found a similar trend.

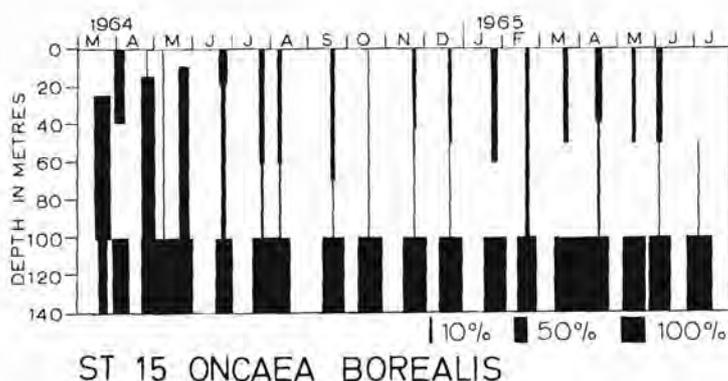


Fig. 67. *Oncaea borealis*, percentage vertical distribution at St. 15 during 1964-65.

Oncaea similis G.O. Sars

A few *O. similis* were taken at St. 15 and 6 in May 1965, in the 100-0 m haul.

In Herdla and Hjeltefjord *O. similis* was found during all seasons with a peak of abundance from October to March (Runnstrøm 1932). Wiborg (1954) recorded it at Sognesjøen in March and September.

Euryte longicauda Philippi

E. longicauda was taken in May 1965 at the outermost St. 18 below 100 m. Sars (1918) found this form frequently clinging to *Laminaria* along the whole Norwegian coast.

COPEPODA HARPACTICOIDA

Unidentified Harpacticoida, the bulk probably *Microcetella norvegica*, were recorded at all stations during all seasons. The main distribution seemed to be in the upper layers.

OTHER ORGANISMS

Coelenterata

The coelenterates were often damaged during the haul and of the more fragile specimens only gelatinous material was retained.

Ctenophora

Beroe cucumis Fabricius occurred frequently at all stations at all depths. *Pleurobracia pileus* occurred occasionally.

Siphonophora

Siphonophors belonging to the family Diphyidae were encountered rather often. Specimens from other families occurred occasionally.

Trachymedusae

Single specimens of *Aglanta digitale* (O.F. Müller) were found in the hauls, mainly in spring and early summer. Other medusae taken by the net were seldom identifiable.

Polychaeta

Only *Tomopteris helgolandica* occurred as an adult in the plankton. Larvae of other polychaetes were occasionally found and are discussed below.

Tomopteris helgolandica Greef

T. helgolandica is widely spread in the Atlantic (Wesenberg-Lund 1935).

In Trondheimsfjorden adults and younger stages of *T. helgolandica* were found in small numbers at all seasons, exclusively in the deepest hauls. The variation in number during 1963-65 is demonstrated in Fig. 68.

Although the material was scanty a significant periodicity of abundance seemed to occur. At St. 15 maxima were found in February 1963, 1964, and 1965, in April-May 1963 and 1964, and in September-October 1963 and 1964. At St. 18 and 15 the maxima partly coincided, and during maximal periods nearly 600 ind/m² were found in average. At St. 6 the number of individuals were significantly reduced and at St. 1 only single specimens were caught.

T. helgolandica prefers the outer part of the fjord, and in Oslofjorden Wiborg (1940) found a similar horizontal distribution. Rae (1949) regards *T. helgolandica* as an indicator of Atlantic water in the North Sea, where it has a seasonal appearance with maxima in autumn. At St. M the presence of *T. helgolandica* indicated inflow of Atlantic water (Østvedt 1955). Probably *T. helgolandica* is able to establish a small population in the deep waters of Trondheimsfjorden, but the main

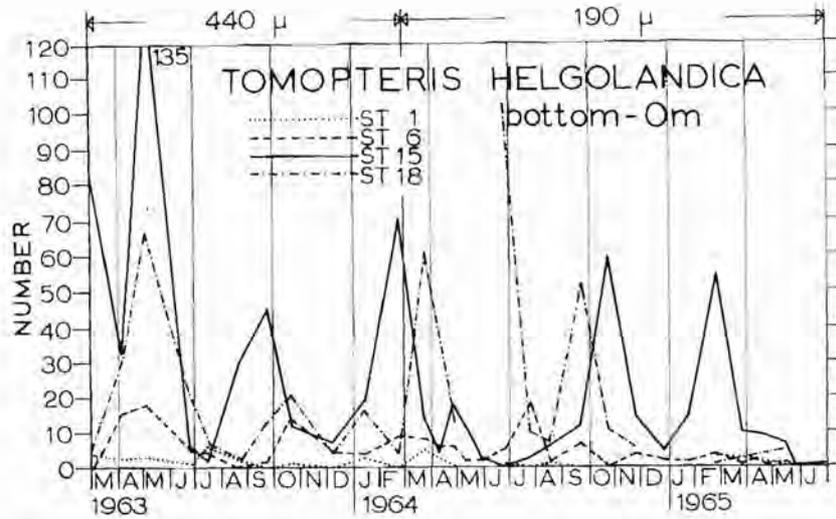


Fig. 68. *Tomopteris helgolandica*, total number at all stations during 1963-65. (Before March 1964 mesh size 440 μ).

stock may be dependent on supply with deep inflows.

Pteropoda

Two Pteropods were recorded in the fjord, *Clione limacina* and *Limacina retroversa*.

Clione limacina (Phipps)

C. limacina was found three times below 100 m in the outer fjord in January-February 1964. Russell (1935) regards *C. limacina* as an indicator of Arctic water.

Limacina retroversa (Fleming)

In Trondheimsfjorden *L. retroversa* has a restricted occurrence in time and space.

The variation in numbers of *L. retroversa* during 1963-66 is shown in Fig. 69. In 1963 maxima occurred in August at St. 18 and in

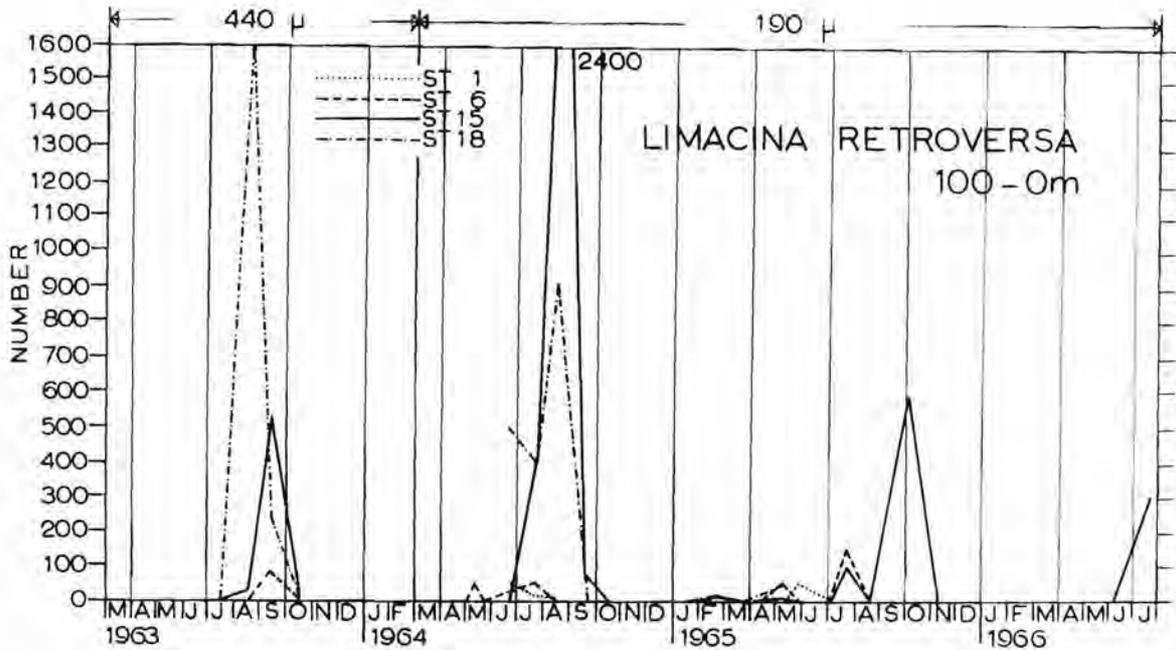


Fig. 69. *Limacina retroversa*, total number in 100-0 m at all stations during 1963-66. (Before March 1964 mesh size 440 μ).

September at St. 15 and 6. In April-May only 10 specimens were recorded at St. 6. In 1963 small specimens easily passed the meshes of the net. In 1964 a few specimens occurred at St. 6 in May. In June *L. retroversa* was relatively abundant at St. 18, and in August the maximum was reached at St. 18 and 15. During summer it occurred in very small numbers at St. 6 and 1. From October 1964 to April 1965 single specimens were encountered at St. 18, while in April-May 1965, a small maximum was found at all stations. A large maximum in 1965 was found in September at St. 15. In 1966 no specimens were found during spring, but in July a summer increase was indicated at St. 15. A general trend of distribution is reduced numbers at the two innermost stations.

In other Norwegian localities *L. retroversa* has been found to be quite variable, but generally the largest numbers occurred in summer and autumn.

In the North Sea *L. retroversa* is considered to be an indicator of Atlantic water (Rae 1949), but the occurrence of small numbers in spring in all parts of the fjord indicates that *L. retroversa* is stationary in Trondheimsfjorden. On the coast Wiborg (1954) recorded single specimens during all seasons.

The summer maxima in the main fjord were obviously influenced

by influx from areas outside the fjord as indicated by the delay in time for maxima inwards and the very significant reduction in numbers at the inner stations. Wiborg (1954) observed a similar delay in time for maxima north along the coast. The absence of a spring stock in 1966 may be due to abnormally low temperatures.

Vertical distribution

L. retroversa is an inhabitant of the upper layers in Trondheimsfjorden, and only a few specimens were taken below 100 m. At St. M it belonged to the surface layers (Østvedt 1955), but was also frequently taken in 600-100 m.

Chaetognata

Of the genus *Sagitta* only *S. elegans* occurred in Trondheimsfjorden. *S. setosa* is recorded on the southern part of the coast, but was not found in Trondheimsfjorden. *Eukrohnia* spp. were abundant in the deeper part of the fjord. Both *E. hamata* (Möbius) and *E. bathypelagica* Alvarino occurred.

Sagitta elegans Verill

The two varieties, *S. elegans elegans* and *S. elegans arctica*

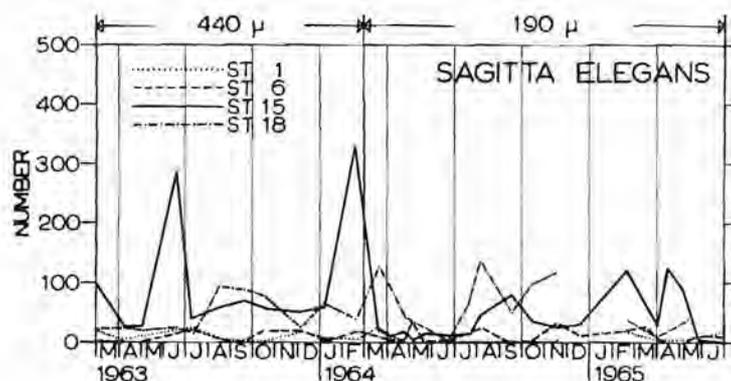


Fig. 70. *Sagitta elegans*, total number at all stations during 1963-1966. (Before March 1964, mesh size 440 μ).

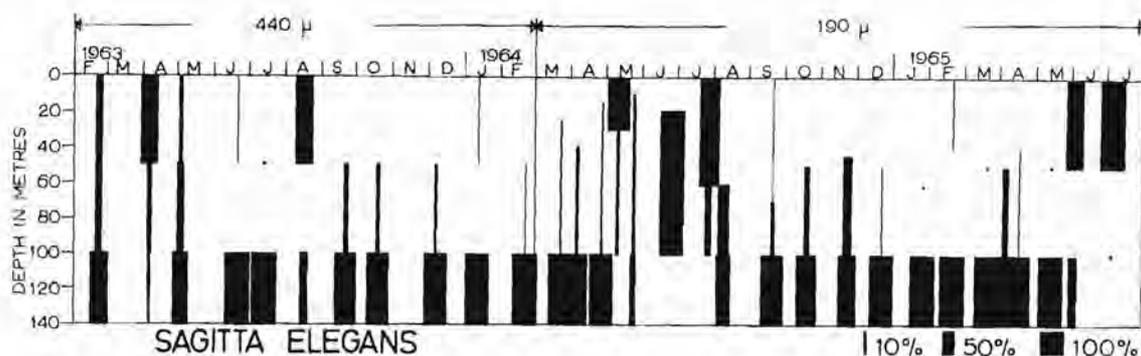


Fig. 71. *Sagitta elegans*, percentage vertical distribution at St. 15 during 1963-1966. (Before March 1964, mesh size 440 μ).

(Fraser 1957) were not separated. The latter has a distribution similar to *C. hyperboreus*.

S. elegans was found regularly in the deep and intermediate layers of Trondheimsfjorden (Fig. 70). No maximal periods can be detected, although prominent peaks occurred, particularly at St. 15. The material is scanty, but it seems evident that the stock is significantly smaller at the inner stations 6 and 1. In Oslofjorden, Wiborg (1940) also found the greatest numbers in the outer fjord. On the western coast *S. elegans* is of minor importance (Wiborg 1954).

In Trondheimsfjorden the main stock of *S. elegans* was found below 100 m (Fig. 71), but also occurred regularly up to the discontinuity layer. In spring and summer, the bulk, mainly small specimens, occurred in the upper 50 m.

Eukrohnia spp.

The bulk of *Eukrohnia* spp. were *E. hamata*, but *E. bathypelagica* also occurred frequently (R. Giskeødegård, pers. comm.). *Eukrohnia* spp. were frequently found below 100 m, but very few specimens were taken in the layer above. Maximal periods seem to occur in spring (Fig. 72). In contrary to *S. elegans*, the greatest numbers were found in inner fjord, with maxima of 9,600 ind/m² and 8,030 ind/m² at St. 1 in March 1964 and 1965 respectively. These maxima consisted mainly of small individuals and a spawning in February of one or both species is indicated. Even

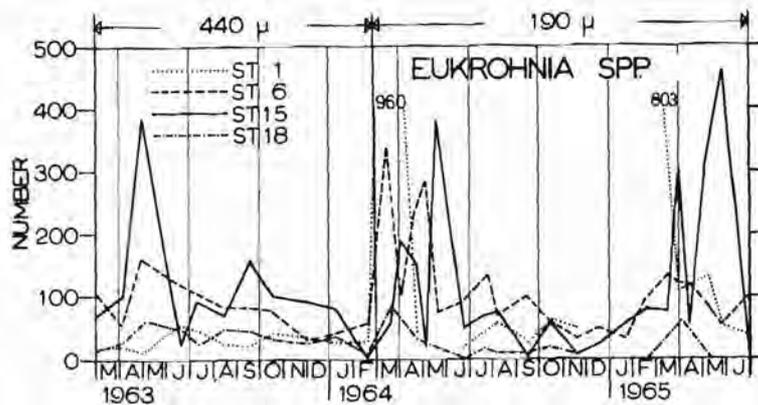


Fig. 72. *Eukrohnia* spp., total number at all stations during 1963-1966. (Before March 1964, mesh size 440 µ).

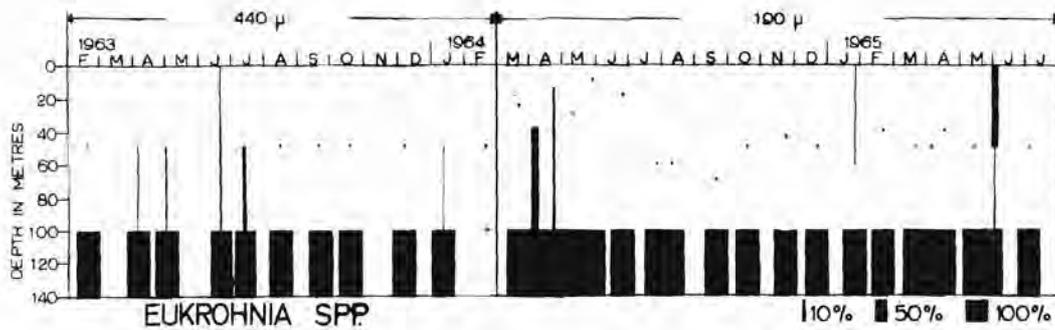


Fig. 73. *Eukrohnia* spp., percentage vertical distribution at St. 15 during 1963-1966. (Before March 1964, mesh size 440 µ).

the smallest individuals tended to avoid the uppermost layer (Fig. 73).

Cladocera

Podon polyphemoides (Leuckart)

Three species of *Podon* were identified: *P. polyphemoides*, *P. leuckarti*, and *P. intermedius*, but *P. polyphemoides* dominated strongly. This species is regarded as a temperate neritic plankton element (Gran 1902).

The variation in number of *P. polyphemoides* during 1963-1966 is

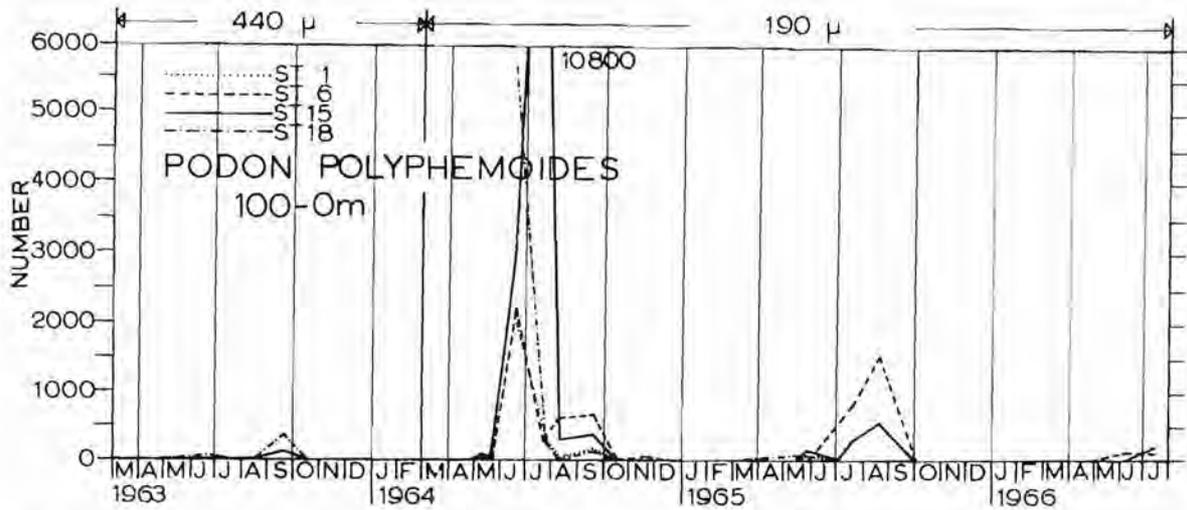


Fig. 74. *Podon polyphemoides*, total number at all stations during 1963-66. (Before March 1964 mesh size 440 μ).

shown in Fig. 74.

The occurrence of *P. polyphemoides* in the fjord was very restricted in time, with peaks in June and August-September.

In the main fjord the June maximum was large in 1964, and very small in 1965 and 1966. The August-September maxima were roughly of the same size in 1964 and in 1965. In 1963 most of the stock probably passed through the net.

A general feature seems to be large fluctuations of *P. polyphemoides* from year to year, and a similar trend is also found on the coast (Wiborg 1954).

A few specimens were recorded in the fjord in May. In Oslofjorden and on the west coast small spring maxima also occur (Gran 1900, Runnstrøm 1932, and Wiborg 1940, 1954). At the southernmost coastal localities and in Oslofjorden the June maximum is most prominent, but the main maximum is delayed northwards, and at Eggum it is found in September. In Hardangerfjorden Gundersen (1953) recorded July and August-September maxima of moderate size, while Lie (1967) found very small maxima in the same locality.

There is a significant reduction in number inwards in Trondheimsfjorden both in summer and autumn, and only in 1964 were a few *P. polyphemoides* found at the innermost station 1. In Oslofjorden an

opposite horizontal distribution was found, with the largest numbers in the inner fjord (Wiborg 1940).

The maxima were obviously related to the temperature increase in the upper 100 m. This trend may indicate a direct temperature dependence, giving a local stock of *P. polyphemoides* a rapid increase. The optimum temperature for *P. polyphemoides* in the Baltic is assumed to be 10-15°C (Ackefors 1969). The horizontal distribution, however, indicates that the summer-autumn maxima of the stock in Trondheimsfjorden also receives a supply from outside the fjord.

Females with embryos and eggs occurred frequently and a new generation was obviously released during the warm season.

P. polyphemoides was always found in the upper 100 m, both above and below the thermocline. Harder (1957) found that *P. polyphemoides* was situated in or near the discontinuity layer.

Evadne nordmanni Lovén

A number of specimens of *Evadne* were examined in periods of abundance and all belonged to *E. nordmanni*. This species probably dominates completely in Trondheimsfjorden. *E. nordmanni* was earlier considered to be entirely neritic. Gran (1902) suggested it as an indicator of coastal water, but Kielhorn (1952) found that *E. nordmanni* was able to establish populations in the open sea.

The variation in numbers per haul of *E. nordmanni* during 1963-66 is shown in Fig. 75.

In 1963 small numbers occurred at St. 6 in April-May, but the maximum of the year was not found until June at St. 18 and 15. In September a second small maximum occurred at St. 15. During 1963 small specimens were not sampled adequately. In 1964 St. 6 again showed a small maximum in April-May, followed by a maximum at all stations in June-July. At St. 18 the stock exceeded 300,000 ind/m² in July. At St. 15 a small peak occurred in August. In 1965 a maximum perhaps occurred at St. 15, 6, and 1 in April/May, but was overshadowed by a large maximum in May-June. In 1966 no April-May maximum was recorded, but a maximum in June or later was indicated.

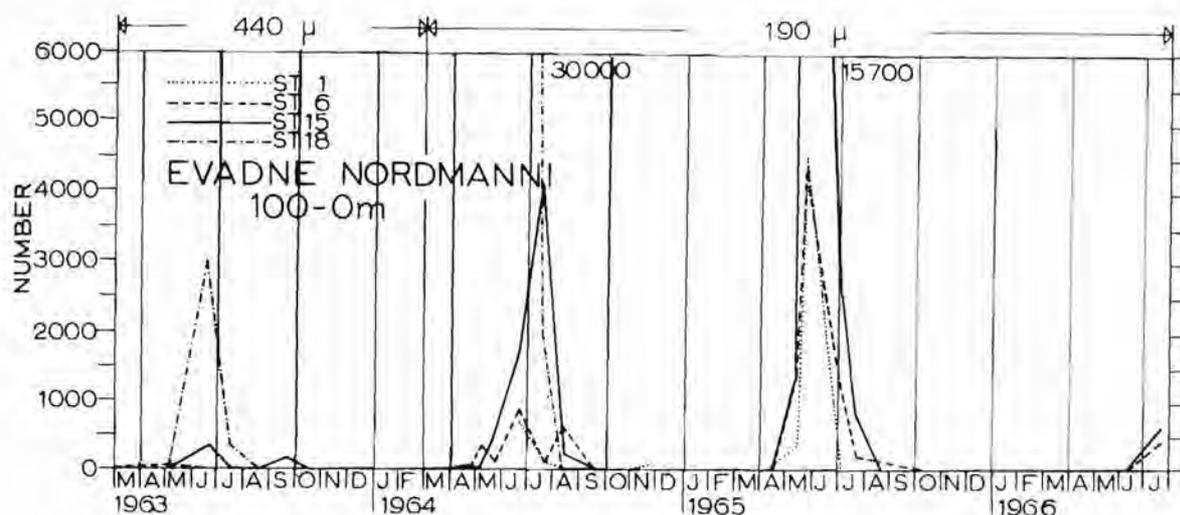


Fig. 75. *Evadne nordmanni*, total number at all stations during 1963-66. (Before March 1964 mesh size 440 μ).

The spring stock was small and was found mainly in the fjord proper. The summer maxima were much larger, particularly at the outermost station but with decreasing number in the inner fjord. The maxima were found simultaneously at all stations. The absence of *E. nordmanni* in spring 1966 followed by a delayed summer occurrence may be related to extremely cold water.

On the southern west coast the stock of *E. nordmanni* normally is large, and Sognesjøen has maxima of more than 40,000 ind/m² in June (Wiborg 1954), while in Hardangerfjorden very small stocks are recorded (Gundersen 1953, Lie 1967).

Normally *E. nordmanni* seems to occur earlier in the plankton than *P. polyphemoides* and this difference is probably related to a lower optimum temperature for *E. nordmanni*.

In Trondheimsfjorden females with embryos and eggs formed the majority of the stock, and *E. nordmanni* obviously propagated significantly in the fjord. During winter only stray specimens were encountered, and the bulk of the winter stock was evidently in resting position.

Vertical distribution

E. nordmanni was always found in the upper 100 m, and mainly in 50-0 m both spring and summer. It seems to prefer the uppermost layers, above the thermocline. On the west coast Wiborg (1954) took nearly all *E. nordmanni* in the upper 50 m, while Gundersen (1953) recorded that in August the layer below 50 m was preferred in Hardangerfjorden.

Isopoda

A few individuals were taken now and then in the deep hauls, mainly at St. 6 and 15, but were not determined to species.

Ostracoda

Only species of the genus *Conchoecia* have been recorded in Trondheimsfjorden. In Norwegian waters, three species are found regularly in the plankton, *C. elegans*, *C. borealis*, and *C. obtusata* (Gran 1902, Wiborg 1954, and Østvedt 1955). In the present material several species probably occur.

In the deeper hauls *Conchoecia* spp. were frequently found. The variation in numbers per haul in the main fjord during 1963-66 is demonstrated in Fig. 76. A significant periodicity was recognized with maximal periods in May-June and September-October. The concentration was of the same magnitude at the three outer stations, while the innermost station showed smaller numbers. Maximal values were above 10,000 ind/m² in May 1964, while average values were of the order of 2-3,000 ind/m². In spring 1963 and 1965 the outermost and the innermost stations showed few specimens compared to 1964.

In coastal localities (Wiborg 1954) *Conchoecia* spp. were found in small numbers except at Skrova where stocks up to 3,000 ind/m² were recorded. The peaks of abundance on the coast were found in January-February at a time when minimal numbers occurred in Trondheimsfjorden.

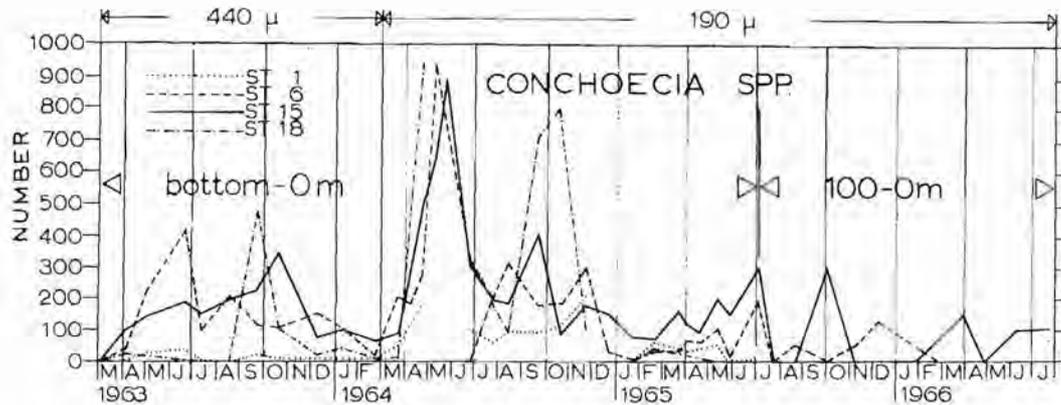


Fig. 76. *Conchoecia* spp., total number at all stations during 1963-66. (Before March 1964 mesh size 440 μ).

In Oslofjorden (Wiborg 1940) very few specimens were found inside Drøbak while in the outer fjord maxima occurred in April-May.

During spring and autumn small specimens, either small species or new broods, dominated. On the coast small individuals were present at all seasons, but the main propagation might have taken place in January-February (Wiborg 1954). In Oslofjorden Wiborg (1940) recorded maxima of small individuals in December and February.

The main stock of *Conchoecia* spp. in Trondheimsfjorden was found below 100 m, but significant numbers migrated above that layer although they were never found above the thermocline. *Conchoecia* spp. seem to have their main distribution below 50-100 m (Wiborg 1940, 1954, 1955 and Østvedt 1955). The Ostracods, however, are excellent swimmers and McHardy & Bary (1965) report that *C. elegans* is distributed throughout the water column except near the surface and undertakes extensive diurnal migrations.

Amphipoda

Temisto abyssorum (Boeck)

T. abyssorum was frequently taken below 100 m, mainly at the outer stations 18 and 15. Peaks of abundance occurred in summer and autumn, and more than 100 specimens were caught in July and October 1964

Scina borealis G.O. Sars

S. borealis occurred several times in 1964, mainly at the outer stations 18 and 15 in July-September. It was always taken in the deepest hauls.

Mysidacea

The Mysidacea caught by the net showed a peculiar distribution in the fjord. At St. 6 they occurred in nearly every haul below 100 m in small numbers, from 1 to 25 specimens, while at the outer stations only stragglers occurred. The bottom sledge samples showed that mysids were much more common near the bottom.

Euphausiacea

Adult Euphausiacea easily escaped the net by swimming and occurred only occasionally in the samples. Nauplii, metanauplii, calyoptopis, and furcilia stages were found in small numbers during restricted periods.

The variation in numbers in the main fjord during 1963-66 is demonstrated in Fig. 77.

Two maxima seemed to occur annually in spring and summer.

In 100-0 m spring maxima occurred in April-May each year and probably at all stations. A summer-autumn maximum was found at St. 18 and 15 in August-September 1963 and August 1964. This maximum could be traced at St. 6. The spring maximum showed the largest numbers. Both maxima seemed to be a little delayed inwards in the fjord, and the numbers were generally reduced in the inner part.

In the layer below 100 m a similar distribution in time and space was indicated. The spring maximum below 100 m seemed to occur in April, generally a little earlier than in the layer above, while the autumn maximum was nearly absent. In June-July a small peak was observed at St. 15 and 6.

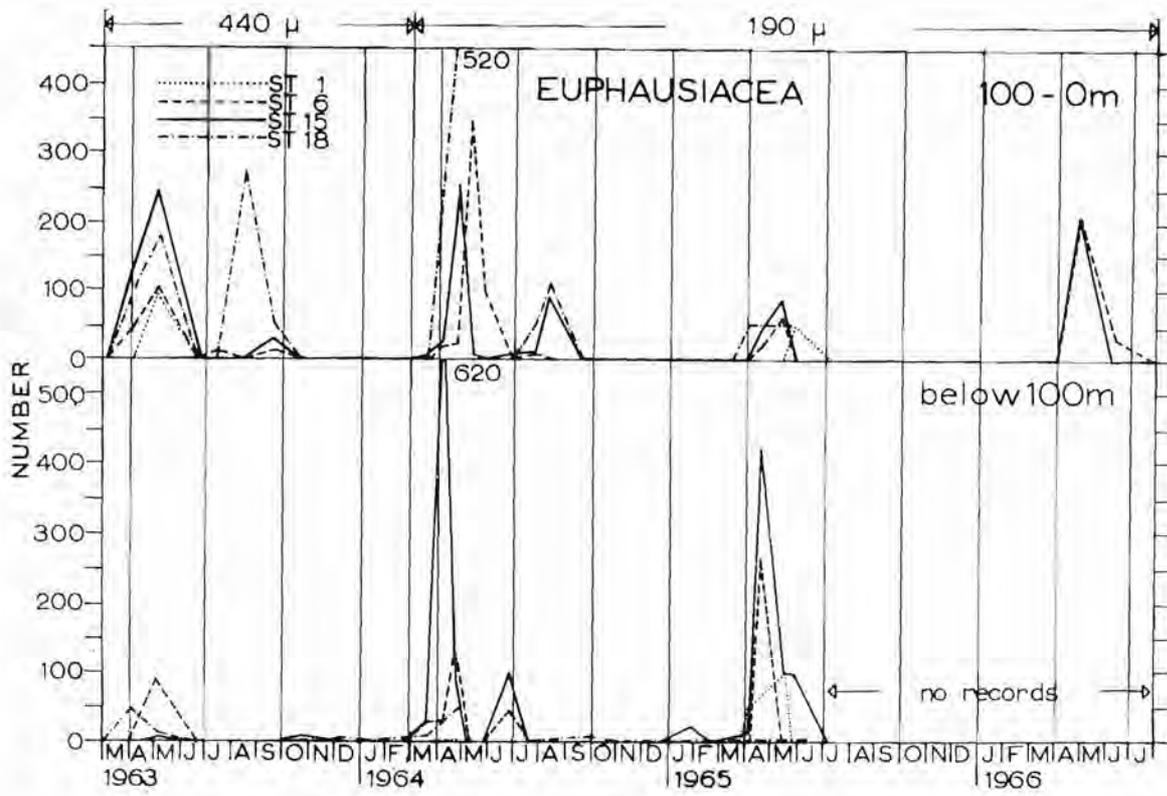


Fig. 77. Euphausiacea, total number below 100 m and in 100-0 m at all stations during 1963-66. (Before March 1964 mesh size 440 μ).

The general pattern of this distribution indicates that young stages of Euphausiacea migrate above 100 m in spring. The delay of maxima inwards the fjord in spring is not combined with a parallel reduction in numbers. The autumn maximum is significantly delayed inwards, and the parallel reduction of the number indicates that immigration is probably of importance.

According to P. Myklebust (pers. comm.) adults of *Meganyctiphanes norvegica*, *Nematocelis megalops*, *Thysanoessa inermis*, *T. raschii*, and *T. longicaudata* occurred in samples taken with an Isaac Kidd Midwater Trawl in Trondheimsfjorden in 1968 and 1969. The most important species in the fjord is *Meganyctiphanes norvegica* and according to P. Myklebust larvae of this species were responsible for the main bulk of all maxima during 1963-66.

Decapoda

Decapod larvae occurred during all seasons except winter, and at all stations although they were less frequent at the innermost station. *Munida* larvae dominated. A few *Pasiphaea tarda* were caught in the deepest hauls. Other types of Decapoda larvae were not determined

Copelata

Three genera are reported from Norwegian coastal water by Wiborg (1954), *Oikopleura*, *Fritillaria*, and *Appendicularia*. The latter has only occasionally been recorded, while the two former genera were rather abundant. The routine handling of the zooplankton samples easily damages these fragile animals and it was found to be difficult to separate the genus *Oikopleura* into species with certainty in all samples.

In Trondheimsfjorden *O. dioica*, *O. labradoriensis*, and *F. borealis* f. *acuta* were identified, while *Appendicularia* sp. did not occur or escaped notice.

In Fig. 78, showing the variation during 1964-66, the two genera are taken together as Copelata. Two main maxima occurred annually, in April-May and August-October. The greatest abundance was found in spring and autumn 1964. At St. 1 the stock was very small.

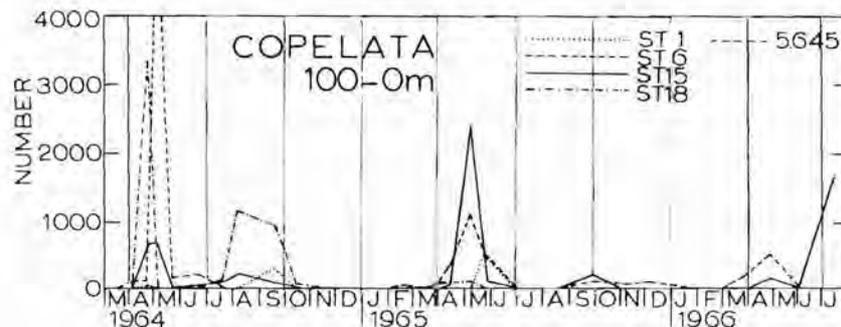


Fig. 78. Copelata, total number in 100-0 m at all stations during 1964-66.

Thaliacea

Salpa fusiformis Cuvier was caught in the net only once, in September 1964 at St. 15, but large numbers were observed at the surface in August-September 1963. This species is considered to be an indicator of Atlantic water (Brattstrøm 1972).

Larvae and eggs of fishes

A few fish larvae and a number of fish eggs occurred mainly between April and June at all stations, but were not identified to species.

Larvae and eggs of bottom invertebrates

Larvae of bottom invertebrates often occurred in large numbers, mainly in spring and summer. In winter very few larvae were found.

Cirriped larvae

Balanus spp. dominated, mainly as nauplii, but cypris stages

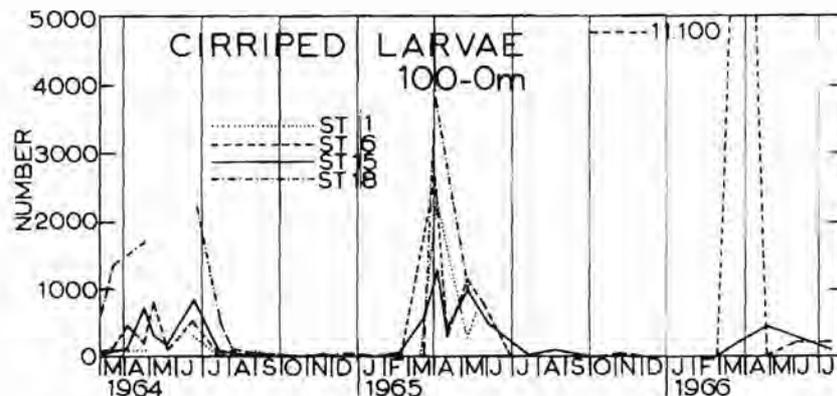


Fig. 79. Cirriped larvae, total number in 100-0 m at all stations during 1964-66.

occurred frequently. Two main peaks occurred, in March-April and May-June (Fig. 79) in all parts of the fjord. All the cirriped larvae kept in the upper 100 m.

Polychaet larvae

Polychaet larvae (Fig. 80) (*Tomopteris helgolandica* excluded) were taken in spring and summer, nearly always in the upper 100 m. Maximal abundance was found in spring.

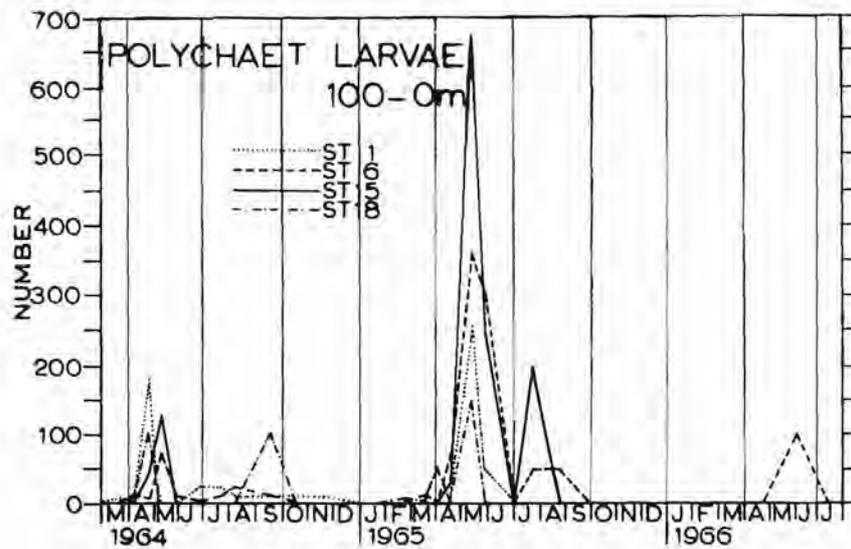


Fig. 80. Polychaet larvae (*Tomopteris helgolandica* excluded), total number in 100-0 m at all stations during 1964-66.

Cyphonautes larvae

Cyphonautes larvae had two peaks of abundance (Fig. 81) in May-June and in August-October. No significant difference between the stations was found. A preference to the upper 100 m is obvious, with the uppermost layers most preferred.

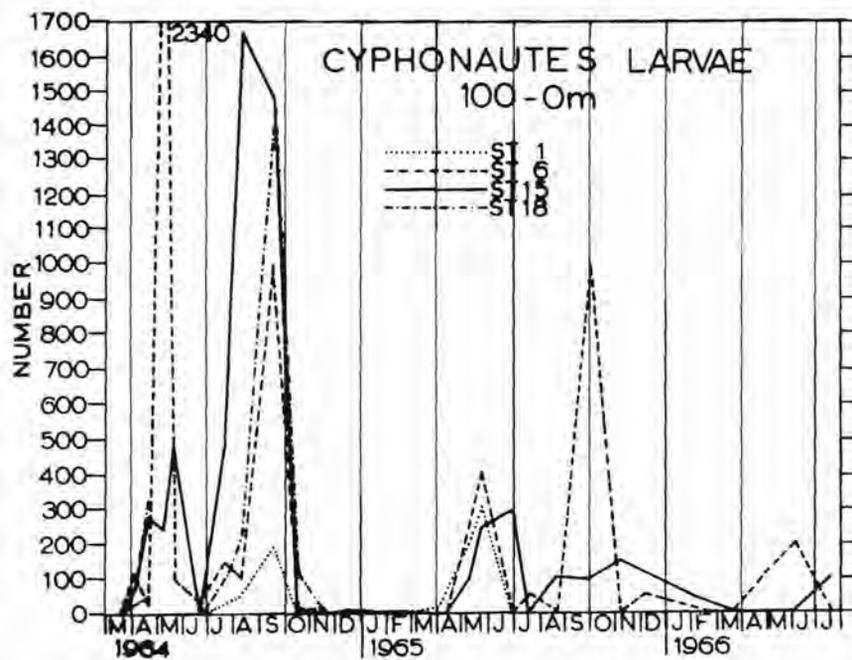


Fig. 81. Cyphonautes larvae, total number in 100-0 m at all stations during 1964-66.

Bivalvia larvae

Bivalvia larvae had two maxima a year (Fig. 82), in May-June and in August-September. During both maxima a high percentage of the

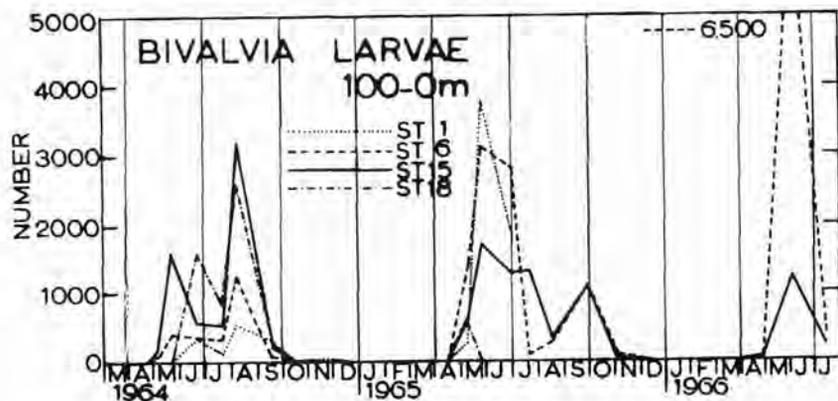


Fig. 82. Bivalvia larvae, total number in 100-0 m at all stations during 1964-66.

larvae resembled *Mytilus edulis*. This bivalve has two main spawnings during the year in Trondheimsfjorden (E. Lande pers. comm.), corresponding to the observed maxima. No significant differences between the stations were found, and nearly all specimens were caught in the upper 100 m.

Echinoderm larvae

Echinoderm larvae were found from March to September at all stations (Fig. 83), mainly in the uppermost layers. Maxima occurred in March-April, May-June, and August-September. Many species are probably represented.

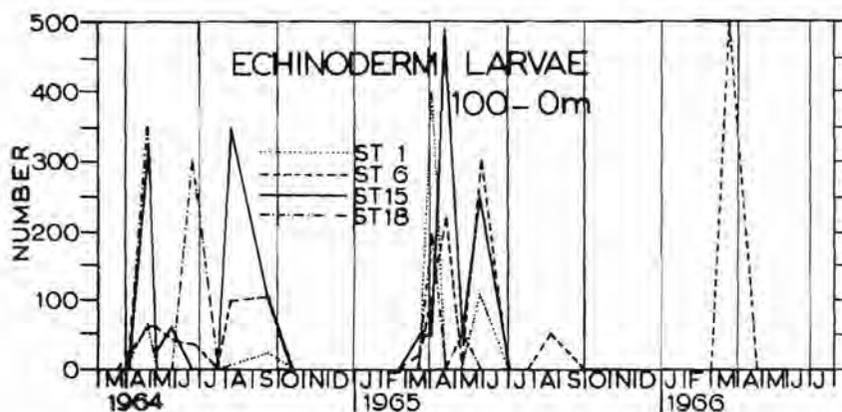


Fig. 83. Echinoderm larvae, total number in 100-0 m at all stations during 1964-66.

Other invertebrate larvae and eggs

Phoronid larvae were found singly in August and September 1969 at St. 1B and 6.

Unidentified eggs and larvae of invertebrates occurred frequently in all parts of the fjord with peaks of abundance in April-July, and were distributed at all depths.

TYPES OF COMPONENTS IN THE ZOOPLANKTON

In the zooplankton in Trondheimsfjorden both autochthonous and allochthonous species occur. Some of the autochthonous species are found during all seasons, but the peaks of abundance may be found during different months. Other species, both autochthonous and allochthonous, have a more restricted temporal occurrence, and a succession of species may be found.

In Fig. 84 the most important species in the zooplankton in terms of total number are arranged according to their occurrence at St. 15 during 1963-65. The ordinate is calculated by the formula

$$Y = \sqrt{\frac{N}{N \text{ max}}}$$

where $N \text{ max}$ is the maximal number of individuals of each species found during the whole period, and N is the actual number.

1. The autochthonous species *C. finmarchicus*, *M. longa*, *P. norvegica*, *Ch. armatus*, *S. minor*, *M. pusillus*, *O. borealis*, *O. spinirostris*, *Conchoecia* spp., *S. elegans*, and *T. helgolandicus* seem to be relatively abundant most of the year, but normally with maxima in spring. *H. norvegicus*, which has a more irregular distribution, should also be added to this group together with *C. hyperboreus* and *P. minutus*.

2. A second main group of autochthonous species represented by *P. elongatus*, *O. similis*, *C. hamatus*, *T. longicornis*, *A. longiremis*, *A. clausi*, *E. nordmanni*, *P. polyphemoides*, and *L. retroversa*, shows greater seasonal variation, with prominent maxima in summer-autumn when local propagation probably is combined with immigration.

The first six of these species are arranged in a matrix of product-moment correlation coefficients, shown in Fig. 85, calculated for the whole sampling period 1963-66.

Three of the species, *P. elongatus*, *O. similis*, and *T. longicornis*, show a highly significant correlation at all stations, while the others, *C. hamatus*, *L. retroversa*, and *A. longiremis*, give more variable correlation coefficients both mutually and to *P. elongatus*, *O. similis*, and *T. longicornis*. At St. 18, however, most species are significantly correlated.

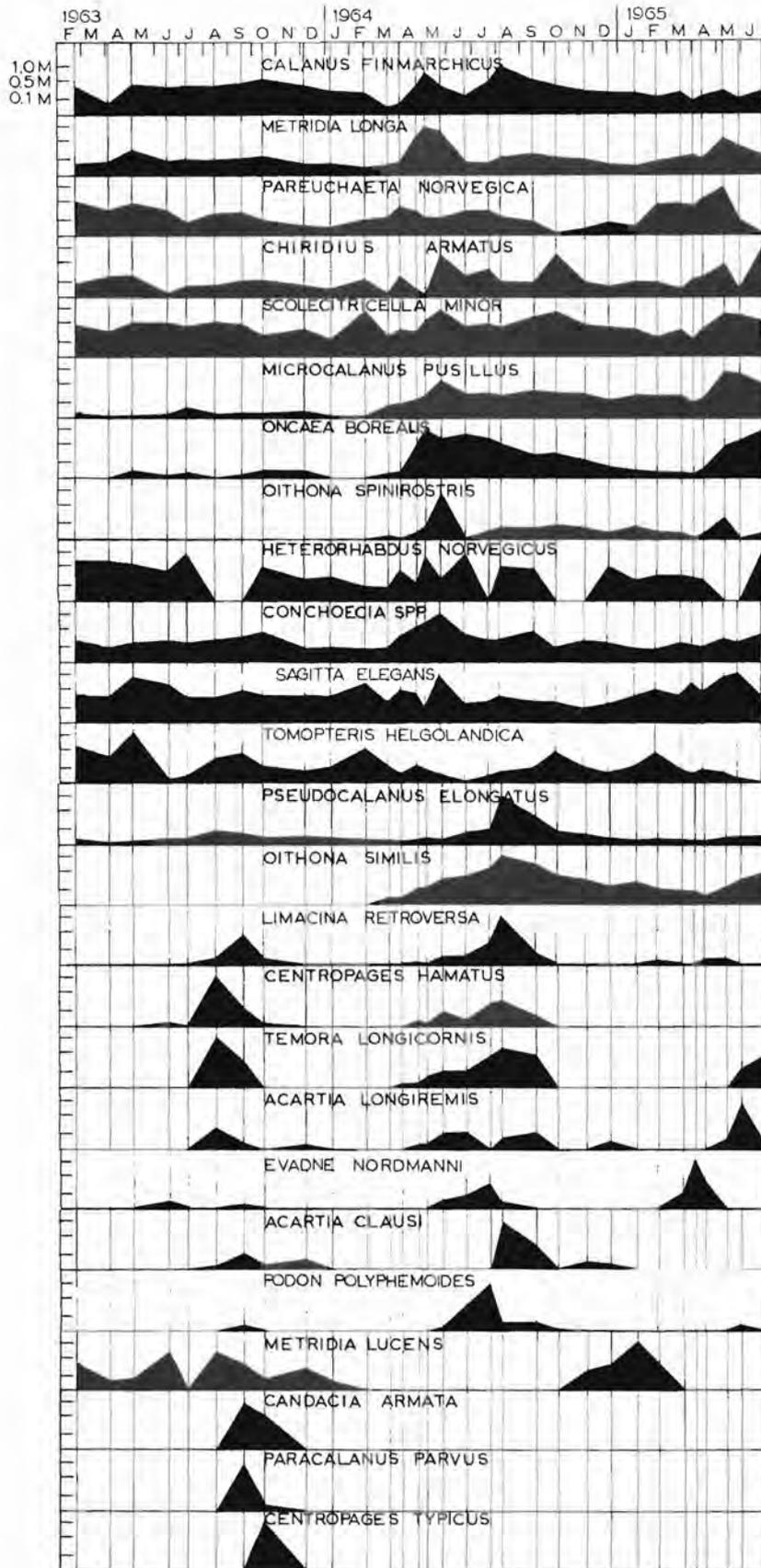


Fig. 84. Types of components in the zooplankton. Left scale indicates 1.0, 0.5, and 0.1 of maximum of Y at St. 15 (see text).

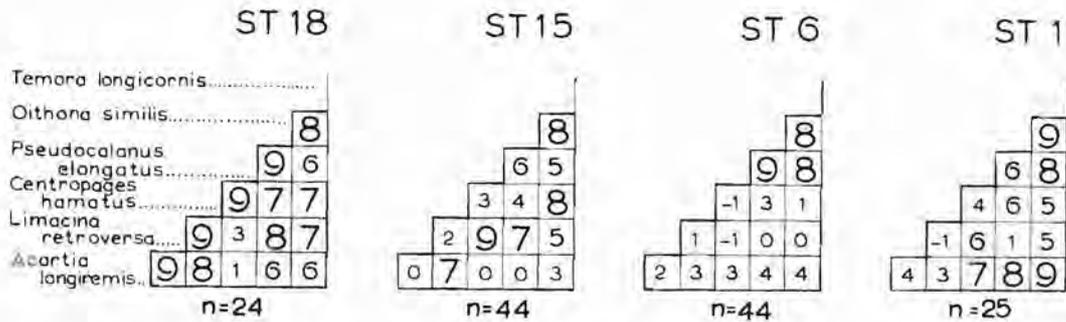


Fig. 85. Correlation matrix for a number of autochthonous species with main maxima in autumn. Critical values for the correlation coefficients at the 0.01 level are $n = 45, r = 0.430$ and $n = 24, r = 0.565$.

The remaining three species in this group, *E. nordmanni*, *A. clausi*, and *P. polyphemoides*, show no significant correlation to the species mentioned above. *E. nordmanni* has an earlier occurrence than *A. clausi* and *P. polyphemoides*.

At St. 18 *E. nordmanni* and *P. polyphemoides* show a correlation coefficient of 1.0, while no significant correlation is found in the fjord proper.

3. The allochthonous species *M. lucens*, *C. armata*, *P. parvus*, and *C. typicus*, have a very restricted occurrence mainly in autumn. These species are found only or mainly in the outer fjord and are not perennial. The matrix of single time-number correlation coefficient for these species for the period 1963-66 is given in Fig. 86. *C. typicus*, *C. armata*, and *M. lucens* show a highly significant correlation at St. 6.

A. patersoni, *R. nasutus*, and *S. fusiformis* are also allochthonous forms.

M. lucens keeps to deeper water than the other species, and may persist in these layers throughout autumn and winter.

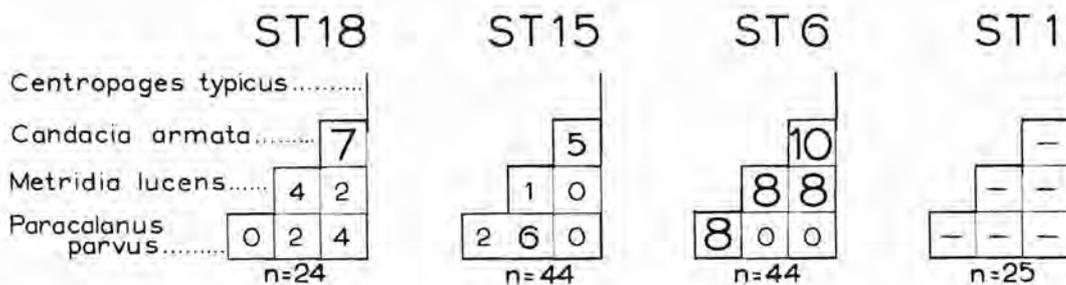


Fig. 86. Correlation matrix for a number of allochthonous species. Critical values of correlation coefficient see Fig. 85.

Scolecithricella minor, *Oithona spirostris*, and *Oncaea borealis* often shown fairly significant correlation to the phytoplankton species *Skeletonema costatum*, *Thalassionema nitzschioides*, *Gonyaulax tamarensis*, and *Peridinium trochoideum* at St. 1 and 15. *T. nitzschioides* seems to accompany these copepods particularly at St. 1.

Of the next main group of autochthonous copepods, which have their main maximum in autumn, *Pseudocalanus elongatus* and *Acartia longiremis* seem also correlated to *Thalassionema nitzschioides*. The bulk of this group, however, *Temora longicornis*, *Centropages hamatus*, *Oithona similis*, and *Limacina retroversa* show a seasonal distribution similar to another group of phytoplankton species, *Ceratium lineatum*, *Ceratium fusus*, and *Coccolithus huxleyi*. The species *Acartia clausi*, *Podon polyphemoides*, and *Evadne nordmanni* seem to have an occurrence similar to *Coccolithus huxleyi*, *Nitzschia delicatissima*, and *Thalassiosira decipiens*. At the outermost station 18, *Podon polyphemoides*, *Evadne nordmanni*, and *Peridinium trochoideum* have identical seasonal variations with correlation coefficient 1.0.

SUMMARY

1. Zooplankton samples were collected every month or every fortnight from February 1963 to July 1966 at permanent stations in Trondheimsfjorden on the West Coast of Norway. The samples were taken in single hauls with a 0.1 m² Juday net. Simultaneously, data on temperature, salinity, oxygen, and phytoplankton were collected.

2. Topographically, Trondheimsfjorden consists of four main basins, separated by thresholds. The hydrographic data indicate an estuarine circulation in the upper layers of Trondheimsfjorden. Inflows at deep and intermediate levels occur several times a year, but both the numbers and the strength of the inflows are reduced successively when the thresholds are passed inwards in the fjord.

3. The copepods dominated the zooplankton during all seasons. In the upper 100 m the variations were mainly due to succession of different species, while in the deeper layers the variations were due to fluctuations of permanent members of the community. *Calanus finmarchicus*

was the dominating copepod at all seasons and in all layers. In autumn, however, a number of small zooplankton were important. (*Pseudocalanus elongatus*, *Temora longicornis*, *Centropages hamatus*, *Acartia longiremis*, *Oithona similis*, *Limacina retroversa*, *Podon polyphemoides*, *Evadne nordmanni*.)

4. The volume of the zooplankton was measured by the displacement method. The variations in the upper 100 m in the main fjord indicated that in the outer fjord, two or three maxima occurred annually, while in the inner part the number of peaks was reduced. Below 100 m the volume maximum occurred in summer and autumn. In both layers the volume varied from year to year as well as from the outer to the inner fjord. The fluctuations seemed to some extent to be correlated to hydrographic events, indicating a relation between zooplankton abundance and water exchange with areas outside the fjord.

5. The different copepods and non-copepods were analysed in terms of variation of number, stage distribution, propagation, and vertical distribution. For a number of specimens, length distribution was also measured. For each species its relation to environmental conditions is discussed.

ACKNOWLEDGEMENTS

The investigation was supported by Norges Almenvitenskapelige Forskningsråd, and the preparation of this paper was supported by The Royal Norwegian Society of Sciences and Letters, The Museum.

I am greatly indebted to Mr. D. Rustad, former curator of Trondheim biological station, who initiated the investigation, to Professor E. Sivertsen, Professor Kr.Fr. Wiborg, and Mr. E. Sakshaug for valuable discussions, to Mr. P. Wendelbo for his cooperation in preparing the hydrographic data, and to Mr. E. Lande for sampling assistance.

Valuable technical assistance was given by Mrs. I. Harder (typing) and Mr. A. Nohre (drawing).

REFERENCES

- Ackefors, H. 1969. Ecological Zooplankton Investigation in the Baltic Proper 1963-65. *Inst. Mar. Res. Lysekil, Ser. Biol. Rep.* (18): 1-137.
- Beyer, F., Å. Dybwad & J. Versvik. 1967. Zooplankton. *Oslofjorden og dens forurensningsproblemer. I. Undersøkelsen 1962-65. Delrapport nr. 5. Oslofjordprosjektet.* Norsk Institutt for Vannforskning, Blindern.
- Bigelow, H.B. 1926. Plankton of the Offshore Waters of the Gulf of Maine. *Bull. Bur. Fish., Wash.* 40 II: 1-509.
- Bigelow, H.B. & M. Sears. 1939. Studies of the water of the Continental Shelf, Cape Cod to Chesapeake Bay. III. A volumetric study of the Zooplankton. *Mem. Mus. comp. Zool. Harv.* 54 (4): 183-378.
- Bogorov, B.G. 1932. Material on the biology of the copepods of the Barents and the White Seas. *Byull. gosud. okeanogr. Inst.* 4.
- 1946. Peculiarities of Diurnal Vertical Migrations of Zooplankton in Polar Seas. *J. mar. Res.* 6 (1): 25-32.
- Bogorov, B.G. & E. Preobrayenskaya. 1934. On the weight characteristics of the plankton organisms of the Barents Sea. II. Copepods. *Byull. vses. Inst. ryb. Khoz. Okeanogr.* (2).
- Brodskii, K.A. 1950. *Calanoida of the Far Eastern Seas and Polar Basins of the USSR.* Israel Program for Scientific Translations. Jerusalem 1967. 440 pp.
- Brattstrøm, H. 1972. On *Salpa fusiformis* Cuvier (Thaliacea) in Norwegian coastal and offshore waters. *Sarsia* 48: 71-90.
- Cameron, F.E. 1957. Some factors influencing the distribution of pelagic copepods in the Queen Charlotte Island area. *J. Fish. Res. Bd. Can.* 14 (2): 165-202.
- Colebrook, J.M., D.E. John & W.W. Brown. 1961. Contribution towards a plankton atlas of the North-eastern Atlantic and the North-Sea. Part II: Copepoda. *Bull. mar. Ecol.* 5 (42): 90-97.
- Conover, R.J. 1956. Oceanography of Long Island Sound, 1952-1954. VI. Biology of *Acartia clausi* and *A. tonsa*. *Bull. Bingham oceanogr. Coll.* 15: 156-233.

- Conover, R.J. 1964. Food relation and nutrition of zooplankton. *Symp. on experimental Mar. ecology. Narragansett Mar. Lab. Occ. Publ.* (2).
- Damas, D. 1905. Notes Biologiques sur les Copepodes de la Mer Norvegienne. *Publs. Circonst. Cons.perm.int.Explor Mer* (22): 1-23.
- Deevey, G.B. 1956. Oceanography of Long Island Sound, 1952-54. V. Zooplankton. *Bull. Bingham oceanogr. Coll.* 15: 113-155.
- Digby, P.S.B. 1950. The Biology of the Small Planktonic Copepods of Plymouth. *J. mar. biol. Ass. U.K.* 29 (2): 393-438.
- 1954. The Biology of the Marine Planktonic Copepods of Scoresby Sound, East Greenland. *J. Anim. Ecol.* 23: 298-338.
- Elgmork, K. 1955. A resting stage without encystment in the annual cycle of the fresh-water copepod, *Cyclops strenuus strenuus*. *Ecology* 36 (4): 739-743.
- Farran, G.P. 1911. Copepoda. *Bull. trimest. Résult. Crois. périod. Cons. perm.int.Explor.Mer* (2): 81-105.
- 1947. Vertical Distribution of Plankton (*Sagitta*, *Calanus*, and *Metridia*) of the South Coast of Ireland. *Proc. R. Ir. Acad.* 51 B (6): 121-136.
- 1948. Copepods. Suborder: Calanoida. Family Candaciidae. Zooplankton Sheet 13. *Fish. Ident. Zooplankton* (13): 1-4.
- Fish, C.J. 1936 a. The biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull. mar. biol. Lab., Woods Hole* 70 (1): 118-141.
- 1936 b. The biology of *Pseudocalanus minutus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull. mar. biol. Lab., Woods Hole* 70 (2): 193-216.
- Fish, C.J. & M.W. Johnson. 1937. The biology of the Zooplankton Population in the Bay of Fundy and Gulf of Maine with Special Reference to Production and Distribution. *J. biol. Bd. Can.* 3 (3): 189-322.
- Fraser, J.H. 1952. The chaetognatha and other zooplankton of the Scottish area and their value as biological indicators of hydrographical conditions. *Mar. Res.* (2): 1-52.
- Fryer, G. & W.J.P. Smyly. 1954. Some remarks on the resting stages of some freshwater cyclopoid and harpacticoid copepods. *Ann. Mag. nat. Hist., Ser. 12, 7* (73): 65-72.

- Gade, H.G. 1968. Horizontal and vertical exchanges and diffusion in the water masses of the Oslo fjord. *Helgoländer wiss. Meeresunters.* 17: 462-475.
- Gardiner, A.C. 1931. The Validity of Single Vertical Hauls of the International Net in the Study of the Distribution of the Plankton. *J. mar. biol. Ass. U.K.* 17 (2): 449-472.
- Gran, H.H. 1900. Hydrographic-biological studies of the North Atlantic Ocean and the Coast of Nordland. *Rep. Norw. Fishery mar. Invest.* 1 (5): 1-92.
- 1902. Das Plankton des Norwegischen Nordmeeres von biologischen und hydrographischen Gesichtspunkten behandelt. *Rep. Norw. Fishery mar. Invest.* 2 (5): 1-222.
- Gundersen, K.R. 1953. Zooplankton Investigations in some Fjords in Western Norway during 1950-1951. *Fiskeridir. Skr. Havundersøk.* 10 (6): 1-54.
- Hansen, V.K. 1960. Investigations on quantitative and qualitative distribution of zooplankton in the southern part of the Norwegian Sea. *Meddr. Danm. Fisk.- og Havunders. Ny Serie* 2 (23): 1-53.
- Haq, S.M. 1967. Nutritional physiology of *Metridia lucens* and *M. Longa* from the Gulf of Maine. *Limnol. Oceanogr.* 12 (1): 40-51.
- Harder, W. 1957. Das Verhalten von marinem Plankton gegenüber Sprungschichten. *Verh. dt. zool. Ges.* (20) Suppl. Bd.: 444.
- Holme, N.A. 1964. Methods of sampling the benthos. *Adv. mer. Biol.* 2: 171-260.
- Jespersen, P. 1934. The Godthaab Expedition 1928, Copepoda. *Meddr Grønland* 79 (10): 1-166.
- 1939 a. Investigations on the copepod fauna in East Greenland waters. *Meddr Grønland* 119 (9): 1-106.
- 1939 b. The Zoology of East Greenland. Copepods. *Meddr Grønland* 121 (3): 1-66.
- 1940. Investigations on the quantity and distribution of zooplankton in Icelandic waters. *Meddr Komm. Havunders. Serie: Plankton* 3 (5): 1-77.
- Johnson, M.W. 1963. Zooplankton collections from the high Polar Basin with special reference to the Copepoda. *Limnol. Oceanogr.* 8: 89-102.

- Kielhorn, W.V. 1952. The Biology of the Surface Zone Zooplankton of a Boreo-Arctic Atlantic Ocean Area. *J. Fish. Res. Bd. Can.* 9 (5): 223-264.
- Légaré, J.E.H. 1957. The qualitative and quantitative distribution of plankton in the Strait of Georgia in relation to certain oceanographic factors. *J. Fish. Res. Bd. Can.* 14 (4): 521-552.
- Lie, U. 1965. Quantities of Zooplankton and Propagation of *Calanus finmarchicus* at Permanent Stations on the Norwegian Coast and at Spitsbergen, 1959-1962. *Fiskeridir. Skr. Havundersøk.* 13 (8): 5-19.
- 1966. Dyreplankton fra faste stasjoner langs Norskekysten i årene 1963-65. *Fisken Hav.* (4): 1-5.
 - 1967. The natural history of the Hardangerfjord. 8. Quantity and composition of the zooplankton, September 1955-September 1956. *Sarsia* (30): 49-74.
 - 1968. Variations in the quantity of zooplankton and the propagation of *Calanus finmarchicus* at Station "M" in the Norwegian Sea, 1959, 1966. *Fiskeridir. Skr. Havundersøk.* 14 (3): 121-128.
- Lohmann, H. 1908. Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton. *Wiss. Meeresunters. Abt. Kiel N.F.* 10: 129-370.
- Lysholm, B. 1912. Trondheimsfjordens plankton-copepoder. *K. norske Vidensk. Selsk. Skr.* (7): 1-8.
- Marshall, S.M. 1949. On the Biology of the Small Copepods in Loch Striven. *J. mar. biol. Ass. U.K.* 28 (1): 45-122.
- Marshall, S.M. & A.P. Orr. 1952. On the biology of *Calanus finmarchicus*. VII. Factors affecting egg production. *J. mar. biol. Ass. U.K.* 30 (3): 527-548.
- Matthews, J.B.L. 1964. On the Biology of some Bottom-living Copepods (Aetideidae and Phaennidae) from Western Norway. *Sarsia* (16): 1-46.
- McHardy, R.A. & B. McK. Bary. 1965. Diurnal and seasonal changes in distribution of two planktonic ostracods, *Conchoecia elegans* and *Conchoecia alata minor*. *J. Fish. Res. Bd. Can.* 22 (3): 823-840.
- McLaren, I.A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. *J. Fish. Res. Bd. Can.* 20 (3): 685-727.

- Nicholls, A.G. 1933 a. On the Biology of *Calanus finmarchicus*. I. Reproduction and Seasonal Distribution in the Clyde Sea Area during 1932. *J.mar.biol.Ass. U.K.* 19 (1): 83-109.
- 1933 b. On the Biology of *Calanus finmarchicus*. III. Vertical Distribution and Diurnal Migration in the Clyde Sea Area. *J.mar.biol.Ass. U.K.* 19 (1): 139-164.
- 1934. The Development Stages of *Euchaeta norvegica*, Boeck. *Proc. R. Soc. Edinb.* 54 (1): 31-50.
- Rae, K.M. 1949. Some broad changes in the plankton round the north of the British Isles in 1948. *Annls biol., Copenh.* 5: 56-60.
- 1950. The continuous plankton recorder survey; some broad changes in the plankton round the British Isles in 1949. *Annls Biol., Copenh.* 6: 87-91.
- 1951. The continuous plankton recorder survey; the plankton round the north of the British Isles in 1950. *Annls biol., Copenh.* 7: 72-77.
- 1957. The Continuous Plankton Recorder Survey; Plankton around the British Isles during 1955. *Annls biol., Copenh.* 12: 84-87.
- Rae, K.M. & C.B. Rees. 1947. Continuous plankton record: The copepoda in the North Sea, 1938-39. *Hull Bull.mar.Ecol.* 2 (13): 95-132.
- Rees, C.B. 1957. The distribution of *Calanus finmarchicus* (Gunn.) in the North Sea and the north-eastern Atlantic, 1946-1953. *Hull. Bull.mar.Ecol.* 5 (37): 211-246.
- Runnstrøm, S. 1932. Eine Übersicht über das Zooplankton des Herdla- und Hjeltefjordes. *Bergen Mus.Årb. 1931, Naturv. R.* (7): 1-67.
- Russel, F.S. 1935. On the Value of Certain Plankton Animals as Indicators of Water Movements in the English Channel and North Sea. *J.mar.biol.Ass. U.K.* 20 (2): 309-332.
- 1939. Hydrographical and biological conditions in the North Sea as indicated by plankton organisms. *J. Cons.perm.int. Explor.Mer.* 14 (2): 171-192.
- Ruud, J.T. 1929. On the Biology of Copepods off Møre. 1925-1927. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* 56: 1-84.
- Sakshaug, E. 1972. Phytoplankton investigations in Trondheimsfjorden, 1963-66. *K. norske Vidensk. Selsk. Skr.* 1: 1-56.

- Sars, G.O. 1903. *An account of the Crustacea of Norway. 4, Copepoda Calanoida.* Bergen og Oslo 1903. 171 pp.
- 1918. *An account of the Crustacea of Norway. 6, Copepoda Cyclopoida.* Bergen og Oslo 1918. 225 pp.
- Scott, T. 1911. Copepoda. *Bull trimest Résult. Crois. périod. Cons. perm. int. Explor. Mer* (2): 106-149.
- Strømgren, T. 1973. Zooplankton investigations in Borgenfjorden, 1967-1969. *K. norske Vidensk. Selsk. Mus. Miscellanea* 9: 1-37.
- Størmer, L. 1929. Copepoda from the Michael Sars Expedition 1924. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* 56: 1-57.
- Sømme, J. 1934. Animal plankton of the Norwegian coast waters and the open sea. I. Production of *Calanus finmarchicus* (Gunner) and *Calanus hyperboreus* (Krøyer) in the Lofoten area. *Rep. Norw. Fishery mar. Invest.* 4 (9): 1-163.
- Verwoort, W. 1952. Copepods: Suborder Calanoida. Zooplankton. *Fish. Ident. Zooplankton* (42): 1-4.
- Wesenberg-Lund, E. 1935. Tomopteridae and Typhloscolesidae. *Dan. Ingolf-Exped.* 4 (11): 1-16.
- Wiborg, Kr.Fr. 1940. The Production of Zooplankton in the Oslo Fjord in 1933-1934. With Special Reference to the Copepods. *Hvalråd. Skr.* (21): 1-85.
- 1944. The Production of Zooplankton in a Landlocked Fjord, The Nordåsvatn near Bergen, in 1941-42. *Fiskeridir. Skr. Havundersøk.* 7 (7): 1-83.
1951. The whirling vessel, an apparatus for the fractioning of plankton samples. *Fiskeridir. Skr. Havundersøk.* 9 (13): 1-16.
1954. Investigation on Zooplankton in Coastal and Offshore Waters of Western and Northwestern Norway. *Fiskeridir. Skr. Havundersøk.* 11 (1): 1-246.
1955. Zooplankton in Relation to Hydrography in the Norwegian Sea. *Fiskeridir. Skr. Havundersøk.* 11 (4): 1-66.
1958. Quantitative variations of the zooplankton in Norwegian coastal and offshore waters during 1949-56. *Fiskeridir. Skr. Havundersøk.* 12 (1): 1-17.
- Winsor, C.P. & L.A. Walford. 1936. Sampling variation in the use of plankton nets. *J.Cons.perm.int. Explor. Mer.* 11 (2): 190-204.

- With, C. 1915. Copepoda I, Calanoida Amphascandaria. *Dan. Ingolf-Exped.* 3 (4): 1-260.
- Wolfenden, R.N. 1904. Notes on the Copepoda of the North Atlantic sea and the Farøer Channel. *J.mar.biol.Ass. U.K.* 7 (1): 110-146.
- Østvedt, O.-J. 1955. Zooplankton Investigations from Weather Ship M in the Norwegian Sea, 1948-1949. *Hvalråd Skr.* (40): 1-93.

Received October 1973

Printed January 1974

