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Tor Strømgren

VERTICAL DISTRIBUTION AND NUMERICAL VARIATION OF ZOOPLANKTON IN THE UPPER 50 M AT ONE STATION IN TRONDHEIMSFJORDEN

TRONDHEIM 1973

K. norske Vidensk. Selsk. Mus. Miscellanea 14 - 1973

VERTICAL DISTRIBUTION AND NUMERICAL VARIATION OF ZOOPLANKTON IN THE UPPER 50 M AT ONE STATION IN TRONDHEIMSFJORDEN

by

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The Royal Norwegian Society of Sciences and Letters, The Museum

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ABSTRACT

Strömgren, Tor. 1973. Vertical distribution and numerical variation of zooplankton in the upper 50 m at one station in Trondheimsfjorden. *K. norske Vidensk. Selsk. Mus. Miscellanea 14:*

At a permanent hydrographic station (Stn 15 Röberg) in Trondheimsfjorden, Western Norway, zooplankton was collected at short intervals during the periods March-June 1970-1972 and August-October 1970. The samples were taken during daylight hours, by pump, at 0, 2, 5, 10, 20, 30, and 50 m depths.

There was a highly significant linear correlation between Simpson's index of diversity (λ) and the Shannon Weaver index (H). Simpson's index for copepods and that for holoplankton also showed a highly significant correlation. This indicates that in this material the diversity of one systematic unit, the copepods, is representative for the whole holoplanktonic community. Index of diversity increased on average with depth, while the largest variations were found in the upper 5 m.

In unstable and cold waters in March, the zooplankton concentration was low and its vertical distribution scattered. In May and June large stocks of several species, including *Calanus finmarchicus*, were confined to the upper 10 m. This distribution coincided with the formation of steep thermo- and haloclines. In June, species which normally inhabited the uppermost layers, tended to disappear from the 0 and 2 m levels. In general, both vertical distribution and abundance of the various species seemed closely related to both horizontal and vertical water displacements.

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INTRODUCTION

Earlier records of the vertical distribution of holoplankton in Norwegian waters are based on vertical hauls (Wiborg 1940, 1944, 1954, Hansen 1951, Gundersen 1953, and others), and show the distribution in water columns of variable height. However, information is required about plankton concentration at discrete depths, where the environment is well defined. Schram (1968) has sampled meroplankton in Oslofjorden with a plankton pump.

During 1963-1966 an extensive sampling of zooplankton was carried out at several stations in Trondheimsfjorden (Strömgren 1973 a), and one representative station in the outer fjord, Stn 15 Röberg, was chosen for a more detailed investigation of the daytime vertical distribution.

MATERIAL AND METHODS

The material was collected from seven depths: 0, 2, 5, 10, 20, 30, and 50 m, at a permanent hydrographic station, Stn 15 Röberg, in the outer basin of Trondheimsfjorden proper (Fig. 1). A Mono pump with a two inch suction hose was used. The pump was adjusted to deliver approximately 200 litres per minute (see Barnes 1949), and 0.5-1.0 m^3 of water was pumped from each depth. At this low rate, both larval plankton and more mobile organisms such as copepods and cladocerans are probably adequately sampled (Banse 1955, Schram 1968).

Samples were taken at short intervals during the springs of 1970, 1971, and 1972, and during the autumn in 1970. All samples were taken during the daytime. The sampling dates are shown in Table 1.

The water was filtered through a nylon net with mesh size 180 u, and the zooplankton fixed in 5% neutralized formalin. Large samples were sub-sampled in a Wiborg Lea plankton divider (Wiborg 1951) before counting.

Hydrographic data from the same sampling depths were obtained with Nansen reversing water bottles, each equipped with two reversing thermometers; salinity was determined by the standard

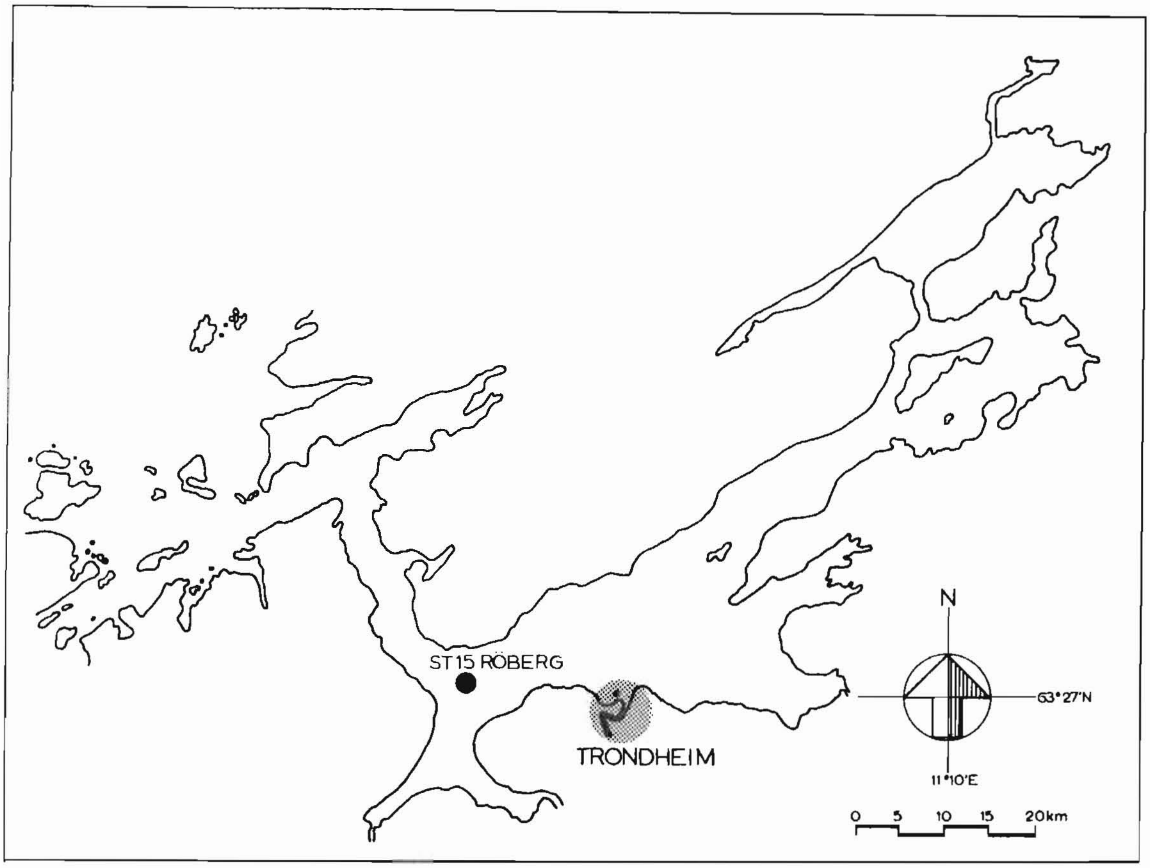

Fig. 1. Trondheimsfjorden, sampling station indicated.

Knudsen titration method. Water transparency was measured with a Secchi disk.

From the values obtained at discrete depths, the total number of the zooplankton in the 50-0 m water column was calculated by linear integration.

Length measurements of carapaces were mede with a stereo-microscope with a built-in micrometer.

HYDROGRAPHY

Isopleths for temperature and salinity during the sampling period are shown in Figs. 2 and 3. The temperature and salinity data for each sampling depth are reproduced in Tables 1 and 2.

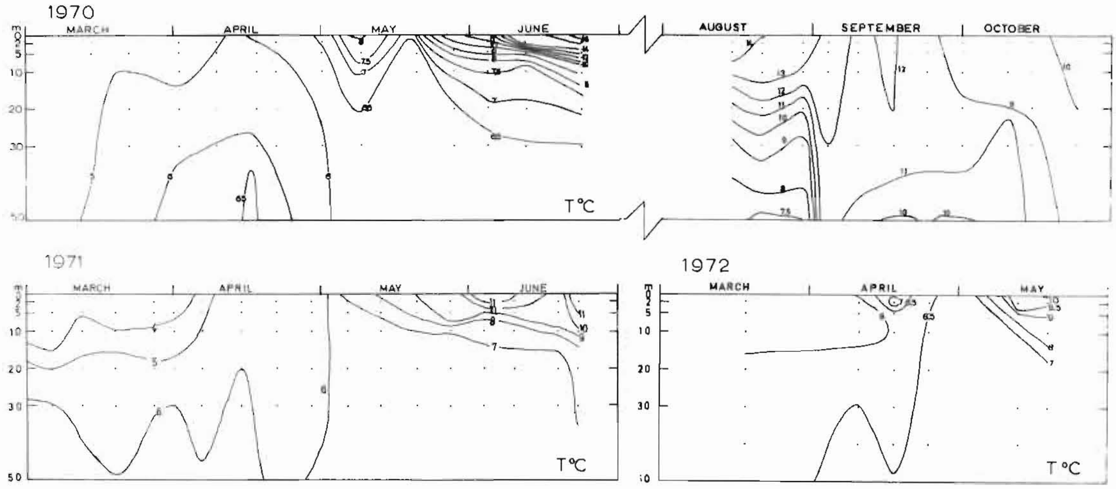

Fig. 2. Temperature isopleths, March 1970 to May 1972 at Stn 15 Röberg.

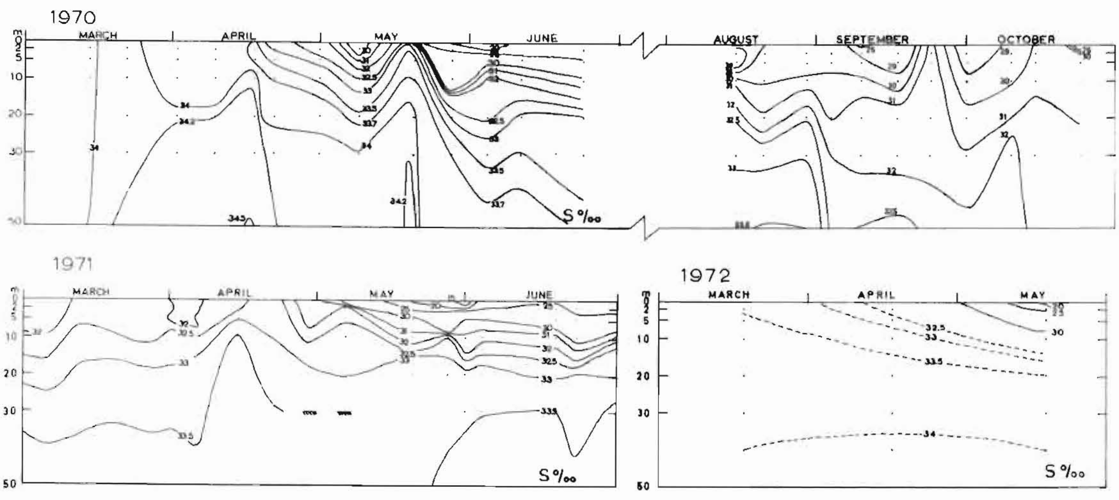

Fig. 3. Salinity isopleths, March 1970 to May 1972 at Stn 15 Röberg.

Table 1. Temperature readings, March 1970 to May 1972 at Stn 15 Röberg in Trondheimsfjorden.

1970

Depth in m	March 12	20	April 1	9	17	21	30	May 8	19	27	June 4	11	23	August 14	20	28	September 3	9	16	23	30	October 9	14	23
0	4.78	5.18	4.90	5.10	6.10	6.48	6.60	8.40	6.90	10.30	12.40	15.03	16.90	14.24	14.30	13.45	12.90	11.60	12.18	11.23	10.49	10.04	10.48	8.82
2	4.69	5.15	4.89	[illegible]	5.92	6.28	6.55	7.79	6.41	10.02	10.92	14.83	15.77	14.27	13.54	13.37	12.93	11.31	12.16	11.25	10.60	10.06	10.62	9.14
5	-	5.06	[illegible]	5.07	5.1[illegible]	5.5[illegible]	6.44	7.76	6.44	8.19	8.82	9.53	13.69	14.30	13.49	13.38	12.77	11.60	12.03	11.23	10.59	10.10	10.79	9.61
10	4.67	5.01	[illegible]	5.10	5.72	5.81	6.39	7.16	6.42	7.08	7.53	7.26	9.17	13.09	13.41	12.89	12.60	11.89	12.00	11.30	10.56	10.59	10.82	9.58
20	4.68	5.02	5.12	5.59	5.95	5.63	6.10	-	6.42	6.21	6.80	7.06	7.11	10.57	11.56	10.08	12.60	11.60	12.00	11.51	11.34	11.09	10.98	10.10
30	4.69	5.07	5.91	6.04	6.14	5.78	5.92	6.36	6.32	-	6.42	6.44	6.46	8.56	9.53	8.83	11.96	11.94	11.70	11.20	11.40	10.63	11.06	10.72
50	5.05	5.67	6.36	6.26	6.89	6.27	5.80	6.31	6.21	6.21	6.23	6.15	6.21	7.75	7.26	7.46	11.03	10.23	9.87	10.69	9.82	10.00	11.02	10.70

1971 / 1972

Depth in m	1971 March 5	11	18	26	31	April 6	14	21	29	May 5	12	19	26	June 1	3	18	22	30	1972 March 17	10	April 17	24	May 12	18
0	2,60	4,00	3,60	3,91	3,92	4,72	5,60	5,80	5,85	8,32	8,60	9,00	9,45		11,20	9,62	13,38	12,53	5,69	6,11	6,90	6,27	9,60	10,00
2	2,55	4,00	3,64	3,91	3,95	4,75	5,58	5,60	5,82	6,89	7,47	8,85	9,47		11,10	9,53	12,40	12,45	5,53	5,90	7,06	6,32	9,90	9,73
5	2,65	4,00	3,65	3,92	3,94	4,76	5,73	5,78	5,75	6,39	7,13	8,35	9.48		8,80	9,50	11,26	10,98	5,56	5,90	6,42	6,53	9,05	8,10
10	2,81	4,45	4,18	4,02	4,34	5,03	5,80	5,68	5,76	6,26	6,53	6,99	7,06		7,30	8,30	9,24	7,95	5,54	5,80	6,06	6,70	7,20	8,30
20	4,97	5,27	5,19	5,24	5,10	5,44	6,00	5,80	5,89	6,17	6,30	6,47	6,70		6,70	6,70	7,30	7,20	6,26	6,23	6,04	6,61	6,65	6,70
30	6,07	5,80	5,70	5,92	6,00	5,63	6,12	5,84	5,75	6,20	6,30	6,28	6,54		6,50	6,56	7,12	7,10	6,32	6,50	6,25	6,72	6,81	6,95
50	4,58	6,04	6,10	6,22	6.15	6,14	6,40	5,84	6,10	6,43	6,50	6.40	6,37		6,44	6,60	6,70	7,02	6,40	6,70	6,52	6,79	6,97	[illegible]

Table 2. Salinity readings, March 1970 to May 1972 at Stn 15 Röberg in Trondheimsfjorden.

1970

Depth in m	March 12	20	April 1	9	17	21	30	May 8	19	27	June 4	11	23	August 14	20	28	September 3	9	16	23	30	October 9	14	23
0	33.95	34.07	33.94	33.75	33.75	32.68	32.20	29.85	32.41	15.21	12.67	-	22.94	27.37	28.93	29.40	29.67	24.90	28.35	31.06	27.74	29.61	30.10	27.11
2	33.86	34.09	33.86	33.80	33.60	33.04	-	-	33.49	24.52	21.64	21.58	23.28	27.54	29.40	29.25	29.60	28.59	28.39	31.08	28.86	29.63	30.42	27.83
5	33.89	34.11	33.95	33.80	33.62	33.42	32.65	30.16	33.55	28.64	29.29	28.71	25.66	27.52	29.65	29.25	29.81	29.14	28.57	31.08	28.91	29.61	30.81	30.66
10	33.93	34..1	33.96	33.84	34.13	33.69	33.42	32.56	33.73	32.00	-	31.58	30.37	30.37	29.96	30.50	30.21	30.28	29.34	31.24	29.04	29.96	30.90	30.68
20	33.95	34.11	34.14	34.16	34.27	33.93	33.87	33.58	34.07	33.21	32.95	33.08	32.95	32.45	31.36	32.48	30.97	31.62	31.49	31.62	30.66	31.04	31.20	30.90
30	33.95	34.11	34.33	34.36	34.31	34.11	34.21	34.02	34.16	33.73	33.39	33.51	33.31	32.90	32.81	32.97	32.00	31.92	31.83	31.87	31.08	32.29	31.44	31.51
50	33.96	34.23	34.38	34.47	34.51	34.38	34.18	34.09	34.34	33.96	33.80	33.95	33.62	33.30	33.53	33.55	32.10	32.56	32.65	32.20	32.57	32.38	31.64	32.00

1971 / 1972

Depth in m	1971 March 5	11	18	26	31	April 6	14	21	29	May 5	12	19	26	June 1	3	18	22	30	1972 March 17	10	April 17	24	May 12	18
0	31,82	32,50	32,08	32,23	31,92	31,89	32,25	32,86	31,75	28,73		19,90	23,60	10,85	23,00	24,00	22,15	24,25	33,37		32,13			19,59
2	31,90	32,50	32,20	32,25	32,09	31,95	32,40	32,88	31,78	32,18		23,95	23,65	20,50	25,00	28,60	24,15	24,35	33,34		32,40			23,39
5	31,85	32,50	32,11	32,25	31,90	32,03	32,90	32,90	31,70	32,43		28,50	23,85	29,90	29,85	29,15	25,90	27,15	33,39		32,88			27.64
10	32,02	32,65	32,60	32,40	32,65	32,50	33,60	32,98	32,25	32,77		32,00	32,40	31,20	31,50	31,20	31,50	32,00	33,63		33.26			30.84
20	32,74	33,06	33,10	33,11	33,05	33,18	33,72	33,37	33,17	32,93		33,20	33,10	33,15	33,20	33,00	33,00	33,00	33,91		33,75			33,55
30	33,27	33,30	33,40	33,45	33,48	33,34	33,86	33,54	33,38	33,28		33,20	33,15	33,35	33,40	33,50	33,25	33,60	33,97		33,90			33,95
50	33,55	33,45	33,83	33,80	33,70	33,72	33,99					33,25	33,85	33,70	33,45	33,60	33,65	33,65	34,06		34,12			34,05

March to the middle of April

During this period the conditions seem to be relatively similar in all years. 1971, however, was characterized by low temperatures in the upper 10 m, and reduced salinity in the upper 50 m, while in 1970 and 1972, both temperature and salinity were markedly higher. At the end of March 1970 a small upwelling was indicated.

The last half of April

On the 17th of April 1970, salinity and temperature data indicate an upwelling of slightly warmer and more saline water up to the 10 m level. In 1971 the temperature and salinity data for April 14th indicate a similar trend, up to at least the 5 m level. For 1972 the salinity data are incomplete, but a temporary temperature increase on April 10th, up to the 10 m level, may indicate upwelling as in 1970 and 1971. Upwelling seems to be followed by mixing. From April 21st onwards, in 1970 and 1971, slightly colder and less saline water was found at the 50 m level. Simultaneously, several species normally confined to the uppermost layers showed a deeper distribution than usual. This may indicate that near-surface water had been mixed to at least 50 m depth.

During April, the surface temperature increased gradually. The increase was least marked in 1971.

May-June

This period is characterized by a large supply of melt water.

In 1970 reduced salinity on May 8th indicates that the formation of a brackish top layer has started, but before May 19th, strong winds seem to have driven away this layer and an upwelling of deep water has taken place. The temperature and salinity of the surface layer were then equivalent to those of the 10-20 m level on the preceding date. Towards the end of May and the beginning of June, the influence of river discharge reached its maximum. The steepest gradients in salinity were found between 2 and 5 m depth, and this may indicate the thickness of the brackish layer.

Table 1. Temperature readings, March 1970 to May 1972 at Stn 15 Rõberg in Trondheimsfjorden.

1970

Depth in m	March 12	March 20	April 1	April 9	April 17	April 21	April 30	May 8	May 19	May 27	June 4	June 11	June 23	August 14	August 20	August 28	September 3	September 9	September 16	September 23	September 30	October 9	October 14	October 21
0	4.70	5.10	4.90	5.10	6.10	6.40	6.60	8.40	6.90	10.30	12.40	15.03	16.90	14.24	14.30	13.45	12.90	11.60	12.18	11.23	10.49	10.04	10.48	8.82
2	4.69	5.15	4.89	5.?5	5.92	6.28	6.55	7.79	6.41	10.02	10.92	14.83	15.77	14.27	13.54	13.37	12.93	11.31	12.16	11.25	10.60	10.06	10.62	9.14
5	-	5.06	[illegible]	5.92	5.3?	5.?5	6.44	7.76	6.44	8.19	8.82	9.53	13.69	14.30	13.49	13.38	12.77	11.60	12.03	11.23	10.59	10.10	10.79	9.61
10	4.67	5.01	[illegible]	5.10	5.72	5.81	6.39	7.16	6.42	7.08	7.53	7.26	9.17	13.09	13.41	12.89	12.60	11.89	12.00	11.30	10.56	10.59	10.82	9.58
20	4.83	5.02	5.12	5.59	5.95	5.63	6.10	-	6.42	6.23	6.80	7.06	7.11	10.57	11.56	10.08	12.60	11.80	12.00	11.51	11.34	11.09	10.98	10.10
30	4.69	5.07	5.91	6.04	6.14	5.78	5.92	6.36	6.32	-	6.42	6.44	6.46	8.56	9.53	8.83	11.96	11.94	11.70	11.20	11.40	10.63	11.06	10.72
50	5.05	5.67	6.36	6.26	6.89	6.27	5.80	6.31	6.21	6.21	6.23	6.15	6.21	7.75	7.26	7.46	11.03	10.23	9.87	10.69	9.82	10.00	11.02	10.70

1971 / 1972

Depth in m	1971 March 5	March 11	March 18	March 26	March 31	April 6	April 14	April 21	April 29	May 5	May 12	May 19	May 26	June 1	June 3	June 18	June 22	June 30	1972 March 17	April 10	April 17	April 24	May 12	May 18
0	2,60	4,00	3,60	3,91	3,92	4,72	5,60	5,80	5,85	8,32	8,60	9,00	9,45		11,20	9,62	13,38	12,53	5,65	6,11	6,90	6,27	9,60	10,00
2	3,55	4,00	3,64	3,91	3,95	4,75	5,58	5,60	5,82	6,89	7,47	8,85	9,47		11,10	9,53	12,40	12,45	5,53	5,90	7,06	6,32	8,90	9,75
5	2,65	4,00	3,65	3,92	3,94	4,76	5,73	5,78	5,75	6,39	7,13	8,35	9,48		8,80	9,50	11,26	10,98	5,56	5,90	6,42	6,53	9,05	9,10
10	2,81	4,45	4,18	4,02	4,34	5,03	5,80	5,68	5,76	6,26	6,53	6,99	7,06		7,30	8,30	9,24	7,95	5,54	5,80	6,06	6,70	7,20	8,90
20	4,97	5,27	5,19	5,24	5,10	5,44	6,00	5,80	5,89	6,17	6,30	6,47	6,70		6,70	6,70	7,30	7,20	6,26	6,23	6,04	6,61	6,65	6,78
30	6,07	5,80	5,70	5,92	6,00	5,63	6,12	5,84	5,75	6,20	6,30	6,28	6,54		6,50	6,56	7,12	7,10	6,32	6,50	6,25	6,72	6,81	6,93
50	6,58	6,04	6,10	6,22	6,15	6,14	6,40	5,84	6,10	6,43	6,50	6,40	6,17		6,44	6,60	6,70	7,02	6,40	6,70	6,52	6,79	6,97	[illegible]

Table 2. Salinity readings, March 1970 to May 1972 at Stn 15 Rõberg in Trondheimsfjorden.

1970

Depth in m	March 12	March 20	April 1	April 9	April 17	April 21	April 30	May 8	May 19	May 27	June 4	June 11	June 23	August 14	August 20	August 28	September 3	September 9	September 16	September 23	September 30	October 9	October 14	October 23
0	33.95	34.07	33.96	33.75	33.75	32.68	32.20	29.85	32.41	15.21	32.67	-	22.94	27.37	28.93	29.40	29.67	24.90	28.35	31.06	27.74	29.61	30.10	27.11
2	33.86	34.09	33.86	33.80	33.60	33.04	-	-	33.49	24.52	21.64	21.58	23.28	27.54	29.40	29.25	29.60	28.59	28.39	31.08	28.86	29.63	30.42	27.83
5	33.89	34.11	33.95	33.80	33.62	33.42	32.65	30.16	33.55	28.64	29.29	28.71	25.66	27.52	29.65	29.25	29.81	29.14	28.57	31.08	28.91	29.61	30.81	30.66
10	33.93	[illegible]	33.96	33.84	34.13	33.69	33.42	32.56	33.73	32.00	-	31.58	30.37	30.37	29.96	30.50	30.21	30.28	29.34	31.24	29.04	29.96	30.90	30.68
20	33.95	34.11	34.14	34.16	34.27	33.93	33.87	33.58	34.07	33.21	32.95	33.08	32.95	32.45	31.36	32.48	30.97	31.62	31.49	31.62	30.66	31.04	31.20	30.90
30	33.95	34.11	34.33	34.36	34.31	34.11	34.11	34.02	34.16	33.73	33.39	33.51	33.31	32.90	32.81	32.97	32.00	31.92	31.83	31.87	31.08	32.29	31.44	31.51
50	33.96	34.23	34.38	34.47	34.51	34.38	34.18	34.09	34.34	33.96	33.80	33.95	33.62	33.30	33.53	33.55	32.10	32.56	32.65	32.20	32.57	32.38	31.64	32.00

1971 / 1972

Depth in m	1971 March 5	March 11	March 18	March 26	March 31	April 6	April 14	April 21	April 29	May 5	May 12	May 19	May 26	June 1	June 3	June 18	June 22	June 30	1972 March 17	April 10	April 17	April 24	May 12	May 18
0	31,82	32,50	32,08	32,23	31,92	31,89	32,25	32,86	31,75	28,73		19,90	23,60	10,85	23,00	24,00	22,15	24,25	33,37		32,13			19,59
2	31,90	32,50	32,20	32,25	32,09	31,95	32,40	32,88	31,78	32,18		23,95	23,65	20,50	25,00	28,60	24,15	24,35	33,34		32,40			22,39
5	31,85	32,50	32,11	32,25	31,90	32,03	32,90	32,90	31,70	32,43		28,50	23,85	29,90	29,85	29,15	25,90	27,15	33,39		32,86			27,64
10	32,02	32,65	32,60	32,40	32,65	32,50	33,60	32,98	32,25	32,77		32,00	32,40	31,20	31,50	31,20	31,50	32,00	33,63		33,26			30,84
20	32,74	33,06	33,10	33,11	33,05	33,18	33,72	33,37	33,17	32,93		33,20	33,10	33,15	33,20	33,00	33,00	33,00	33,91		33,75			33,55
30	33,27	33,30	33,40	33,45	33,48	33,34	33,86	33,54	33,38	33,28		33,20	33,15	33,35	33,40	33,50	33,25	33,60	33,97		33,90			33,95
50	33,55	33,45	33,83	33,80	33,70	33,72	33,99					33,25	33,85	33,70	33,45	33,60	33,65	33,65	34,06		34,12			34,05

March to the middle of April

During this period the conditions seem to be relatively similar in all years. 1971, however, was characterized by low temperatures in the upper 10 m, and reduced salinity in the upper 50 m, while in 1970 and 1972, both temperature and salinity were markedly higher. At the end of March 1970 a small upwelling was indicated.

The last half of April

On the 17th of April 1970, salinity and temperature data indicate an upwelling of slightly warmer and more saline water up to the 10 m level. In 1971 the temperature and salinity data for April 14th indicate a similar trend, up to at least the 5 m level. For 1972 the salinity data are incomplete, but a temporary temperature increase on April 10th, up to the 10 m level, may indicate upwelling as in 1970 and 1971. Upwelling seems to be followed by mixing. From April 21st onwards, in 1970 and 1971, slightly colder and less saline water was found at the 50 m level. Simultaneously, several species normally confined to the uppermost layers showed a deeper distribution than usual. This may indicate that near-surface water had been mixed to at least 50 m depth.

During April, the surface temperature increased gradually. The increase was least marked in 1971.

May-June

This period is characterized by a large supply of melt water.

In 1970 reduced salinity on May 8th indicates that the formation of a brackish top layer has started, but before May 19th, strong winds seem to have driven away this layer and an upwelling of deep water has taken place. The temperature and salinity of the surface layer were then equivalent to those of the 10-20 m level on the preceding date. Towards the end of May and the beginning of June, the influence of river discharge reached its maximum. The steepest gradients in salinity were found between 2 and 5 m depth, and this may indicate the thickness of the brackish layer.

In 1971 the salinity decrease at the surface was recorded on May 5th, and apart from a temporary increase at the end of May, an absolute minimum, of only 10.85^{o}/oo, was recorded on the first day of June (Table 2). As in 1970, the thickness of the brackish top layer seems to be in the order of 5 m, increasing towards the end of June.

In 1972 a salinity of 19.59^{o}/oo was recorded on May 18th, and a development similar to 1971 is indicated.

During May and June, the vernal warming is evident all years. In 1970, the temperature of the upper layers in June was particularly high, compared to 1971.

Due to freshwater supply, a surface outflow would be expected. Wendelbo (1970) assumed the velocity of this current to be of the order of 50 cm/sec. Accordingly, a strong counter current would be expected below the halocline. Simultaneously vertical transport of water was occasioned by entrainment (E. Sakshaug pers. comm.).

August-October

In the middle of August temperature and salinity gradients were less steep and the surface salinity was markedly increased. From the August 28th to the September 3rd 1970, the temperature increased by 2.52^{o}C, and the salinity decreased by 1.51^{o}/oo at 30 m depth. This may indicate that mixing has taken place. On the other hand, the salinity data show a net loss of salt in the upper 50 m, while there is a net gain of heat. This would indicate an introduction of warm and less saline water. Similar influxes of warm water into Trondheimsfjorden in autumn in previous years are described by Wendelbo (1970) and Strömgren (1974). The influx seems to continue throughout September.

On September 23rd 1970, a sudden increase in salinity in the upper 10-20 m may be related to strong winds, which may have driven the surface water away.

In the middle of October net increases in temperature and salinity were recorded, obviously due to an influx.

Temperature and salinity gradients

The average temperature and salinity gradients in the upper 10 m during periods of significant stratification are shown in Table 3. The steepest temperature gradients were found between 2 and 5 m at the end of May 1970, and in the upper 5 m at the beginning of June the same year. Throughout June the steepest gradients were found successively deeper down. At the beginning of May 1971, steep gradients occurred in the 0-2 m layer, while in June 1971 the situation was similar to that in June 1970.

Table 3. Temperature and salinity gradients, March 1970 to May 1972 at Stn 15 Rõberg in Trondheimsfjorden.

	1970									1971									1972	
Depth in m	May			June			August			May				June					May	
	8	19	27	4	11	23	14	20	28	5	12	19	26	1	3	18	22	30	12	18
0- 2	0.30	0.25	0.14	0.74	0.10	0.77	0.02	0.43	0.04	0,72	0,57	0,08	0,01		0,05	0,05	0,49	0,04	0,15	0,13
2- 5	0.01	0.01	0.61	0.70	1.77	0.69	0.01	0.02	0.00	0,17	0,11	0,17	0,00		0,77	0,01	0,38	0,49	0,28	0,22
5-10	0.12	0.01	0.22	0.26	0.45	0.90	0.22	0.02	0.10	0,03	0,12	0,27	0,48		0,30	0,24	0,40	0,66	0,37	0,12
10-20	-	0.00	0.09	0.07	0.02	0.20	0.25	0.19	0.28	0,01	0,02	0,05	0,04		0,06	0,16	0,19	0,08	0,06	0,17

	1970									1971									1972	
Depth in m	May			June			August			May				June					May	
	8	19	27	4	11	23	14	20	28	5	12	19	26	1	3	18	22	30	12	18
0-2	-	0.04	4.65	4.50	-	0.17	0.08	0.24	0.08	1,73		2,03	0,03	4,83	1,00	2,30	1,00	0,05		1,40
2-5	-	0.02	1.37	2.55	2.38	0.79	0.01	0.08	0.00	0,08		1,52	0,07	1,13	1,62	0,18	0,58	0,93		1,75
5-10	0.48	0.04	0.67	-	0.57	0.94	0.57	0.06	0.25	0,07		0,70	1,71	0,26	0,33	0,41	0,72	0,97		0,64
10-20	0.10	0.03	0.12	-	0.30	0.26	0.21	0.14	0.20	0,02		0,12	0,07	0,20	0,17	0,18	0,35	0,10		0,27

The salinity gradients were steepest in the 0-2 m layer at the end of May 1970 and in the upper 5 m at the beginning of June 1970, while in the middle of June the maximum gradient occurred in the 5-10 m layer. In 1971 significant gradients occurred in the upper 5 m from the beginning of May, while in June the trend was similar to that in 1971.

LIGHT CONDITIONS

Secchi disc measurements (Table 4) in 1970 indicated reduced light penetration from the end of April to the first week of June. Similar conditions were also recorded on September 9th and 30th, and on

Table 4. Cloud cover and Secchi disc depths, March 1970 to May 1972 at Stn 15 Röberg in Trondheimsfjorden.

1970

	March		April					May			June			August			September					October		
Date	12	28	1	9	17	21	30	8	19	27	4	11	23	14	20	28	3	9	16	27	30	9	14	23
Cloud cover	○	◔	◑	●	●	◔	●	○	●	●	◔	●	○	◔	◑	●	◑	◑	◑	●	◕	●	●	●
Secchi disc depths	14	17	8	5	8	6	4	3	-	3	3	-	6	4	6	6	-	2	6	7	5	8	8	4
Brownish water	-	-	-	-	-	-	X	X	-	-	X	-	X	-	-	-	-	X	-	-	X	-	-	X

1971

	March					April				May				June				
Date	5	11	18	26	31	6	14	21	29	5	12	19	26	1	3	18	22	30
Cloud cover	◕	◕	◑	◕	●	○	◕	◕	◑	◕	●	●	◕	◕	●	●	◑	●
Secchi disc depths	10	9	10	6	3		5	7	9	8	11	3	6		3	4		

1972

	March		April		May	
Date	17	10	17	24	12	18
Cloud cover	◔	◔	◑	◑	●	◑
Secchi disc depths	1		7		4	5

October 23rd. In 1971 low Secchi disc readings were recorded on April 31st, May 19th, and in the middle of June. In March 1972 an exceptionally low value was recorded.

The cloud cover at Trondheim on the sampling dates is shown in the same table. The Trondheim meteorological station values are probably quite representative for the cloud cover at Stn 15.

COMPOSITION OF THE ZOOPLANKTON

Copepoda dominate the zooplankton at all depths, both numerically and in respect of biomass. Six copepod species *(Calanus finmarchicus, Pseudocalanus elongatus, Temora longicornis, Microcalanus pusillus, Oncaea borealis,* and *Oithona similis)* contributed on average the bulk of the total number of organisms. This is in agreement with earlier observations in Trondheimsfjorden (Strömgren 1973 a, b). The number of species differed slightly with depth (Table 5). The number of specimens, however, was largest in the 2-20 m samples, and within this zone, the depth of maximum concentration varied with season.

In March-April, temperature and salinity in the upper 50 m were relatively homogenous, and a scattered vertical distribution was the norm. In May-June, when the water becomes stratified, the upper 2-10 m showed the highest concentrations.

Table 5. Cumulated occurrence of the species at different depths at Stn 15 Röberg in Trondheimsfjorden.

	0	2	5	10	20	30	50
Calanus finmarchicus	x	x	x	x	x	x	x
Paracalanus parvus	x	x	x	x	x	x	x
Pseudocalanus elongatus	x	x	x	x	x	x	x
Microcalanus pusillus	x	x	x	x	x	x	x
Chiridius armatus	0	0	0	0	x	x	0
Pareuchaeta norvegica	x	x	x	x	x	x	x
Scolecithricella minor	0	0	0	x	x	x	x
Temora longicornis	x	x	x	x	x	x	x
Metridia longa	0	0	0	0	x	x	x
Metridia spp.	x	x	x	x	x	x	x
Centropages hamatus	x	x	x	x	x	x	x
Centropages spp.	x	x	x	x	x	x	x
Acartia longiremis	x	x	x	x	x	x	x
Acartia clausi	x	x	x	x	0	x	x
Acartia spp.	x	x	x	x	x	x	x
Oithona similis	x	x	x	x	x	x	x
Oithona spinirostris	x	0	x	x	x	x	x
Oncaea borealis	x	x	x	x	x	x	x
Oncaea borealis, male	x	x	x	0	x	x	x
Oncaea similis	0	0	0	0	0	0	x
Microcetella norvegica with eggs	x	x	x	x	x	x	x
Microcetella norvegica without eggs	x	x	x	x	x	x	x
Unidentified harpacticoids	x	x	x	x	x	x	x
Unidentified nauplii	x	x	x	x	x	x	x
Tomopteris helgolandicus	0	0	x	x	x	x	x
Limacina retroversa	x	x	x	x	x	x	x
Sagitta elegans	x	x	x	x	x	x	x
Podon polyphemoides	x	x	x	x	x	x	x
Evadne nordmanni	x	x	x	x	x	x	x
Ostracoda	x	x	x	x	x	x	x
Euphauciacea	x	x	x	x	x	x	x
Fritillaria borealis	x	x	x	x	x	x	x
Oikopleura dioica	x	x	x	x	x	x	x
Salpa fusiformis	0	x	0	0	0	x	x
Fish eggs	x	x	x	x	x	0	0
Fish larvae	x	x	x	x	0	x	0
Cirriped larvae	x	x	x	x	x	x	x
Polychaet larvae	x	x	x	x	x	x	x
Bivalv larvae	x	x	x	x	x	x	x
Echinoderm larvae	x	x	x	x	x	x	x
Cyphonautes larvae	x	x	x	x	x	x	x
Decapod larvae	0	x	x	x	x	x	x
Ascidiacea eggs	x	0	0	0	0	0	0
Ascidiacea larvae	0	0	x	0	x	x	x
Total number of copepod species	14	13	14	15	16	17	17
Total number of holoplanktonic species	23	23	24	25	26	28	27

x = present

0 = absent

DIVERSITY

The diversity of the copepods and of the total holoplankton was calculated by three different formulae: Simpson's index $\lambda = 1 - \sum p_i^2$ (Simpson 1949), the Shannon Weaver index $\underline{H} = -\sum p_i \ln p_i$ (McArthur and McArthur 1961, Patten 1962), and Margalef's index $d = \frac{S - 1}{\ln N}$ (Margalef 1958). For Simpson's formula, the unbiased estimator $1 - \frac{\sum n (n - 1)}{N (N - 1)}$ was used, for the Shannon Weaver the approximation $- \sum (N_i/N \ln (N_i/N))$. All three holoplankton indexes have been calculated for all dates at all depths, a total of 350 samples. In Figs. 4-5 the

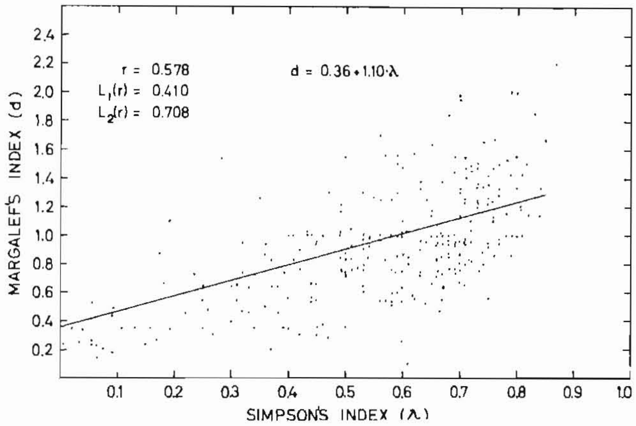

Fig. 4. Correlation between Simpson's index (λ) and Margalef's index (d). Correlation coefficient, 95% confidence limits, and regression line indicated.

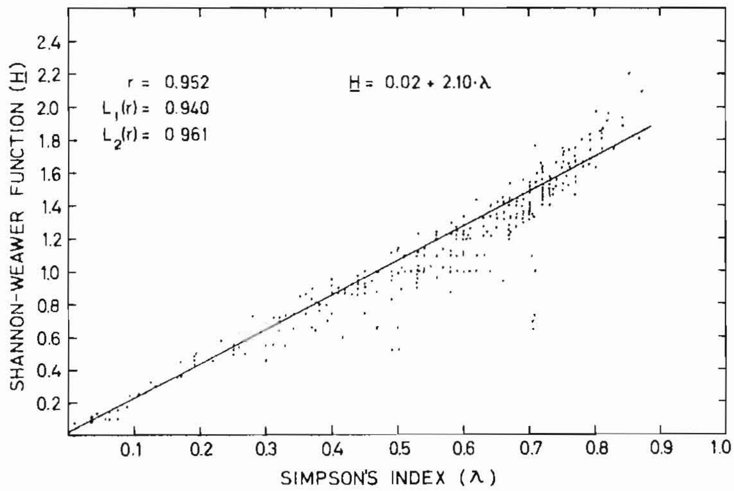

Fig. 5. Correlation between Simpson's index (λ) and the Shannon Weaver function ($\underline{H}$). Correlation coefficient, 95% confidence limits, and regression line indicated.

Simpson index is compared with the Margalef index and the Shannon Weaver index. A highly significant linear correlation between the Simpson and the Shannon Weaver indexes is very obvious ($r = 0.952$, $P < 10^{-6}$), while it is less significant between the Simpson and the Margalef indexes ($r = 0.578$, $P < 10^{-2}$). A similar linear correlation between Simpson's and Shannon Weaver's indexes was found also in a littoral community in the same area, but the slope of the regression line differed (Strömgren et al. 1973). The Shannon Weaver index is taken from information theory and indicates the amount of information per individual. Its application to biology is assumed to be of great interest (Margalef 1958). However, from a statistical point of view, the Shannon Weaver index is difficult to handle. Great mathematical problems are involved in its estimation, and tedious approximation methods have to be applied to calculate the standard error (Good 1953, Bowman et al. 1971). For Simpson's index these calculations are simple (Simpson 1949), and it may be calculated without bias for all sample sizes greater than unity. In this case, therefore, when it is evident that both the Shannon Weaver and the Simpson indexes yield the same information, the latter is to be preferred.

Many workers have discussed the possibility of using a smaller and more easily identified part, a systematic or an ecological unit, as an indicator of the diversity of the whole system (Margalef 1967, Sanders 1968, Lie 1968). In Fig. 6, Simpson's index of the holoplankton

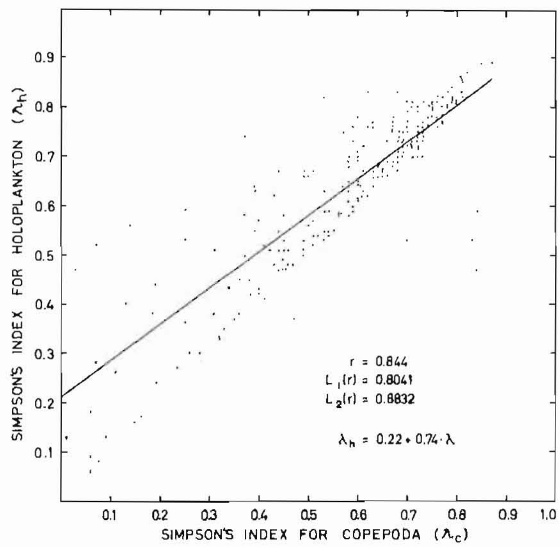

Fig. 6. Correlation between Simpson's index for copepods (λ_c) and that for holoplankton (λ_h). Correlation coefficient, 95% confidence limits, and regression line indicated.

is compared to a smaller systematic sub-unit, the copepods. The total number of data, 350 samples, have been included. There is a highly significant linear correlation between the two units ($r = 0.844$, $P < 10^{-6}$). This indicates that the copepods alone provide a sufficient description, in term of diversity, for the entire holoplanktonic community. The deviation from linearity is greatest when the index value is small. Below λ_c is used.

The average value of the Simpson index and the 95% confidence limits for each depth during the whole sampling period is shown in Fig. 7.

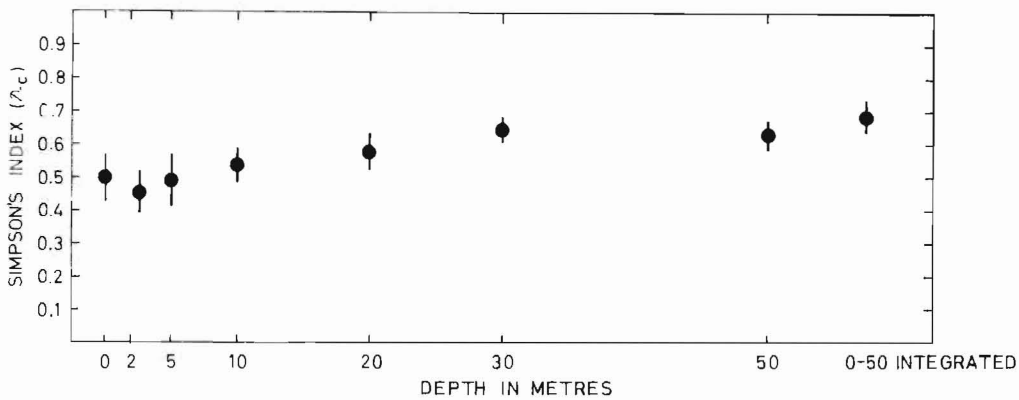

Fig. 7. Average Simpson's index value at the sampling depths. 95% confidence limits indicated.

The lowest average index value was found at 2 m of depth and this value differs significantly from the 20 m index value at the 0.02 level (two-tailed t-test), from the values for the 30 and 50 m samples at the 0.01 level. This trend may indicate that the upper 10 m to some extent have a community different from that in the layer below. The number of species is smaller in the upper 10 m, and the species composition is generally more homogenous. The deepest samples may represent a layer of interchange between surface and deep water. Margalef (1958) states that zones of mixing yield higher diversity indexes for the phytoplankton.

The average values of the Simpson index for each month for the 2 and 50 m samples are shown in Fig. 8, with the 95% confidence limits indicated. For the 2 m samples, June showed a significantly higher value than all other months ($P < 0.001$). For the 50 m samples, March was significantly different from April, May, and June ($P < 0.001$).

The difference between the 2 and 50 m samples was significantly only in March ($P < 0.001$) and in September ($P < 0.001$).

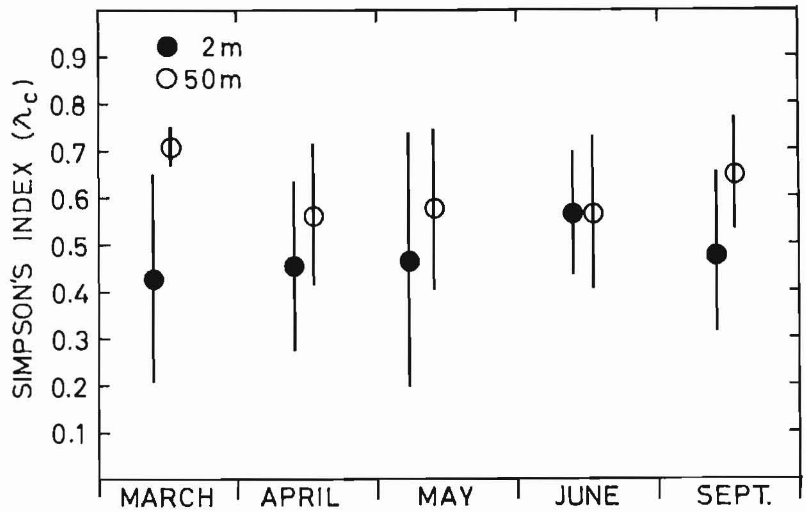

Fig. 8. Seasonal variation in Simpson's index at 2 and 50 m, given as the average for the same months during the whole period, with 95% confidence limits indicated.

A more detailed impression of the variation in time of Simpson's index for the 2 and 50 m samples is given in Fig. 9. The 2 m samples showed considerable variation over short periods, as well as large annual differences, while the 50 m samples have higher values and a greater stability. This pattern indicates a less diverse holoplanktonic community, influenced by rapid environmental changes, at 2 m than at 50 m. The variation in diversity showed no significant relationship to temperature or salinity, or to gradients of these factors.

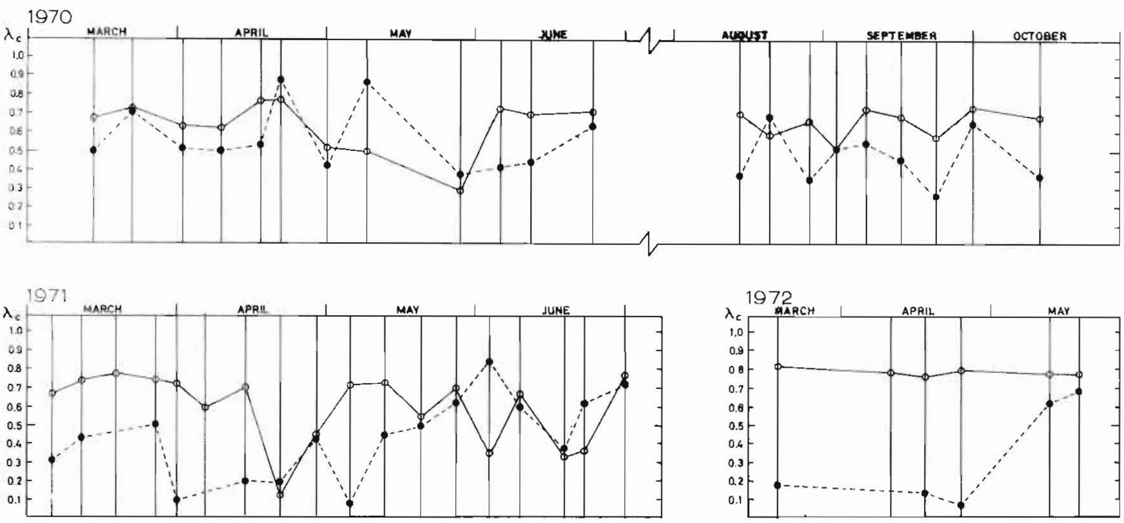

Fig. 9. Variation of Simpson's index at 2 m (dotted line) and 50 m (solid line).

VERTICAL DISTRIBUTION AND NUMERICAL VARIATION

Calanus finmarchicus Gunnerus

In Trondheimsfjorden the nauplii and copepodite stages III-I of *C. finmarchicus* normally keep to the upper 50 m, while older stages tend to stay below 100 m, except during spring (Strömgren 1973 a, b).

During March and the beginning of April, before the main spring spawning, relatively few nauplii and copepodite stages of *C. finmarchicus* occurred (Figs. 10-13), with a scattered vertical distribution.

The main spawning in April produced very large numbers of nauplii, especially in 1971 and 1972. The number of nauplii seems to be correlated with the number of females (Table 6). In 1972 spawning started slightly earlier than in the other years, and the main spawning appeared to be spread over a longer period.

Both in 1970 and 1971 the nauplii showed a scattered vertical distribution, particularly during maximum abundance, while in 1972 nearly the whole stock was recorded in the 2 m and 5 m samples.

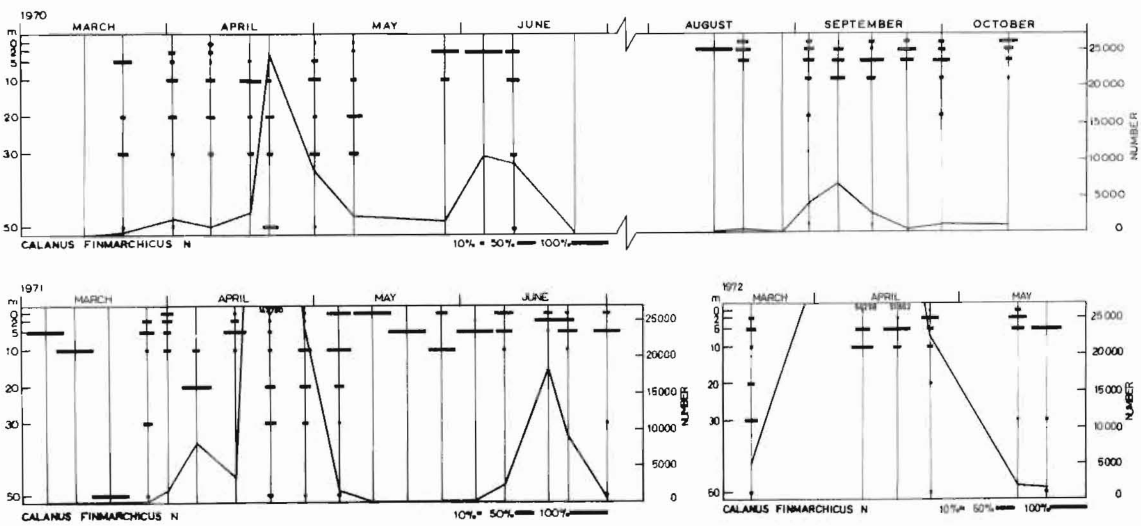

Fig. 10. *Calanus finmarchicus*, nauplii, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

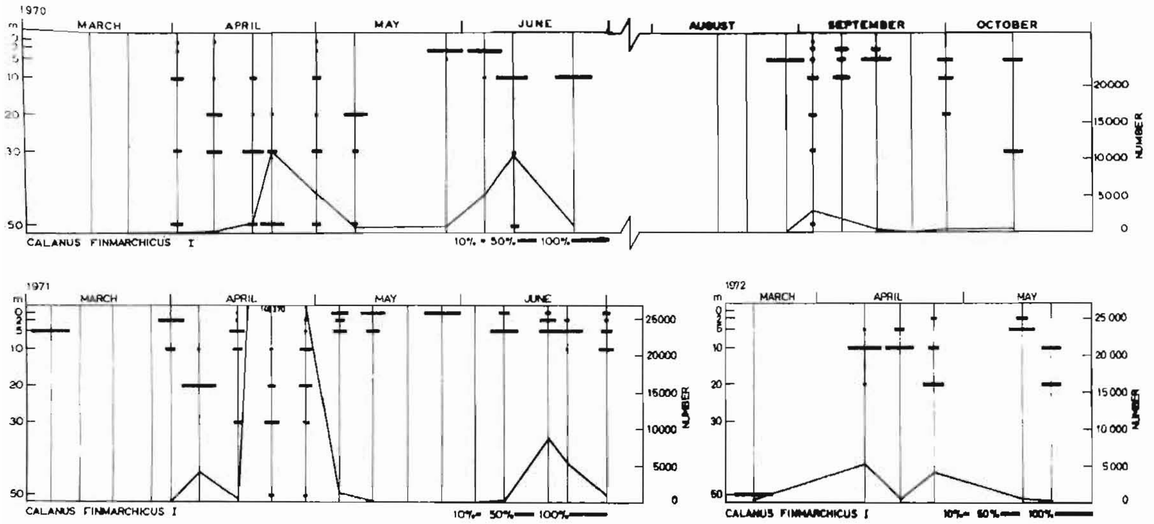

Fig. 11. *Calanus finmarchicus*, copepodite stage I, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

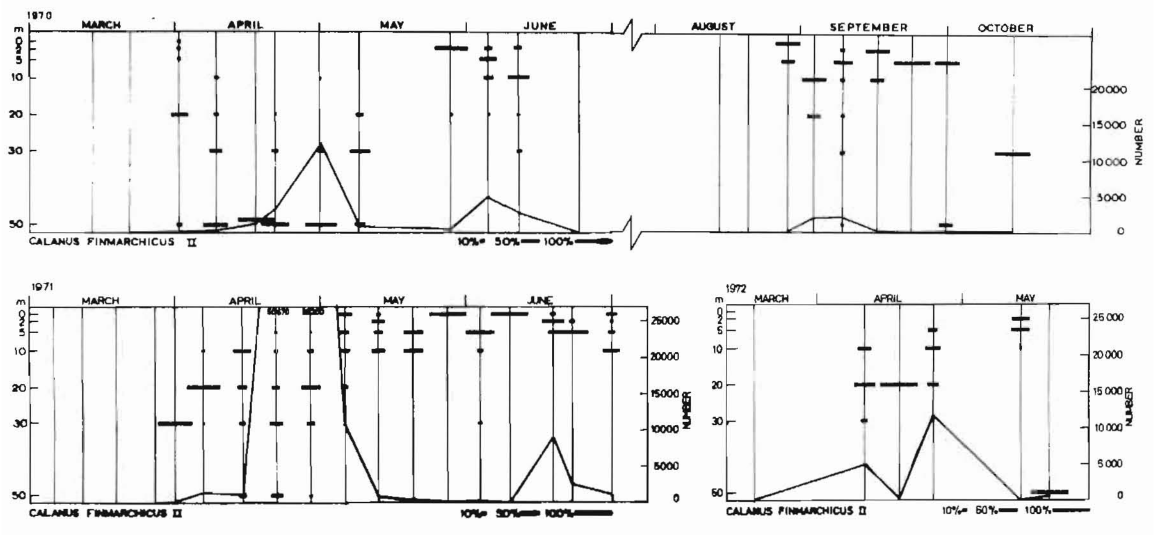

Fig. 12. *Calanus finmarchicus*, copepodite stage II, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

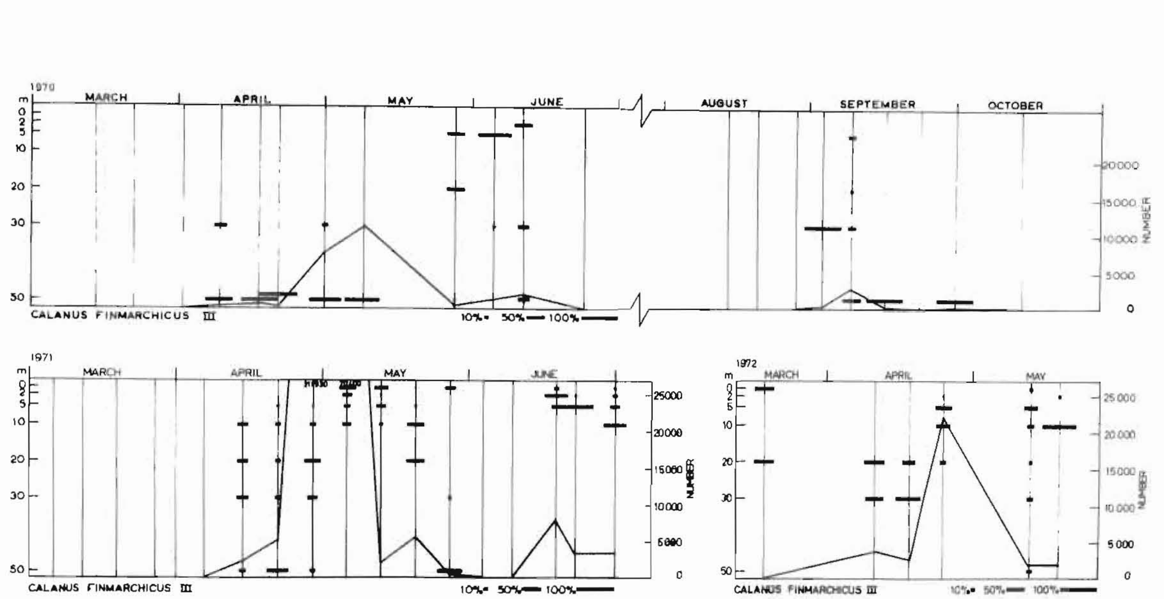

Fig. 13. *Calanus finmarchicus*, copepodite stage III, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

In 1970, the nauplii developed into a moderate stock of copepodite stages III-I, while in 1971 the rich spawning was followed by large numbers of all copepodite stages. In 1972, however, there was a significant decrease in numbers from nauplii to copepodite stages III-I, and minima of these stages occurred in the middle of April. This may indicate that the nauplii, which were produced earlier in April, did not develop further at this locality. The later April brood, however, had some success, and copepodite stages V-IV were quite numerous in the beginning of May (Table 6).

Both the vertical distribution and the trend of development indicate that special conditions prevailed in 1972. The anomalous development during April 1972 may be related to the restricted vertical distribution of the nauplii that year, as compared to 1970 and 1971.

In May rather small numbers of nauplii and young copepodite stages of *C. finmarchicus* were recorded. Copepodite stages V-IV, however, showed maxima in the beginning of the month.

A second main spawning appeared to take place in June in 1970 and 1971 followed by maxima of copepodite stages III-I. The June maxima were significantly smaller than the spring maxima, and nearly all specimens were recorded in the upper 5-10 m in both years. The April and

Table 6. *Calanus finmarchicus*, males, females, and copepodite stages V-IV, calculated number below 1 m^2 in 0-50 m.

Date			V	IV
12.03.70	0	400	0	200
20.03.70	0	0	0	0
01.04.70	0	400	0	0
09.04.70	0	0	0	0
17.04.70	0	0	0	0
21.04.70	0	0	0	0
30.04.70	0	0	0	14000
08.05.70	0	0	0	3000
27.05.70	0	200	2400	2000
04.06.70	0	0	0	8500
11.06.70	0	0	0	5000
23.06.70	0	1500	1000	1400
14.08.70	0	0	2400	0
20.08.70	0	0	3500	0
28.08.70	0	0	300	0
03.09.70	0	0	0	3000
09.09.70	0	2000	0	10000
16.09.70	0	0	0	2000
23.09.70	0	0	0	0
30.09.70	0	0	0	2000
14.10.70	0	0	0	0
05.03.71	360	21840	9790	80
11.03.71	1800	12980	6800	500
18.03.71	460	3880	2200	450
26.03.71	0	1330	0	400
31.03.71	1100	4500	300	0
06.04.71	0	1800	0	0
14.04.71	0	1700	1200	4100
21.04.71	0	0	0	0
28.04.71	0	0	59500	777900
05.05.71	7500	3200	156000	995800
12.05.71	1200	200	112800	141900
19.05.71	800	1600	140700	196750
26.05.71	500	13420	171560	56300
03.06.71	200	1900	9300	1400
09.06.71	4150	22000	33650	2450
18.06.71	600	14000	26000	24400
22.06.71	2300	6600	13700	40900
30.06.71	0	2000	27600	36400
17.03.72	0	0	800	400
10.04.72	400	3400	4200	16400
17.04.72	0	0	11000	24000
24.04.72	0	3000	36140	193680
12.05.72	750	300	48200	72350
18.05.72	0	9500	300520	24540

June maxima thus seem to differ both in size and vertical distribution. This change in vertical distribution seems to take place early in May, and may be related to hydrography. On the other hand, Marshall et al. (1934) have shown that different generations of *C. finmarchicus* may have different vertical distributions, and even different populations may behave in the same way (Russell 1934).

During the period April-June, very few specimens were taken in the 0 m samples in 1970 and 1972, while in 1971 all stages were frequent in the surface layer during the same period, especially copepodite stages III and IV in the first week of May.

Small numbers occurred in autumn 1970, with a small peak at the beginning of September. Normally, the bulk of the younger stages remained in the upper 10 m, but during this peak they were found significantly deeper than they were on the preceding and subsequent sampling.

The spring spawning seems to have started simultaneously in 1970 and 1971, with maximum of nauplii the 20th and 21st of April, with a successively delay until maximum of copepodite stage III in the first week of May. During spring, this development thus requires approximately two weeks. The June spawning occurred significantly earlier in 1970 than in 1971, but in both cases, the development into copepodite stage III needed significantly shorter time than during spring. The more rapid development in June is obviously due to increased temperature.

Normally the greatest maxima of *C. finmarchicus* coincided with low temperature and high salinity, but significant numbers also occurred during more extreme conditions. In June 1970 a moderate stock of nauplii and copepodite stages III-I were found in water with a salinity of 21.58 - 21.64 $^{o}/oo$, but when the salinity fell below 20 $^{o}/oo$ very few, if any, young *C. finmarchicus* occurred. In late May 1971, females and copepodite stages V-IV were taken in significant numbers at a salinity of 23.85 $^{o}/oo$. Males, however, were not observed at salinities below 31.50 $^{o}/oo$. Young stages were frequent at temperatures above 14^{o}C.

Paracalanus parvus (Claus)

The allochthonous copepod *P. parvus* was found in the pump samples in September 1970, when a significant maximum occurred in the beginning of the month (Fig. 14). Smaller numbers were found throughout the autumn and a slight increase was indicated in the middle of October.

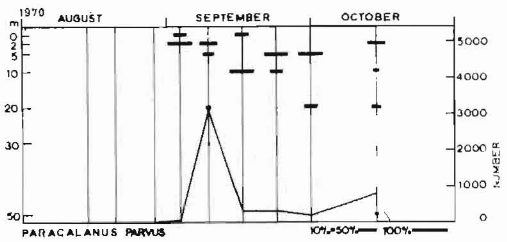

Fig. 14. *Paracalanus parvus*, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

The bulk of individuals occurred in the upper 5 m. A single specimen was found in the 2 m sample on the 9th of June 1971.

Pseudocalanus elongatus Boeck

In Trondheimsfjorden small spring stocks of *P. elongatus* normally occur both above and below 100 m, while in summer and autumn large maxima are found mainly above 100 m depth, probably in the upper 50 m (Strömgren 1973 a, b).

The spring stock of *P. elongatus*, copepodite stages III-I and V-IV, was rather small in all years, especially in 1972 (Figs. 15-16). A significant summer stock was recorded only in 1970, with a maximum in the first week of June. During this maximum, copepodite stages III-I were recorded only in the 10 and 5 m samples, while the older copepodite stages were distributed at deeper levels.

As for *C. finmarchicus*, the vertical distribution was generally shallower from the beginning of May onwards. This trend was most pronounced in 1971.

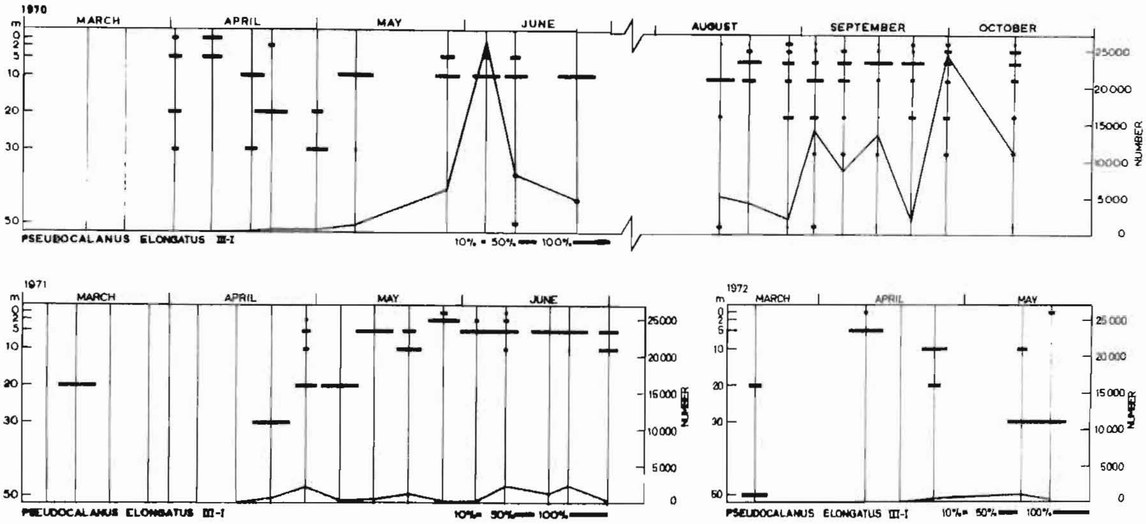

Fig. 15. *Pseudocalanus elongatus*, copepodite stages III-I, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

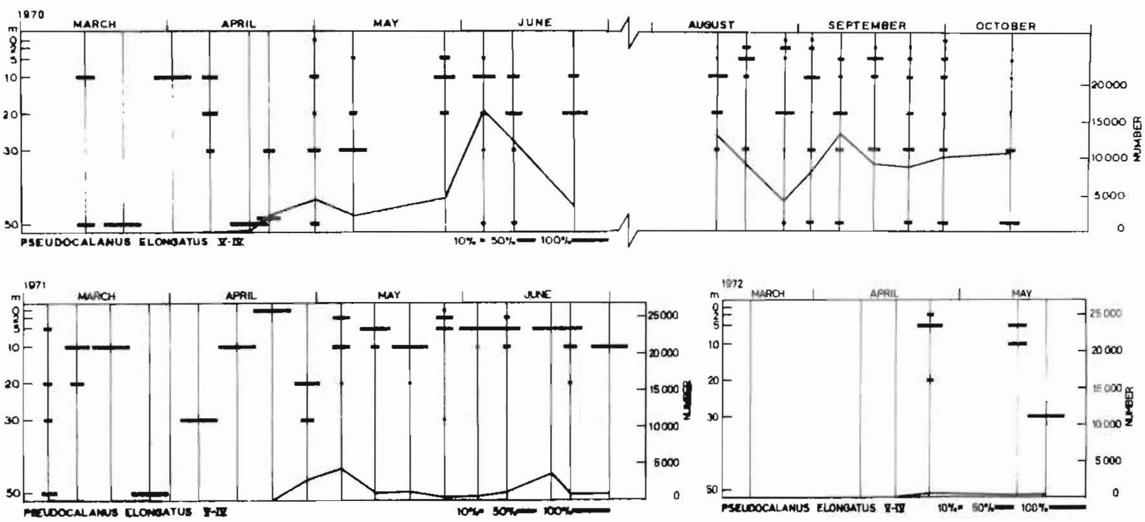

Fig. 16. *Pseudocalanus elongatus*, copepodite stages V-IV, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

In autumn 1970, relatively large numbers of copepodites were present, with a more scattered vertical distribution than in spring, although the bulk of them were normally found in the 5 and 10 m samples. A pronounced minimum at the end of September 1970 was followed by a large maximum at the September-October transition.

Adults were scarce until May. More females occurred in May-June 1971 than during the same period in 1970, and while the 1970 females were taken exclusively at the 20 m level and below, they were found higher up in 1971. This trend parallels that found for *C. finmarchicus*. In summer and autumn 1970 both females and males were more abundant, with the bulk of them distributed below 10-20 m depth (Fig. 17).

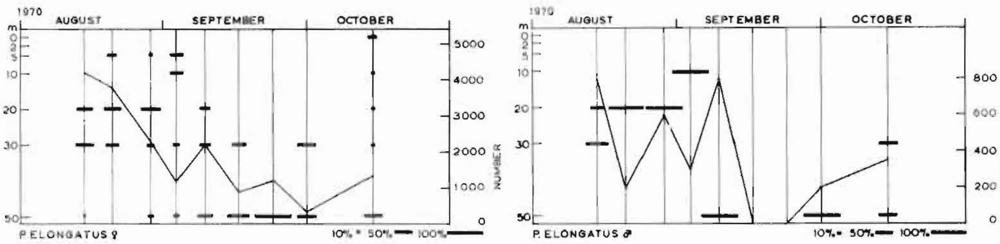

Fig. 17. *Pseudocalanus elongatus*, males and females, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

In 1970 a change in size distribution of females is indicated from the end of June to the middle of August (Fig. 18). The smaller females in August may represent a summer generation.

At all seasons there was a general tendency for the younger stages to keep nearer to the surface, although very few specimens were recorded in the 0 m samples in May and June. The largest numbers were generally found in the 5 and 10 m samples, and *P. elongatus* seems to keep below the discontinuity layer. This accords with observations from the Baltic (Ackefors 1969) and from Oslofjorden (Hansen 1951).

Normally the adults and copepodite stages V-IV kept to salinities above 31 $^{o}/oo$, but during May-June 1971, relatively many males, females and copepodite stages V-IV were taken at salinities of 29.15 $^{o}/oo$, 28.50 $^{o}/oo$, and 19.15 $^{o}/oo$, respectively. Copepodite stages

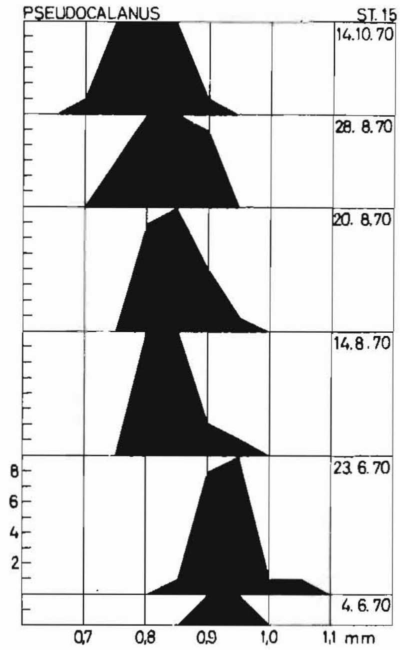

Fig. 18. Size distribution of female *Pseudocalanus elongatus* during June-October 1970.

III-I were encountered at a salinity close to 19.90 ^{o}/oo. During May-June only stray specimens were taken at temperatures above 10^{o}C, but the autumn generation of copepodite stages III-I was very abundant in 1970 at a temperature of 13.49^{o}C.

Microcalanus pusillus G. O. Sars

Very few copepodite stages III-I of *M. pusillus* were recorded, due to the mesh size used, but the older stages were satisfactorily retained by the net.

Both copepodite stages V-IV and females were scarce during March-April 1970, while they were slightly more numerous during the same period in 1971, and in 1972 a small maximum was recorded in the middle of April (Figs. 19-20). Large numbers were recorded at the end of May and the end of June in all years. Prominent minima occurred on the 4th of June 1970, the 3rd and 30th of January 1971, and on the 24th of April 1970. As a rule, *M. pusillus* was found in the samples from 20 m and deeper, and very often the largest numbers occurred in the deepest samples. *M. pusillus*, however, has its main distribution below 50 m depth (Strömgren 1973 a), and those taken by the pump are obviously

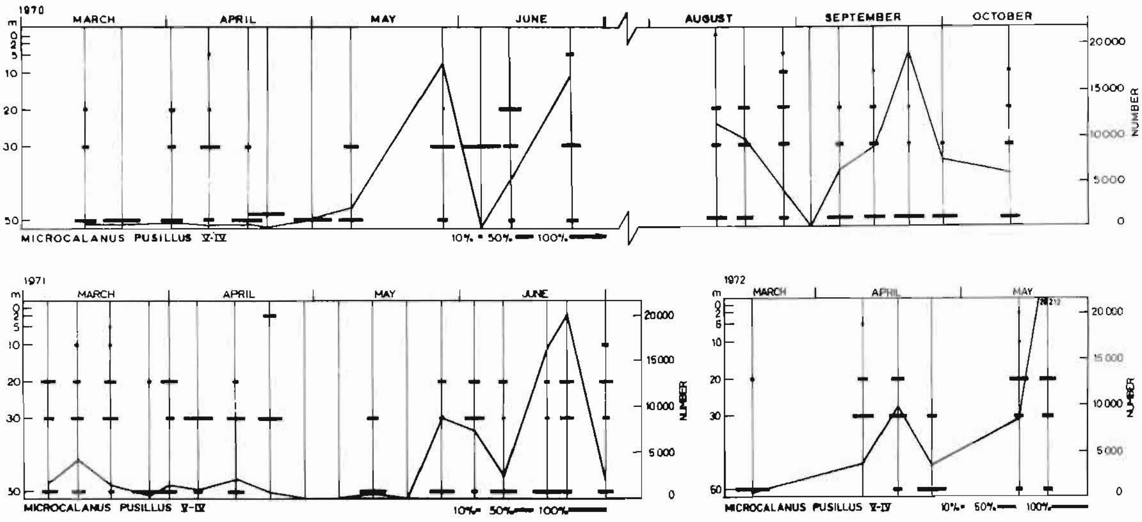

Fig. 19. *Microcalanus pusillus*, females, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

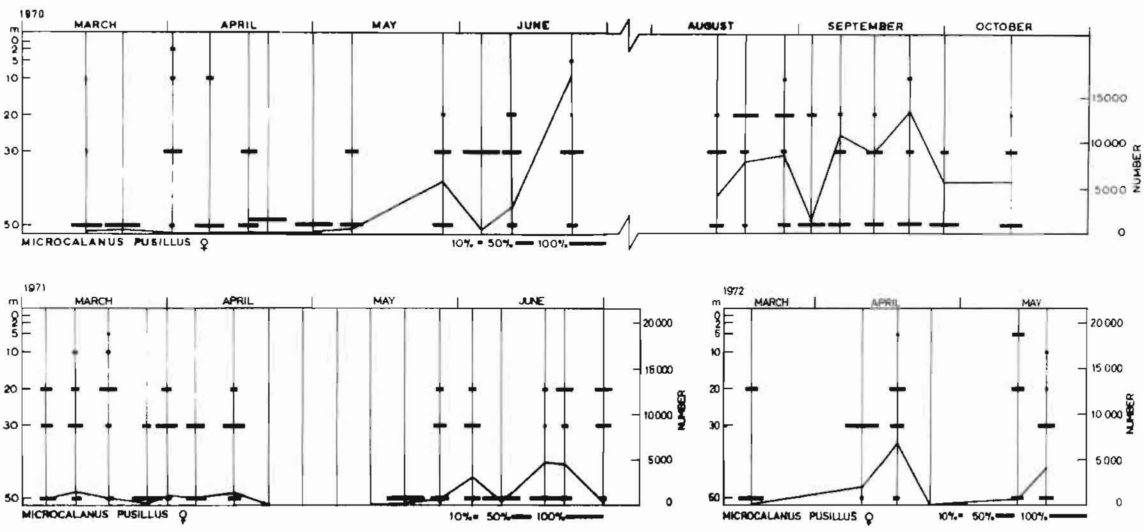

Fig. 20. *Microcalanus pusillus*, copepodite stages V-IV, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

invaders from the layer below. On several occasions, they have been indicators of upwelling or other hydrographic events bringing deep water nearer to the surface. This may explain the fact that the finds of *M. pusillus* seemed to vary inversely to those of the young stages of *C. finmarchicus* and of other species or stages which normally live in the surface layer.

Females generally tended to remain deeper than the copepodite stages. Males were very scarce and probably have a deeper distribution than other stages (Strömgren 1973 a).

Females and copepodite stages V-IV of *M. pusillus* were normally found at salinities above 32 °/oo.

Temora longicornis Müller

In Trondheimsfjorden *T. longicornis* keeps to the upper 50 m (Strömgren 1973 a, b).

Large numbers of copepodite stages of *T. longicornis* occurred in June and August 1970, and significant numbers were present from the beginning of May that year (Figs. 21-24). The adult stages were also numerous in June, and were also recorded in significant numbers from mid-April. In 1971 and 1972, however, very few *T. longicornis* occurred at all.

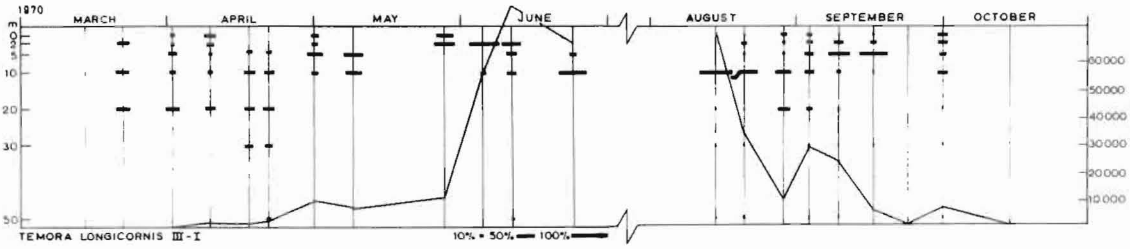

Fig. 21. *Temora longicornis*, copepodite stages III-I, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

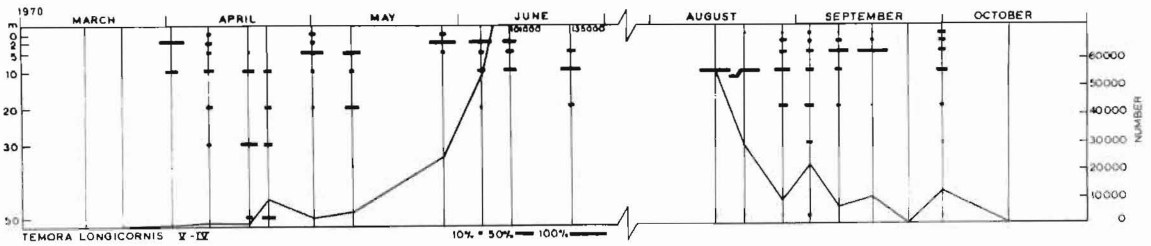

Fig. 22. *Temora longicornis*, copepodite stages V-IV, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

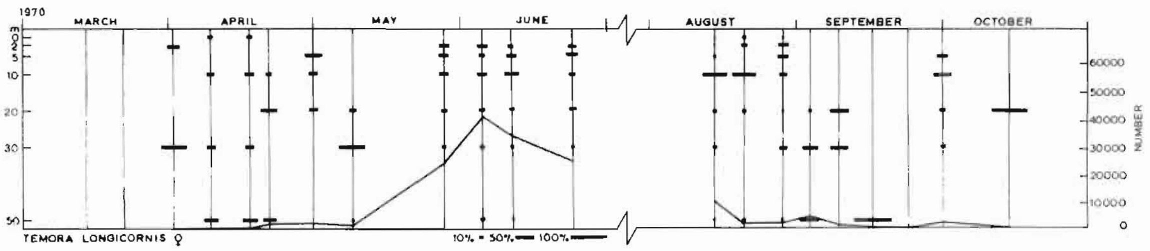

Fig. 23. *Temora longicornis*, females, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

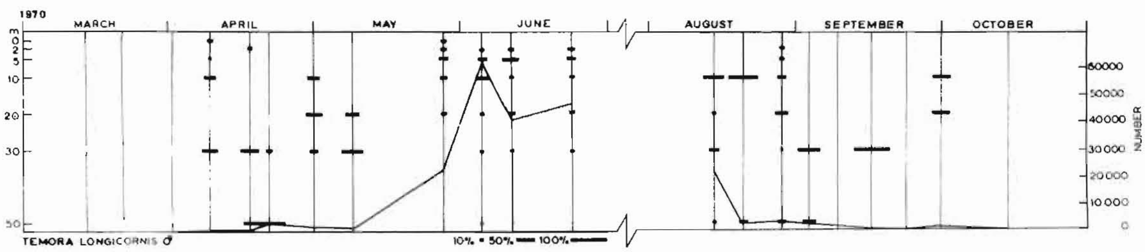

Fig. 24. *Temora longicornis*, males, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

All copepodite stages showed a distinctly higher vertical distribution from the beginning of May in all years, independent of the stock size, and with maximal abundance in the 2-10 m samples. The adults showed a similar change in vertical position from the beginning of May, although generally a deeper distribution was indicated. In the middle of April 1970 an unexpectedly deep distribution of all stages was observed.

At the end of May 1970 all stages occurred in the surface samples. During the large maximum in June the same year, however, few copepodites occurred in the 0 m samples, and at the end of this month the 2 m samples, too, were poor in *T. longicornis*. A simultaneous reduction in size may indicate the presence of a new generation of smaller females. A tendency to keep away from the surface layers seems to coincide with low surface salinities.

The rich stock of adults and copepodite stages V-IV found during May-June 1970 can scarcely be related to the very small spring stock. It may be assumed that a fresh supply of a stock of mature or premature stages has given rise to the prominent maximum of the younger stages found throughout June. The increase in size of females from the 8th to the 27th of May (Fig. 25) also indicates that a new population has been introduced.

During August-October 1970 the bulk of all copepodite stages were taken in the upper 10 m, especially in the 10 and 5 m samples. The large numbers found on the first sampling date in August indicate the presence of a large summer stock. On the 23rd of September *T. longicornis* was absent in all samples, and the small females which were found at the end of that month may indicate the presence of a new population.

The vertical distribution in June 1970, with large concentrations in the upper 10 m, may be related to the prevailing high temperatures or to the steep temperature and salinity gradients in the layer immediately below. Both in Oslofjorden (Hansen 1951) and in the Baltic (Ackefors 1969), *T. longicornis* was shown to thrive near or at the thermocline.

All stages of *T. longicornis* were found at the surface on the 27th of May 1970, but on the 4th and the 11th of June they were absent from this layer. On the 23rd of June all copepodite stages were found at 5 m or below, while the adults still occupied the 2 m layer. This distribution was evidently not determined by temperature or salinity. A tolerance of a salinity as low as 15.21 $^{o}/oo$ was demonstrated

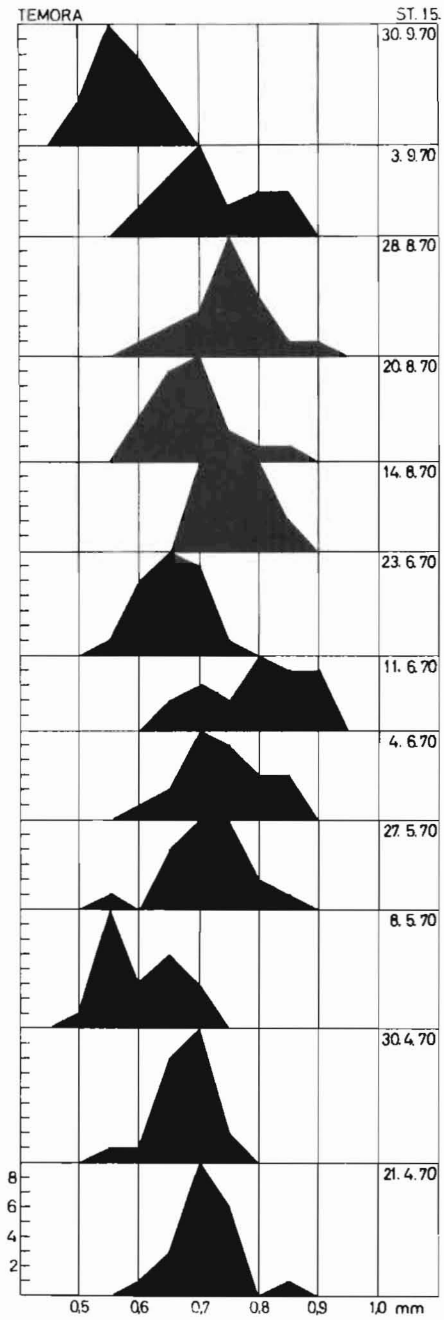

Fig. 25. Size distribution of female *Temora longicornis* during April-September 1970.

on the 27th of May 1970 for all stages, while on the 11 th and 23rd of June the surface salinities were significantly higher. Their absence from the surface in June may have been due to dispersion by surface currents.

Metridia longa (Lubbock)

Both *M. longa* and *M. lucens* Boeck may sometimes occur in the fjord, the latter as immigrants during autumn (Strömgren 1973 a). No specimens of *M. lucens* were identified in the pump samples during 1970-1972. Nauplii and copepodite stages of *Metridia* occurred only during the period March-May, and undoubtedly belonged to *M. longa*.

Maxima of nauplii and copepodite stage I (Fig. 26) were found at the transition April/May in 1970, but a small peak was also found at the beginning of April. Copepodite stage II showed a similar occurrence but was less abundant. Both nauplii and copepodite stage I seemed to have an irregular depth distribution during the middle of April, paralleling that of *C. finmarchicus* and other species. In 1971 and 1972 very few *M. longa* were observed.

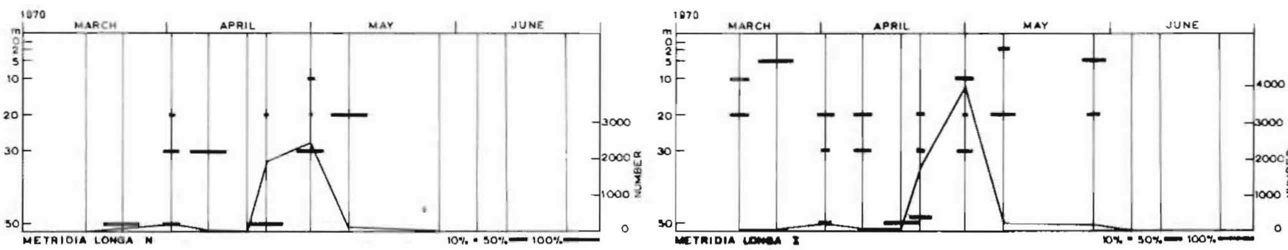

Fig. 26. *Metridia longa*, nauplii and copepodite stage I, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

Older copepodite stages occurred singly and a few adults were also recorded in the deepest samples in June 1971. During 1963-1966 all stages of *M. longa* were normally absent from the upper layers (Strömgren 1973 a), and the pump samples hardly provide a true picture of the variation of the stock.

Centropages hamatus Lilljeborg

In 1970 all copepodite stages of *C. hamatus* showed a similar numerical variation, with peaks in the middle of April, at the end of May, in June, in September, and at the September/October transition (Figs. 27-28). In 1971 and 1972 only a few *C. hamatus* were recorded, in the upper 5 m exclusively.

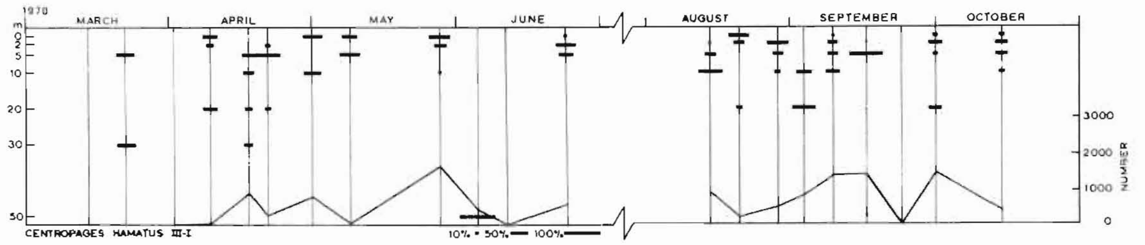

Fig. 27. *Centropages hamatus*, copepodite stages III-I, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

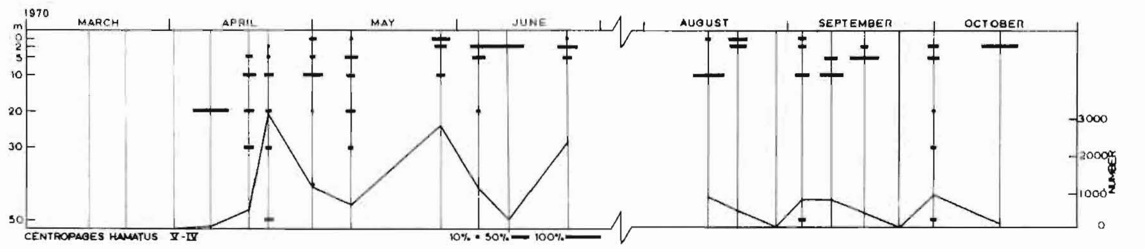

Fig. 28. *Centropages hamatus*, copepodite stages V-IV, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

All copepodite stages were normally found in the upper 20 m, with maximal concentrations in the upper 10 m. In June 1970 a maximum occurred at 5 m depth. A slightly deeper distribution was found in the middle of April 1970.

Females were rather scarce, while males occurred in significant numbers during April-June 1970 (Fig. 29).

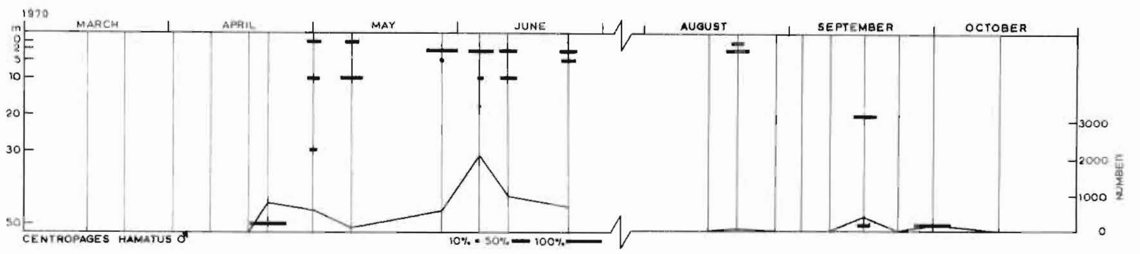

Fig. 29. *Centropages hamatus*, males, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

Except in the middle of April 1970, the adults kept nearer to the surface than the copepodites. A similar distribution of adults was also recorded in Oslofjorden by Hansen (1951).

The bulk of the *C. hamatus* population tended to stay in or above the discontinuity layer, and in Trondheimsfjorden all stages were found regularly at the surface. Hansen (1951) listed *C. hamatus* as a species which mainly occurred in the warm surface water. Significant numbers occurred at a salinity of 15.21 ^{o}/oo at the end of May 1970, while no specimens occurred at a salinity of 12.67 ^{o}/oo at the beginning of June the same year.

Acartia clausi Giesbrecht and Acartia longiremis Lilljeborg

Both *A. clausi* and *A. longiremis* occur in the fjord proper (Strömgren 1973 a). The youngest stages of these species are difficult to separate. Adults of *A. clausi* suddenly appeared on the 9th of September 1970, but two weeks later no specimens remained. A second occurrence was observed on the 14th of October the same year. In both these cases *A. clausi* occurred together with *P. parvus* and indicated an influx of warm water. In 1971 and 1972 no *A. clausi* were recorded, except for a single male in May 1972.

A. longiremis occurred at all seasons in all 3 years, and nearly all the copepodite stages III-I belong undoubtedly to this species.

Small peaks of *Acartia* spp. (Fig. 30) and *A. longiremis* (Figs. 31-33) were recorded in the middle of April 1970. In June 1970 a very pronounced maximum of all stages occurred and because the large number of adults and copepodite stages can scarcely have been derived from such a small **local** stock, a supply from other areas is indicated.

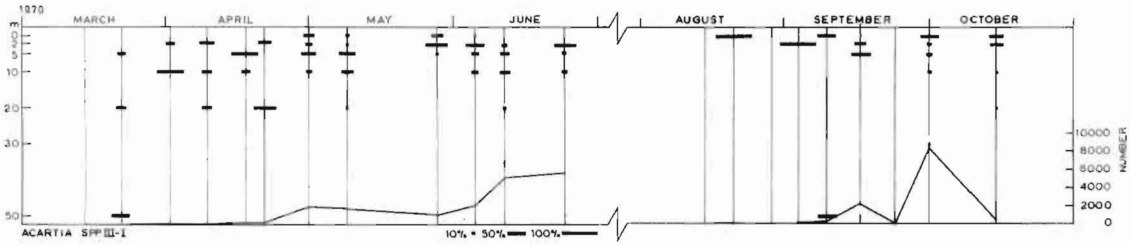

Fig. 30. *Acartia* spp., copepodite stages III-I, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

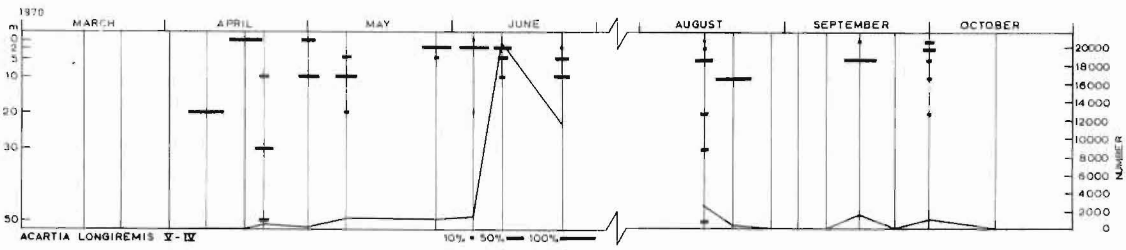

Fig. 31. *Acartia longiremis*, copepodite stages V-IV, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

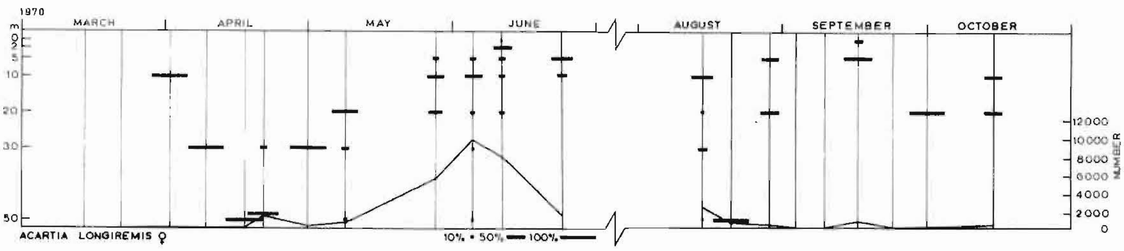

Fig. 32. *Acartia longiremis*, females, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

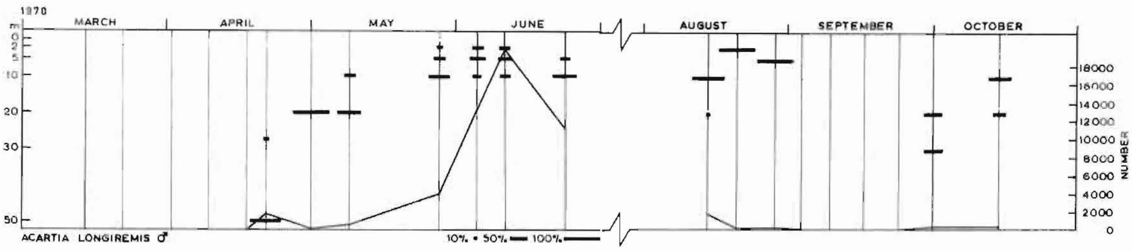

Fig. 33. *Acartia longiremis*, males, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

Small numbers occurred in the middle of September 1970 and a peak of copepodite stages III-I was found at the transition September/October. On the 3rd, 9th, and 23rd of September 1970, all stages of *Acartia* were virtually absent. In 1971 and 1972 all stages occurred, but in very small numbers.

The highest concentration was observed in the upper 20 m, but the older the stage, the more scattered the distribution. Significant numbers of young copepodites were found at the surface, but the bulk of *Acartia* tended to stay near the discontinuity layer. During 1971 and 1972 nearly all specimens were taken in the 0-5 m samples. A deeper vertical distribution than normal was found in the middle of April 1970. In Nordåsvannet, Wiborg (1944) found that *A. longiremis* kept mainly within the upper 15 m.

Copepodite stages V-IV and adults of *A. longiremis* seemed to prefer water with a salinity above 21 $^{o}/oo$, while copepodite stages III-I of *Acartia* spp. were found at significantly lower salinities (15.21 and 12.67 $^{o}/oo$) in 1970.

A scarcity of *A. longiremis* in 1971 and 1972 coincided with large numbers of *C. finmarchicus*. A similar inverse relation between these two species is recorded earlier in Trondheimsfjorden (Strömgren 1973 a, b).

Oithona similis Claus

In Trondheimsfjorden *O. similis* was found mainly in the upper 100 m during May-September, while during the rest of the year a significant part of the stock was recorded below 100 m as well (Strömgren 1973 a, b).

O. similis occurred in almost all pump samples (Fig. 34). During March-April the stock was small in all years, except for a peak at the end of April 1971. During March, 1970 and 1971, *O. similis* was rather evenly distributed at all depths, whereas in April the 0-5 m samples contained only small numbers and maximum abundance was found in the 10-30 m samples.

At the end of May 1970 a very large maximum occurred, with nearly all the specimens (180,000 ind./m^3) concentrated in the 10 m sample. In general a higher vertical distribution was recorded in May and this situation prevailed also for the large stocks found in June 1970 and 1971, with the bulk in the 10 and 5 m samples. Very few specimens were taken in the 0 m samples. *O. similis* tended to keep below the discontinuity layer during the March-June period.

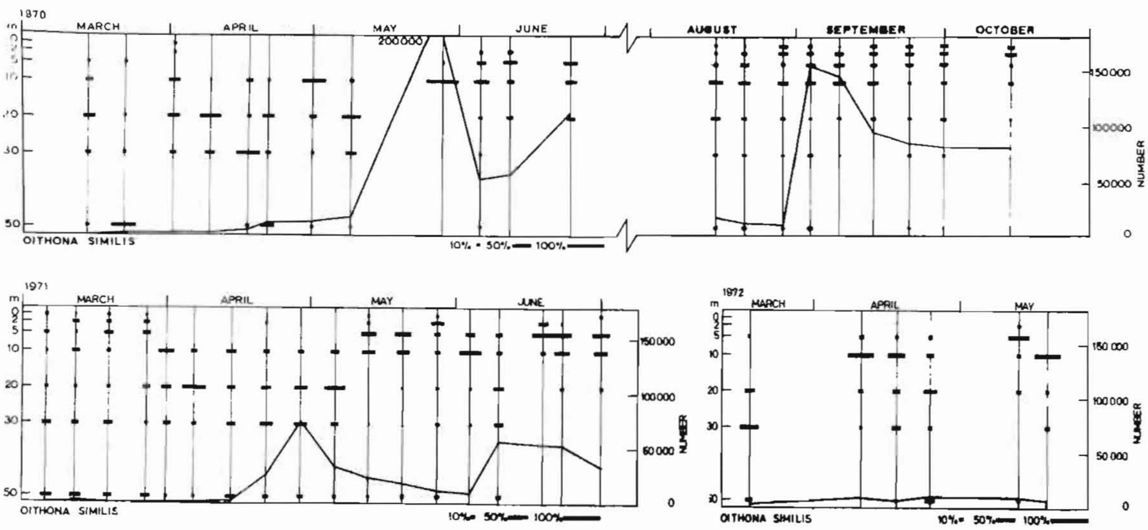

Fig. 34. *Oithona similis*, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

In autumn a large stock was found mainly in the upper 10 m and significant numbers were recorded in the 0 m samples.

Practically no specimens were recorded at a salinity of 15.21 ^{o}/oo, or less, and large stocks were normally found at significantly higher salinities. In the Baltic, *O. similis* is reported at salinities below 10 ^{o}/oo, although it seems to require 12-13 ^{o}/oo for spawning (Ackefors 1969). Mankowski & Ciszewski (1962) found that in the Baltic, *O. similis* was the only copepod whose distribution was at all closely correlated with salinity.

Oncaea borealis G. O. Sars

In Trondheimsfjorden the main stock of *O. borealis* keeps below 100 m, but indications of upward migration have been found during March-May and at shallow localities very large stocks may occur in the 0-30 m layer (Strömgren 1973 a, b).

O. borealis did not occur in significant numbers in the pump samples until the end of April (Fig. 35). Prominent maxima were found at the end of May 1970 and at the end of April 1971, while in 1972 no maximum was recorded. This trend shows a striking similarity to that for *O. similis*. In autumn 1970, however, the stock was small.

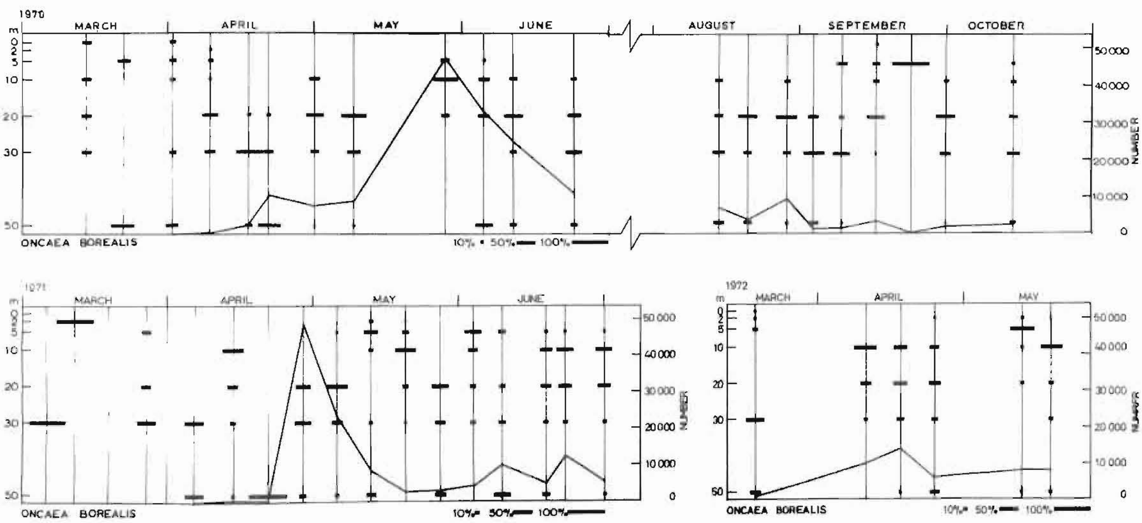

Fig. 35. *Oncaea borealis*, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

O. borealis showed a scattered vertical distribution during the whole observation period and no significant change in the vertical position was observed during May. The 0 and 2 m samples were generally poor in *O. borealis*, and this species was usually abundant only in water with salinity above 28-30 ^{o}/oo.

A few males of *O. borealis* were caught during spring in 1970 and 1972.

Microsetella norvegica Boeck

M. norvegica (Fig. 36) proved to be a variable species, showing rapid changes in abundance, especially during the autumn of 1970. During March-April in all years, the bulk of the population was found in the 20 and 30 m samples. In May and June, however, the 10 m samples, below the discontinuity layer, were generally richest. In the 0, 2, and 5 m samples, only a few specimens occurred during the March-June period. The largest numbers of *M. norvegica* were found in autumn 1970.

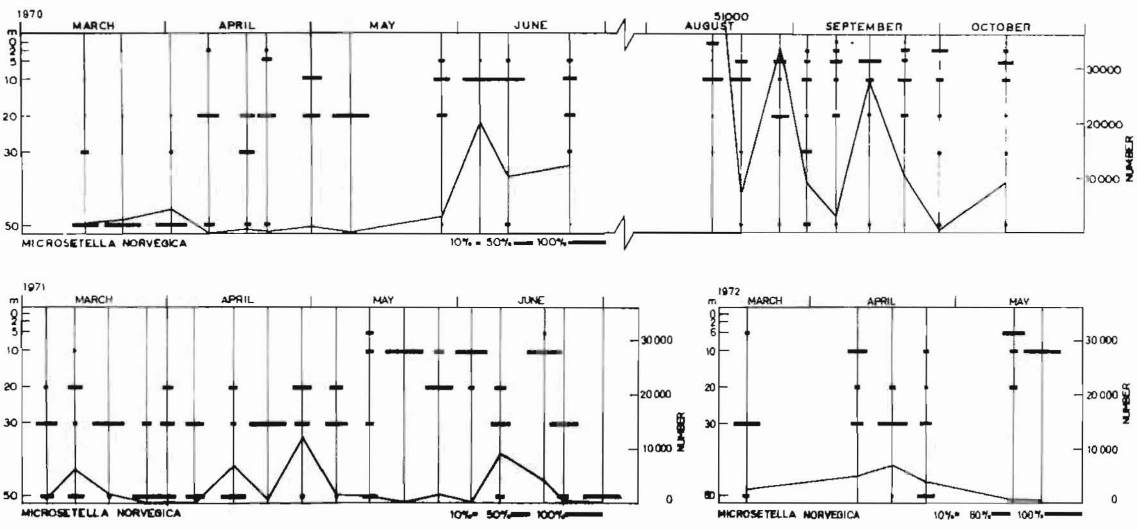

Fig. 36. *Microsetella norvegica*, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

Females of *M. norvegica* with eggs were frequent at all seasons, with a peak of abundance in August 1970. Nearly all specimens of *M. norvegica* were taken at salinities above 30 °/oo.

Limacina retroversa Fleming

L. retroversa is an inhabitant of the surface layers in Trondheimsfjorden and practically the whole stock can be expected to be encountered within the upper 50 m (Strömgren 1973 a, b).

The largest stocks of *L. retroversa* were recorded during June and August 1970 (Fig. 37), seemingly coincident with a high sea temperature. In 1971 *L. retroversa* was less abundant and was very scarce during April-May 1972.

In May nearly the whole stock was found in the upper 10 m, while during August-October a slightly deeper distribution was indicated, probably related to temperature conditions.

L. retroversa was recorded at a salinity of 15.21 °/oo at the end of May 1970, but was absent from water with a salinity of 12.67 °/oo at the beginning of June the same year, although it was very abundant in the layers immediately below.

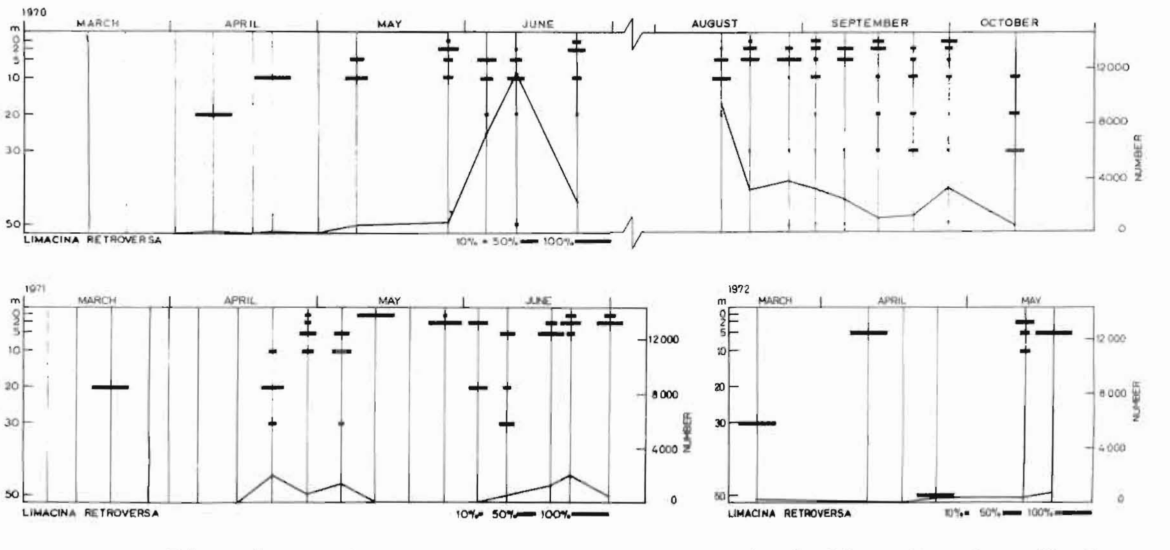

Fig. 37. *Limacina retroversa*, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

Evadne nordmanni Lovén

Maxima of *E. nordmanni* were recorded in the middle of June and in August 1970 (Fig. 38). Smaller numbers occurred during 1971 and in 1972 the stock was very small. *E. nordmanni* thus showed a numerical variation very similar to that of *L. retroversa*, with maxima correlated with high sea temperatures. The bulk of the stock was normally found in the upper 5 m at all seasons. In Oslofjorden Hansen (1951) found that *E. nordmanni* kept close to the surface.

The largest numbers of *E. nordmanni* were found at salinities above 21.50 $^{o}/oo$, while below this level only small stocks were recorded. *E. nordmanni* is known to be very euryhaline, and in the Baltic the optimal salinity lies within the range 4-35 $^{o}/oo$ (Ackefors 1969).

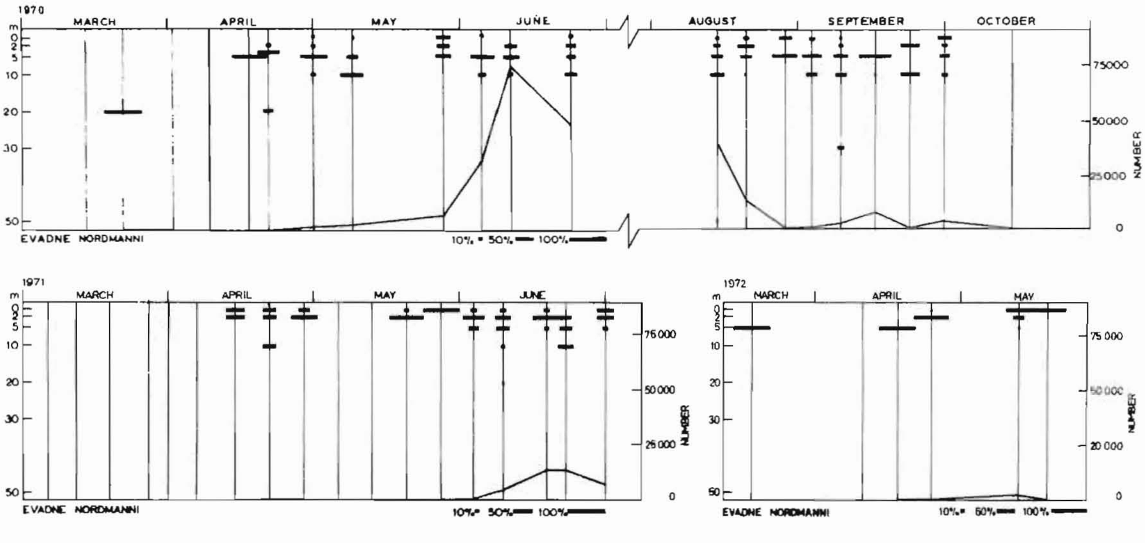

Fig. 38. *Evadne nordmanni*, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

Podon polyphemoides (Leuckart)

The largest numbers of *P. polyphemoides* were observed during June and in the middle of August 1970 (Fig. 39). Large stocks may also be assumed to have been present during the July of that year. A second peak occurred in the middle of September 1970. At the beginning and end of that month, *P. polyphemoides* was almost absent. In June 1971 only small numbers occurred.

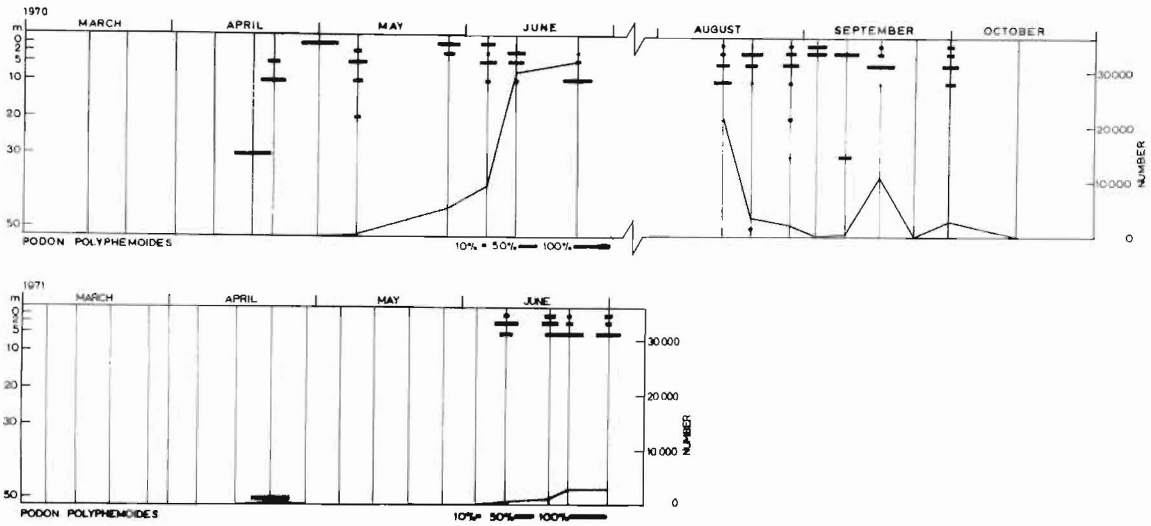

Fig. 39. *Podon polyphemoides*, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

Practically the whole stock was encountered in the upper 10 m and at the end of June a very high concentration was found in the 10 m samples. In Oslofjorden the bulk of the *P. polyphemoides* population was found in the warm surface water (Hansen 1951), and in Dramsfjorden above the 5 m depth (Beyer 1954). Both in numerical variation and in vertical distribution, *P. polyphemoides* resembled *L. retroversa* and *E. nordmanni*, but appeared to be more or less absent from the uppermost layers during its maximal abundance in June 1970.

P. polyphemoides is very euryhaline (Ackefors 1969) and the observed surface salinties were well within the range for the species. The temperature conditions seemed to be very favourable during June 1970.

The peak in the middle of September that year coincided with a small temperature increase in the upper 10-20 m.

Fritillaria borealis Lohmann

F. borealis is a typical spring species, showing a maximum in April in all 3 years (Fig. 40). Practically the whole stock was found in the upper 20 m, when abundant in the upper 10 m. It was frequently observed at the surface.

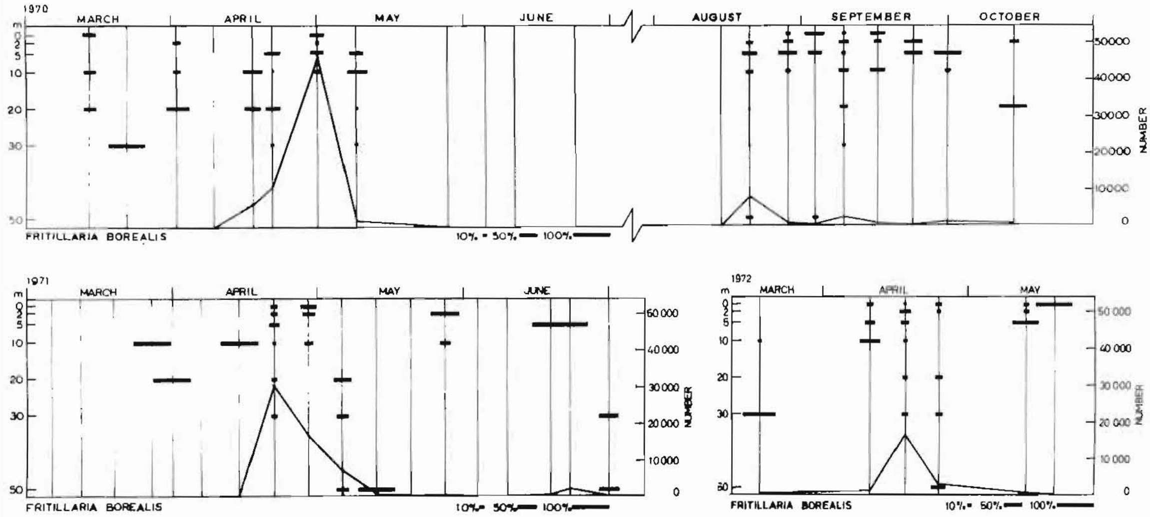

Fig. 40. *Fritillaria borealis*, percentage vertical distribution (left scale) and calculated number below 1 m^2 in 0-50 m (right scale).

The maximal concentrations of *F. borealis* coincided with sea temperatures below 7°C and salinities above 32 ‰ in the upper 10 m. The numerical variation of *F. borealis* in 1970 paralleled that of *M. longa*. A similar trend was also observed in the same area during 1963-1966 (Strömgren 1973 a).

Oikopleura spp.

During 1963-1966 two species of *Oikopleura* were identified from the fjord: *O. dioica* Fol and *O. labradoriensis* Lohmann (Strömgren 1973 a).

In the middle of August 1970 large numbers of *Oikopleura* spp. were observed, indicative of a summer maximum, while no specimens were recorded earlier in the year. During the years 1967-1969, *Oikopleura* spp. reached its maximum during the August-September period.

Other organisms

Juvenile stages of *Pareuchaeta norvegica* (Boeck), mainly nauplii, were relatively frequent during April-June.

Scolecithricella minor Brady, females and copepodite stages, occurred in small numbers at all seasons, mainly in the deepest hauls.

Oithona spinirostris Claus was most frequent during May-June in all years.

Eggs, nauplii, and metanauplii of euphausids were relatively numerous during March-April in all years. The highest concentrations were found in April 1971.

In the deepest samples a few ostracods occurred during March-April in all years, as well as in the autumn in 1970.

The larvae of chaetognaths were most frequent during May-June.

A few *Salpa fusiformis* Cuvier, 59 specimens in all, were recorded on the 15th of October 1970, mainly at 2 m depth. *S. fusiformis* is regarded as an indicator of Atlantic water (Wiborg 1954, Brattström 1972).

Cirriped larvae were abundant from April to June, while smaller numbers occurred during August-October 1970. They occurred mainly in the upper 20 m.

Polychaeta larvae also showed a maximum abundance during the period April-June, with peaks at the April/May and May/June transitions. Later in the year they were insignificant. Maximal concentrations were generally found at 10 m depth. Very few specimens occurred near the surface.

Cyphonautes larvae were unimportant during the spring, but in September large concentrations were recorded. They had a rather scattered vertical distribution.

Echinoderm larvae showed significant peaks in June and from the end of August to the beginning of September, mostly in the samples from the 5 and 10 m depths.

Bivalve larvae were most abundant during May-June, being then mostly present in the upper 10 m. In autumn their vertical distribution was more scattered.

DISCUSSION

A diurnal migration has been shown to occur in most species, but in stratified neritic waters the movements are commonly depressed (Banse 1964, and others). As all samples during 1970-1972 were taken during daylight hours, these consequently indicate maximal depths. However, controversial patterns are known to occur in several species, for example the occasional daytime aggregations of *C. finmarchicus* at the surface (Marshall & Orr 1955, and others). Hydrographic and biotic factors, as well as the physiological state of the animal, may modify the customary vertical distribution.

During March in all years, the concentration of zooplankton was very low, expecially in the upper 20 m. Below this level only *M. pusillus*, *O. similis*, and harpacticoids, mainly *Microsetella norvegica*, occurred in any numbers. During this period the water was cold, less than 6.5°C, no stratification occurred, and phytoplankton was scarce. *M. pusillus* has been shown, however, to be rather independent of phytoplankton blooms (Marshall 1949), and *M. norvegica* and *O. similis* may exhibit a similar relationship.

The number of *C. finmarchicus* nauplii reached a maximum at the end of April in all years. The diatom maximum in Trondheimsfjorden is generally found during the first half of April (Sakshaug 1972), and the spawning of *C. finmarchicus* is obviously related to that (cfr. Marshall 1949, and others). In 1970 and 1971 the number of copepodites corresponded to the number of nauplii, but in 1972 the nauplii maxima occurred simultaneously with minima of the older copepodite stages. This trend coincided with the different vertical distribution of the nauplii in 1972 and a simultaneous maximum for the deeper-living copepod *M. pusillus*. A reduction of the temperature in the uppermost layer may indicate that the surface water had been swept away by strong winds and, in that case, the young copepodite stages of *C. finmarchicus* may have been transported away from the area.

Many species showed a deeper vertical distribution than normal on April 21st 1970. For most of them, this shift in distribution coincided with an increase in numbers. On the other hand, species which normally have a deep distribution (e.g. *M. pusillus*) showed a significant minimum at the same date. A similar trend was indicated in the middle of April 1971 and perhaps also at the end of April 1972. The distribution pattern indicates that surface water had been introduced down to at least 50 m depth. The hydrographic development during 1970 and 1971 supports this assumption. Salinity data are lacking for this period in 1972. The small maxima, or small numerical increases, which were recorded for several species, may have been due to their adoption of a greater depth range rather than to higher concentrations at given depths. For species which mainly spawn in spring (e.g. *C. finmarchicus*), however, large maxima occurred.

At the beginning of May in all years, the younger stages of *C. finmarchicus* reached a minimum, probably due to their development into older copepodite stages followed by migration to deeper layers. A simultaneous change in vertical distribution, however, may indicate a horizontal displacement of subsurface water, which would likewise have led to a loss of *C. finmarchicus*. A number of species which had produced small stocks in April also generally showed minima at the beginning of May (*P. elongatus, T. longicornis, C. hamatus, A. longiremis, F. borealis, L. retroversa*). In several cases these minima also coincided with a higher vertical distribution.

Both the decreases in numbers and the changes in vertical distribution may be related to the counter-current to the brackish-water runoff, which may have brought in water of different quality.

The preference for the uppermost layers became more significant throughout May and June, but large populations were not produced in the upper 10 m during 1970. In 1971 and 1972 most species were much less numerous. This difference is obviously related to the very high surface temperature recorded in 1970, which improved the performances of the temperate species.

During May-June in all years, a pronounced stratification was established, with a brackish top layer. Two types of vertical distribution may be noted during this period. The first type is represented by a group of species 80-95% of whose stock was found in the upper 10 m. This group consists of all stages of *T. longicornis, C. hamatus, A. longiremis*, all copepodite stages of *P. elongatus*, nauplii and copepodite stages II-I of *C. finmarchicus*. *E. nordmanni, P. polyphemoides, L. retroversa*, and *O. similis* showed similar distributions. The bulk of these organisms had their maximal abundance in

2-5 m depth, although some of the older stages showed maxima at 10 m.

The second group is smaller and less homogenous. *O. borealis* showed a scattered distribution in June, while more than 90% of *M. pusillus* was found in the 30-50 m samples. The number of surface species seemed to vary inversely to the number of *M. pusillus*.

The vertical distribution of the first group corresponds to the stratification in the upper layers, and the preference of many species for the 2 and 5 m depths seems related to the steep gradients for temperature and salinity (Table 3). Their vertical distributions might thus be explained by aggregation near to a barrier or sharp gradient. Discontinuity layers, especially sharp haloclines, are generally considered to stop or reduce vertical migration (Hansen 1951, 1960, Petipa et al. 1960, Banse 1964, and others) and layering itself is suggested to lead to accumulations of zooplankton (Harder 1952). It seems evident that the increased temperature in the upper 10 m improves development, but most of the species were able, earlier in the year, to produce significant stocks during conditions similar to those now found below 10 m. Thus temperature alone may not explain a success restricted to the uppermost layers.

On the other hand, brackish-water runoff in May and June must have generated a counter-current flowing into the fjord. At the beginning of the period this inflowing water may have been poor in zooplankton and also unfavourable for growth of the actual species concerned. Production would thus have been confined to a narrow water layer and only few individuals migrated to the layer below. At the beginning of June a rapid increase of adults and copepodite stages V-IV of *T. longicornis* coincided with increasing numbers of *P. polyphemoides, E. nordmanni,* and *L. retroversa*, and a slightly deeper distribution was indicated for some other species. Simultaneously, *M. pusillus* showed a minimum. This may indicate that in this case the counter-current had brought in immigrants which, under the favourable temperature conditions at the sample station, produced the large numbers recorded later in the month.

The observed biological differences between the upper 5-10 m and the layers below may be due to their belonging to different water bodies. It is a well known fact that apparently identical water masses may have different biological properties (Fraser 1952, and others) and evidently may retain their identity for some time (Bowen &

Sugihara 1957, Banse 1959). The phytoplankton did not show gradients similar to the zooplankton during May and June (E. Sakshaug, pers. comm.) and thus the zooplankton distribution can hardly be explained by food relations.

Several numerically important species (*P. polyphemoides*, *E. nordmanni*, *C. hamatus*, *T. longicornis*, *A. longiremis*, *L. retroversa*) were observed in significant numbers at the surface in late May 1970, but in early June the same year only *P. polyphemoides* and a few *E. nordmanni* remained in this layer, although the salinity records were well within the known range for most of the species and the high temperatures might have been expected to provide favourable conditions. On the other hand, a reduced salinity implies a strong supply of freshwater and probably indicate surface runoff into the fjords derived from the rivers (Strömgren 1974). In that case increased surface runoff may explain the apparent submergence of most species in early June 1970, because reproduction was unable to keep pace with loss except for species with a high fecundity, such as *P. polyphemoides*, which may have been further favoured by the optimal temperature conditions. Species which normally tend to occupy the uppermost layers are most severely exposed to runoff. The small stock of *A. longiremis* copepodites and the decreasing number of females and copepodites of *C. hamatus* in June 1970 may be explained in that way. Hansen (1951) showed that *C. hamatus* kept above the discontinuity layer in summer. The sensitivity of *C. hamatus* to surface runoff is also indicated by its apparent absence from Hardangerfjorden (Gundersen 1953, Lie 1967), discussed by Strömgren elsewhere 1974). Young stages of *C. finmarchicus* were evidently able to occupy the near-surface layers in spite of salinities below 25 ^{o}/oo, so this important species, too, may be influenced by surface runoff. *T. longicornis*, *L. retroversa*, and *E. nordmanni* also showed small maxima during June 1970. They were probably favoured by the high temperature, but because they had a slightly deeper distribution than *C. hamatus* they were perhaps less exposed to runoff.

An irregular depth distribution of surface species was again observed between the 3rd and 9th of September 1970, and as in April the most important species simultaneously showed a peak in numbers. This depth distribution once again coincided with a minimum of *M. pusillus*. Simultaneously a very prominent temperature increase occurred in the surface layer, together with a decrease in salinity. It seems probable that near-surface water had penetrated to depths below 10-20 m. The situation at the beginning of September thus showed a parallel to that found in the middle of April, and the peaks which were observed for some of the species might have been due to a fresh supply, which added to the original stock.

At the end of August a number of species were preferentially found in the 10 m samples (*P. elongatus*, *T. longicornis*, *C. hamatus*, *A. longiremis*, *M. norvegica*, *E. nordmanni*, *P. polyphemoides*, *Oikopleura* spp.).

In the middle of September these same species tended to occur preferentially in the 5 m samples. This distribution showed no direct relationship to temperature or salinity gradients, but may have been related to the hydrographic changes which took place during the first week of September, as indicated by the irregular vertical distribution of the zooplankton.

On the 23rd of September very pronounced minima were recorded for some species (*C. finmarchicus*, *P. elongatus*, and *L. retroversa*), while several others were nearly absent (*T. longicornis*, *C. hamatus*, *A. longiremis*, *O. borealis*, *E. nordmanni*, *P. polyphemoides*, *F. borealis*, and *Oikopleura* spp.). Simultaneously, *M. pusillus* showed a maximum. The temperature and salinity development indicate that the upper 20 m of the water column had been carried away. The inhabitants of this layer were thus reduced in numbers, while deeper living species, like *M. pusillus*, were introduced. This exclusion of several species explain the reduction in the species diversity index (see Fig. 9).

At no season was a significant correlation observed between the vertical distribution of the various species, the Secchi disc measurements or the cloud cover.

The variations in vertical distribution seemed to be very dependent on water movements. The distributions were evidently more related to different water bodies than to the tendency of the species to seek optimal conditions. Discontinuity layers are usually regarded as forming boundaries for vertical movement and thus leed to a vertical stratification of the zooplankton, but a given distribution may just as well be due to the superposition of different water masses possessing different biological properties and different contents of zooplankton. This is in line with the view of Banse (1959, 1964) and others, that the distribution of the zooplankton in neritic areas may be regarded as reflecting the distribution of different water types. Banse (1959) based his interpretation on the T-S relationship, but at Stn 15 in Trondheimsfjorden the water types of the upper 50 m could not be identified by this method. Petipa et al. (1960) found that various zones of different quality might be superposed, but that distribution within any zone depended on the ecological characteristics of the species.

When and where rapid displacement of the water masses may occur, as at Stn 15, the mixing or superposition of different stocks of the zooplankton thus complicates any analysis of species dynamics.

SUMMARY

At a permanent hydrographic station (Stn 15 Röberg) in Trondheimsfjorden, Western Norway, zooplankton was collected at short intervals during the periods March-June 1970-1972, and August-October 1970. The samples were taken during daylight hours, by pump, at 0, 2, 5, 10, 20, 30, and 50 m depths.

During March and April, the salinity was above 31 $^{o}/oo$ at all levels. During May and June river discharge increased greatly, due to melt water, and a pronounced stratification was established with a brackish top-layer in the upper 5-10 m. Simultaneously the vernal warming took place. During August-October 1970 the temperature and salinity gradients were less steep and at the end of this period stability was low.

The hydrographic development was to a great extent ruled by surface runoff, wind-driven displacement of surface water, upwellings, and influxes to different layers. These events were often of short duration, but affected the plankton very much.

Copepoda dominated in the zooplankton. Six copepod species (*Calanus finmarchicus*, *Pseudocalanus elongatus*, *Temora longicornis*, *Microcalanus pusillus*, *Oncaea borealis*, and *Oithona similis*) formed the bulk of the total number of organisms.

A highly significant linear correlation was found between Simpson's diversity index and the Shannon Weaver diversity index. A highly significant linear correlation was also found between Simpson's index for copepods and the same index for holoplankton, indicating that the copepods alone may provide a sufficient description, in terms of diversity, for the holoplankton as a whole. The lowest average diversity for the whole sampling period was found at 2 m depth. The diversity index values fluctuated widely within this layer, while they were more stable for the deepest samples.

Vertical distribution and numerical variation are discussed for all species which were relatively abundant. In March the concentration of zooplankton was low and its vertical distribution scattered. In April the spring burst of *C. finmarchicus* dominated, with maximal abundance in the upper 30 m. In May several species changed their vertical position and throughout May and June the largest concentrations were normally found in the upper 10 m. This change in vertical distribution seemed to be related to transport of water masses and the introduction of water bodies of different origin.

When surface salinity was at its minimum several species disappeared from the surface layer, although they were abundant immediately below. This is assumed to have been due to horizontal transport by the brackish-water runoff, rather than to active migration. In general, both vertical distribution and abundance of most species seemed closely related to both horizontal and vertical water movements.

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