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Tor Strømngren

ZOOPLANKTON AND HYDROGRAPHY IN TRONDHEIMSFJORDEN

ON THE WEST COAST OF NORWAY

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ZOOPLANKTON AND HYDROGRAPHY IN TRONDHEIMSFJORDEN  
ON THE WEST COAST OF NORWAY

by

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ABSTRACT

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An analysis of the relationship between hydrography and the zooplankton in Trondheimsfjorden is presented on a basis of zooplankton samples and hydrographic data collected during 1963-1966 and 1968-1972.

A highly significant correlation was found between the size of the spring generation of the most important copepod species present, *Calanus finmarchicus*, and the discharge of riverine freshwater into the fjord prior to the main spring flood. The brackish water run-off is assumed to transport the juvenile stages of *C. finmarchicus* out of the fjord.

During the late summer and autumn, a highly significant correlation was found between the numbers of *C. finmarchicus*, copepodite stage V, and the salinity below threshold levels. The increased salinity at this season is assumed to indicate an inflow of deep water, which carries with it fresh stocks of *C. finmarchicus*, thus compensating for the vernal loss of the juvenile stages.

Several autochthonous temperate species show a decrease in abundance from the mouth to the inner parts of the fjord during summer and autumn, which is correlated with warm water influxes. The immigrants carried in by these influxes contribute significantly to the local stocks.

A number of allochthonous species are indicators of surface or deep-water inflows in the autumn.

The close relationship found between zooplankton and hydrography, demonstrates that establishment of the stocks of the various species is affected by the complex interaction of several independent biological and physical factors. This probably explains the large temporal and spatial variations of the zooplankton found in Trondheimsfjorden.

A comparison with data from Hardangerfjorden indicates similar relationships between zooplankton and hydrography.

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## INTRODUCTION

In Trondheimsfjorden marked annual variations occur in the composition of the zooplankton and the abundance of the different species. The cause or causes of these variations are not yet fully understood. Several events may determine success or failure, such as food supplies, predation, the reproductive dynamics of the various species and certain abiotic factors, e.g. currents. The long-term investigations made in Trondheimsfjorden, permit an analysis of the relationship between hydrography and the occurrence and abundance of many zooplankton species.

This paper is a discussion of the results of previous investigations in Trondheimsfjorden made during 1963-1966 and 1968-1972 (Strömngren 1973a, b, c; Wendelbo 1970). Comparisons are made with similar investigations in Hardangerfjorden in 1950-1951 (Gundersen 1953) and 1955-1956 (Lie 1967, Saalen 1962). The sampling stations for Trondheimsfjorden are shown in Fig. 1, and the sampling dates during the investigation period are shown in Table 1.

The methods used in sampling the zooplankton, together with their limitations, have been discussed previously (Strömngren 1973a).

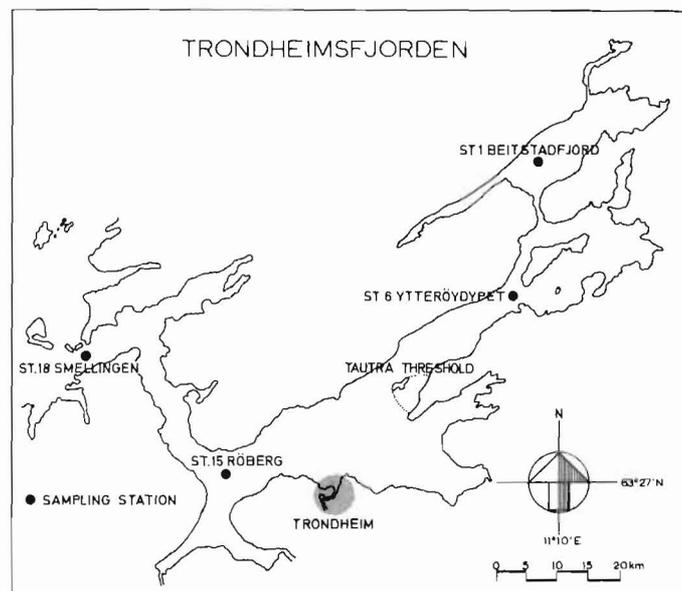
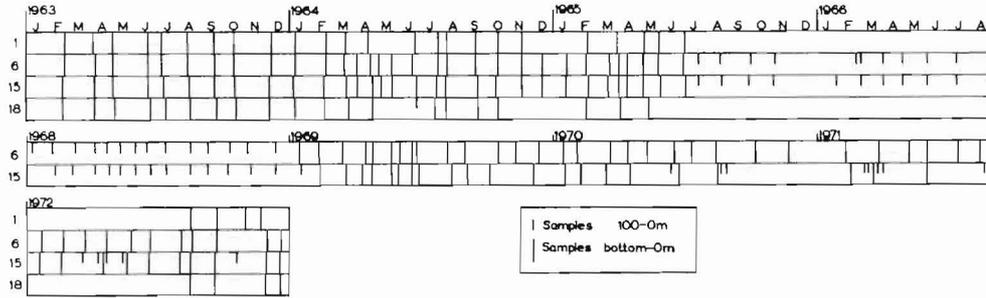


Fig. 1. The positions of the four sampling stations in Trondheimsfjorden.

Table 1. Sampling dates throughout the investigation period



THE INFLUENCE OF BRACKISH WATER RUN-OFF IN SPRING

In Trondheimsfjorden, the copepod *Calanus finmarchicus* Gunnerus comprises 60-80%, on average, of the zooplankton biomass (Strömngren 1973a). The main spawning period of this species in Trondheimsfjorden is in April. Spawning is preceded by a vertical migration of mature adults, or maturing stage V copepodites, to the surface. The development from nauplius to copepodite stage III takes approximately two weeks and takes place in the uppermost water layers. The further development to copepodite stage V, takes a further two weeks and these stages are distributed at significantly deeper levels (Strömngren 1973a, b, c).

During the March-May period in 1963-1966 and 1968-1972 the annual fluctuation in numbers of the spring generation of *C. finmarchicus* normally showed one of two alternative patterns at all the stations sampled (Fig. 2). In 1963, 1966, and 1972 the spring spawning resulted in relatively large stocks of copepodite stages III-IV, while in 1964, 1965, 1968, and 1970 markedly smaller stocks of these copepodite stages were found. In 1969 an intermediate situation occurred. The data for Stn 15 in 1970 and 1971 are insufficient to give a reliable estimate of the size of the spring generation.

Food relationships do not seem to explain these differences. Sakshaug (1973) has shown that diatoms are always abundant in Trondheimsfjorden during spring and no abiotic barriers are found which might cut off *C. finmarchicus* from the food sources. Other possible factors, such as sea temperature, wave exposure, or predation were not found to be correlated with the variation in numbers either. In Table 2 the average number of all the copepodite stages and nauplii

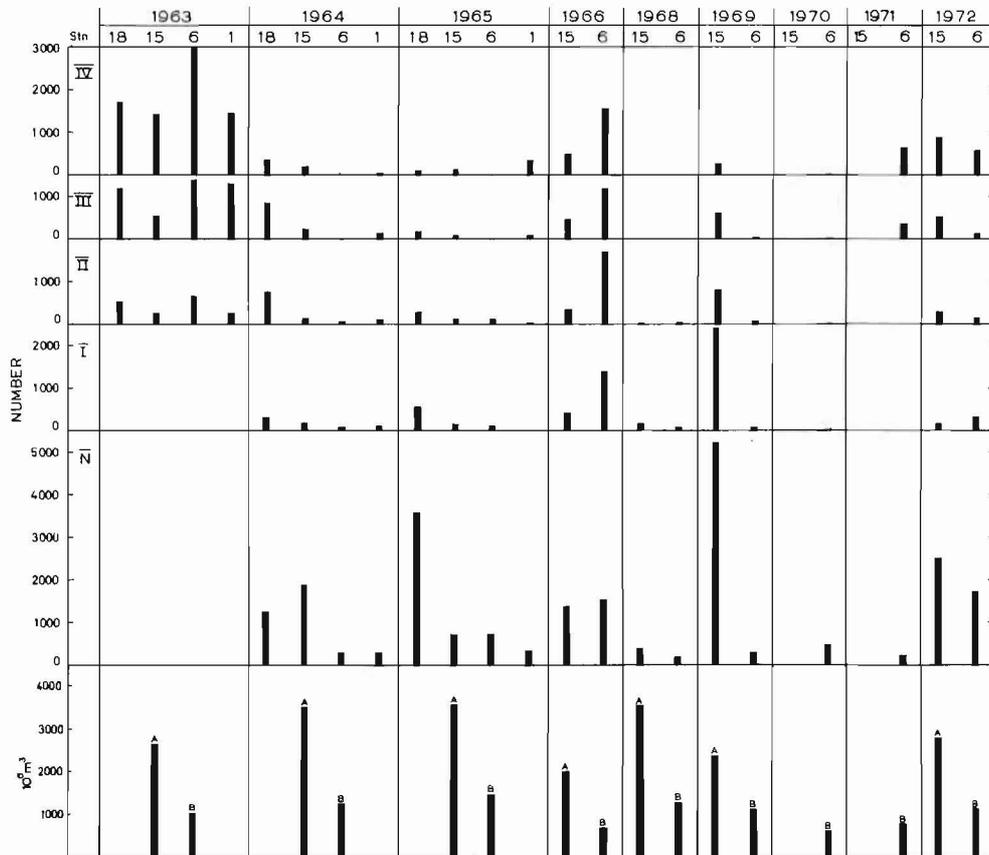


Fig. 2. The average numbers of nauplii and copepodite stages I-IV of *Calanus finmarchicus* found during March-May 1963-1966 and 1968-1972 in the 0-100 m water layer at the various stations. River discharge during March-April to the whole fjord (A) and to the inner fjord (B) in  $10^6 \text{ m}^3$ . (Below)

of the spring generation of *C. finmarchicus* during the various years is compared with the relative strength of the freshwater discharge into the fjord during March and April in the same years, that is in the period when the formation of the spring generation of *C. finmarchicus* is at a critical phase, but before the main spring flood. Zooplankton samples from the beginning of March to the first third of May are included. The numerical order of years at Stns 1 and 6 is compared to the discharge into the inner fjord basin, at Stns 15 and 18 to the total discharge to the fjord. The estimate of the freshwater discharge is based partly on direct measurements, partly on precipitation data (Wendelbo 1970). The primary data has been furnished by Norges Vassdrags- og Elektrisitetsvesen, Hydrologisk

Table 2. Average numbers of copepodite stages I-V and nauplii of *Calanus finmarchicus* during the period March - first third of May, ranked according to the volume freshwater discharge in  $10^6 \text{ m}^3$  recorded during March-April. The standardized variable ( $\alpha$ ) and significance level are indicated

											$\alpha = \frac{x - Ex}{\sqrt{\text{var } x}}$	P (x ≤ α)	
Stn 18	F	2675	3510	3560								+ 2.59	0.005
	$\overline{\text{nC}}$	>4665	3605	4824									
	Year	1963	1964	1965									
Stn 15	F	1984	2353	2675	2740	3510	3560	3589					
	$\overline{\text{nC}}$	3865	10387	>2825	3496	1353	1519	1150					
	Year	1966	1969	1963	1972	1964	1965	1968					
Stn 6	F	609	680	740	1067	1101	1154	1272	1273	1461			
	$\overline{\text{nC}}$	780	8880	1350	>5318	730	1990	574	533	1241			
	Year	1970	1966	1971	1963	1969	1972	1964	1968	1965			
Stn 1	F	1067	1273	1461								+ 2.59	0.005
	$\overline{\text{nC}}$	>3164	705	2198									
	Year	1963	1964	1965									

avdeling. A rank correlation between the average number of *C. finmarchicus* and the freshwater discharge for all stations combined shows a highly significant inverse correlation at the 0.005 level.

This supply of freshwater to the fjord gives rise to a brackish top-layer, and the salinity in the upper 10 m during spring is closely correlated with the freshwater supply (positive correlation, significant at the 0.005 level). The depths of the brackish layer increased toward the mouth of the fjord, at which point it may reach to a depth of 15 m (Wendelbo 1970). Since the juvenile stages of *C. finmarchicus* tend to keep to the uppermost layers, lowered salinity might affect the development into older stages. This view may find support in the highly significant positive correlation found between the numbers of *C. finmarchicus* and the salinity at 5 m depth recorded at the turn of the months March-April and April-May (see Table 3). The salinity at 5 m depth is significantly correlated with the salinity at both the 0 m and 10 m levels ( $P < 0.001$ ) and may indicate the conditions found in the brackish water layer.

However, the salinities recorded are well within the limits which are known to be suitable for the successful development of *C. finmarchicus* (Marshall & Orr 1955), and salinity in itself is not considered decisive for the success of the spring generation of *C. finmarchicus* in Trondheimsfjorden.

The discharge of freshwater by the rivers gives rise to an estuarine circulation in the fjord (Wendelbo 1970), and it is assumed that the discharge may be used as an indicator of the degree of brackish water run-off. The velocity of this outflow has not been measured directly in Trondheimsfjorden, but during the spring flood the outflow probably exceeds 50 cm/sec (Wendelbo 1970). Before this, in March and April, a speed of 10 cm/sec is likely when the run-off is high. In this case surface water may theoretically be transported from the innermost basin and out of the fjord within 16 days.

The nauplii and younger copepodite stages of *C. finmarchicus* are frequently found in the uppermost layers, and it is commonly accepted that these copepodite stages prefer the near-surface layer (Marshall, Nicholls & Orr 1934, and others). This preferred vertical distribution brings these stages to the surface where they are subject to the outgoing current, and a transport of these juveniles out of the fjord is likely. This washout effect is assumed to be decisive for the

Table 3. Salinity at 5 m depth, ranked according to the numbers of *Calanus finmarchicus* found in the 0-100 m water layer at the end of March and end of April. The standardized variables ( $\alpha$ ) and significance levels are shown for each period

March/April								$\alpha = \frac{x - E_x}{\sqrt{\text{var } x}}$	$P(x \leq \alpha)$
Stn 15	Salinity 5 m	31.46	31.69	31.92	32.54	32.66	32.99	- 2.657	0.004
	<i>Calanus finmarchicus</i>	320	493	490	805	1000 <sup>x</sup>	2140		
	Year	1968	1964	1971	1965	1963	1966		
Stn 6	Salinity 5 m	31.17	31.36	31.69	31.98	33.10	33.21		
	<i>Calanus finmarchicus</i>	150	530	1771	70	3160	3000 <sup>x</sup>		
	Year	1968	1964	1965	1971	1966	1963		
April/May								- 2.461	0.007
Stn 18	Salinity 5 m	32.01	32.09	32.50					
	<i>Calanus finmarchicus</i>	5620	325	7175					
	Year	1963	1965	1964					
Stn 15	Salinity 5 m	27.75	29.99	30.86	31.98	32.00 <sup>xx</sup>	32.79		
	<i>Calanus finmarchicus</i>	2610	910	1990	5301	13200	5790		
	Year	1965	1964	1968	1963	1969	1966		
Stn 6	Salinity 5 m	29.22	29.45	31.11	31.67	32.30	32.54		
	<i>Calanus finmarchicus</i>	420	900	720	2000	10476	400	14600	
	Year	1964	1965	1968	1971	1963	1969	1966	
Stn 1	Salinity 5 m	30.10	30.57	31.11					
	<i>Calanus finmarchicus</i>	1372	4040	6423					
	Year	1964	1965	1963					

<sup>x</sup> Estimated value

<sup>xx</sup> Interpolated value

success of the spring generation of *C. finmarchicus*.

Transport of the juvenile stages of *C. finmarchicus* away from the breeding areas by the surface current has been reported by many workers (Bigelow 1926, Fish 1936, Sherman 1965, Ussing 1938). Similar relationships between the size of larval fish stocks and run-off are discussed by several other workers (Dahl 1899, Sund 1924, Lillelund 1965, Dons unpublished). In the inner part of Trondheimsfjorden, near Stn 6 Denstadli (1972) recorded that strong year classes of cod (*Gadus morhua*) corresponded to years rich in *C. finmarchicus*. This may be due to food relations, although transport may be taken into account.

The estuarine circulation in the fjord may reintroduce *C. finmarchicus* by the in-going counter-current. Gran (1900) suggested that a proportion of the large stocks of *C. finmarchicus* found in the fjords of Northern Norway during June and July were derived from an influx in May. This type of circulation seems to be of minor importance for the stocks of *C. finmarchicus* in Trondheimsfjorden.

The described loss of *C. finmarchicus* during spring and summer would make difficult the maintenance of a fjord population, were it not for the fact, shown later, that deep inflows in late summer and autumn bring with them new stocks of the older copepodite stages, particularly copepodite stage V.

A comparison with the observations from Hardangerfjorden during 1956-1957 (Lie 1967) and 1950-1951 (Gundersen 1953) also indicate that in spring the highest surface salinities recorded are associated with the largest numbers of *C. finmarchicus* present, and if surface salinity is indicative of freshwater discharge and run-off, a similarity to Trondheimsfjorden is thus indicated.

Data from Skjomen, a fjord in Northern Norway, also indicate that river discharge may influence *C. finmarchicus* in a similar way (Strömngren 1974). However, in both these cases the material is so scanty to allow closer interpretation.

In Trondheimsfjorden a number of the more temperate, smaller copepod species, which reach their main maxima during the summer and autumn (e.g. *Pseudocalanus elongatus*, *Temora longicornis*, *Centropages hamatus*, *Limacina retroversa*, *Podon polyphemoides*, *Evadne nordmanni*), usually show a smaller secondary peak in spring. The low, absolute numbers of these species in spring is probably related to

the low water temperature, but as they tend to keep near to the surface, like the juvenile stages of *C. finmarchicus*, they must also be subject to the same outward drift, which will contribute to a reduction of the spring stock.

One species, *Acartia longiremis*, however, seems to show a different behaviour. *A. longiremis* seems to be inversely correlated with *C. finmarchicus* during the main river flood period in May-June (Strömngren 1973 a, b, c). This may be due to a different response to freshwater discharge; *A. longiremis* probably keeps below the brackish layer. In the Strait of Georgia, Legare (1957) also found that the main peaks of *A. longiremis* coincided with flood periods.

#### THE INFLUENCE OF DEEP INFLOWS IN SUMMER AND AUTUMN

In Trondheimsfjorden, the summer and autumn maxima of *Calanus finmarchicus*, below 100 m water depth, are dominated by copepodite stage V. The deep layers were sampled during autumn only in 1963, 1964, 1969, 1970, and 1972 (Table 1). Fig. 3 shows the large annual fluctuations which occurred, as well as the marked differences found between stations, the largest numbers occurring in the outer regions of the fjord (Stns 18 and 15). The annual, and particularly the horizontal, differences in abundance coincided with similar variation patterns of the salinity.

Salinity in the fjord basins is dependent on inflows. In the deeper layers of Trondheimsfjorden repeated deep inflows take place throughout the year (Wendelbo 1970). The summer and autumn inflows are characterized by water of a high salinity. Both the frequency and strength of the inflows are successively reduced by the sills separating the various basins. In Norwegian fjords water with a salinity above 35 ‰ is regarded as being of Atlantic origin. At the outer stations 18 and 15, influx of oceanic or deep coastal water is revealed by the occurrence of salinities close to 35 ‰. Within the Tautra threshold (Fig. 1) salinity is generally lower and at Stns 6 and 1 an inflow of water is indicated by records of salinities above 34.6 ‰ and 34.2 ‰ respectively.

In the summer of 1963 a deep inflow of saline water first occurred at Stn 18 in July and progressively later further in,

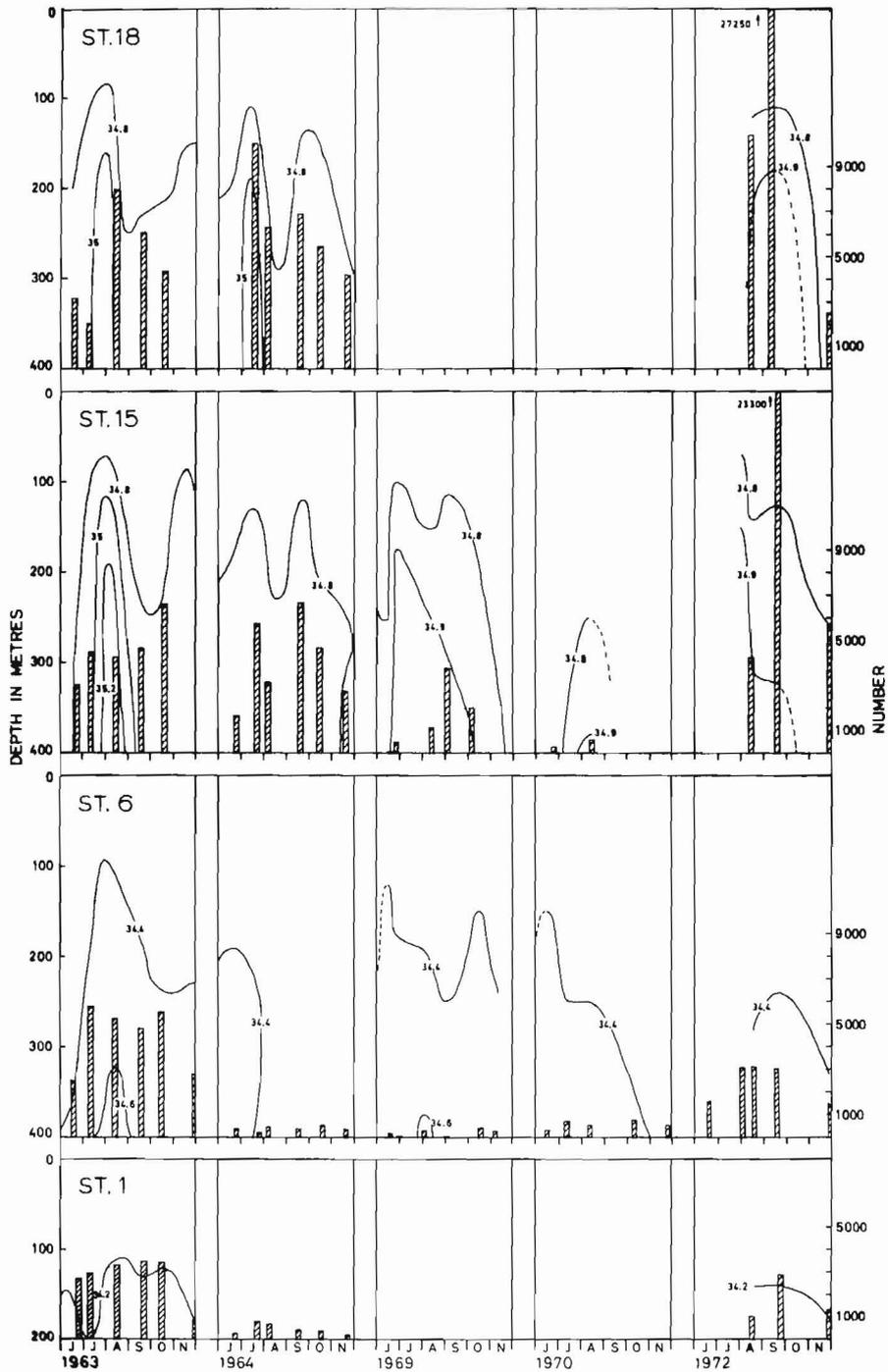


Fig. 3. The number of copepodite stage V of *Calanus finmarchicus* found below the 100 m level at the four stations in Trondheimsfjorden during June-November 1963, 1964, 1969, 1970, and 1972 (right-hand scale), and the salinity isopleths for the same period (left-hand scale).

culminating at the innermost station in August-September (Fig. 3). This inflow was very strong and produced salinities above 35.2<sup>o</sup>/oo even at Stn 15 in August. In the outer part of the fjord, the direction of flow was reversed during the interval between the sampling dates of August 14th and September 19th, but at the beginning of October the outer basins were once again subject to water influx.

In 1964 the inflow at Stns 18 and 15 in July seemed fairly strong and a salinity of 35<sup>o</sup>/oo was recorded in August at Stn 18. At the two innermost stations only a very weak inflow was indicated. After a temporary reversal in July-August, a second inflow took place in September at the two outer stations.

In 1969 influxes occurred in July and September at Stn 15, of approximately the same order as in 1964. At Stn 6 the position of the 34.4 isopleth indicates inflows during June-July and in October, interrupted by a temporary, but significant, outflow during August-September. The second inflow occurred later at Stn 6 than at Stn 15.

In 1970 a very weak inflow occurred at Stn 15 in August; an inflow which can also be traced at Stn 6.

In 1972 quite a strong inflow was recorded at all stations.

In Fig. 3, the comparison between variations in numbers of *C. finmarchicus*, stage V, and the salinity changes seems to indicate a direct relationship between inflows and increased numbers of *C. finmarchicus*. The strong inflow in the autumn of 1963, which reached all the fjord basins, corresponded with marked maxima of *C. finmarchicus*. In 1964, when a significant inflow took place in the outer fjord whilst the basins within the Tautra threshold were little affected, the *Calanus* stock showed a corresponding distribution, with considerable numbers in the outer fjord and a very small stock in the inner part. During the outflow in August at the outer stations, minima of *C. finmarchicus* occurred simultaneously. In 1969 inflows were moderate and the numbers of *C. finmarchicus* were also moderate at Stn 15. Both were insignificant at Stn 6. This may have been related to the August-September outflow, which coincided with a minimum of *C. finmarchicus*. Although no data exist for *C. finmarchicus* after August 1970 at Stn 15, a weak inflow that year corresponded with small stocks of *C. finmarchicus*, while the strong inflow in 1972 was accompanied by large numbers of *C. finmarchicus*.

Table 4. Average salinities at a given level below the threshold depths ( $\bar{S}_{\text{depth}}$ ) during August-October in the various years, ranked according to the corresponding average numbers of copepodite stage V of *Calanus finmarchicus* present below 100 m depth ( $\bar{N}$ ). Standardized variable ( $\alpha$ ) and significance levels are shown for all data combined

							$\alpha = \frac{x - E_x}{\sqrt{\text{var } x}}$	$P(x \leq \alpha)$							
Stn 18	$\bar{S}_{400}$	34.950 <sup>x</sup>	34.930	34.880				- 2.825	0.003						
	$\bar{N}$	18850 <sup>x</sup>	6120	6100											
	Year	1972	1964	1963											
Stn 15	$\bar{S}_{400}$	35.010	34.910 <sup>x</sup>	34.907	34.890	34.860 <sup>xx</sup>	- 2.825			0.003					
	$\bar{N}$	5130	12000 <sup>x</sup>	2300	4800	600 <sup>xx</sup>									
	Year	1963	1972	1969	1964	1970									
Stn 6	$\bar{S}_{300}$	34.573	34.495 <sup>x</sup>	34.493	34.435	34.387					- 2.825	0.003			
	$\bar{N}$	5230	3110 <sup>x</sup>	270	680	500									
	Year	1963	1972	1969	1970	1964									
Stn 1	$\bar{S}_{200}$	34.283	34.270	34.137									- 2.825	0.003	
	$\bar{N}$	3470	1940	470											
	Year	1963	1972	1964											

<sup>x</sup> Average for August-September

<sup>xx</sup> Single value for August

at all stations.

The salinity below threshold depth during the autumn may be used as an indicator of the strength and the course of the deep inflows. Table 4 shows the average number of *C. finmarchicus*, copepodite stage V, below the 100 m level during the period August-October and the average salinity recorded at a given depth below the threshold during the same months. A rank test for all stations combined, shows a highly significant correlation between these two variables ( $P < 0.003$ ). This may indicate that much of the autumn stock of *C. finmarchicus*, stage V, is apparently carried in together with the deep inflows. This supply may compensate for the loss of the younger stages of *C. finmarchicus* with the spring run-off, discussed earlier in this paper.

A comparison of the hydrographic data (Saelen 1962) and the variations in the quantity of zooplankton at the 100-300 m and 300-800 m levels for Hardangerfjorden (Lie 1967), indicates that a similar relationship also exists there.

Salinity isopleths, based on some unpublished material and on data given by Saelen, are presented for Stn A during 1950-1951 (Fig. 4) and for Stns H5, H6, and H7 during 1955-1956 (Fig. 5). As mentioned earlier, Stn H7 is almost identical with Stn A, while Stns H6 and H5 are situated further inside the fjord.

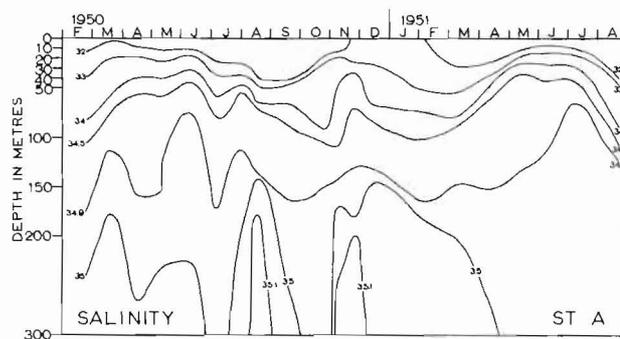


Fig. 4. Salinity isopleths for Stn A in Hardangerfjorden, during 1950-1951. Based on unpublished data (Institute of Marine Research, Bergen).

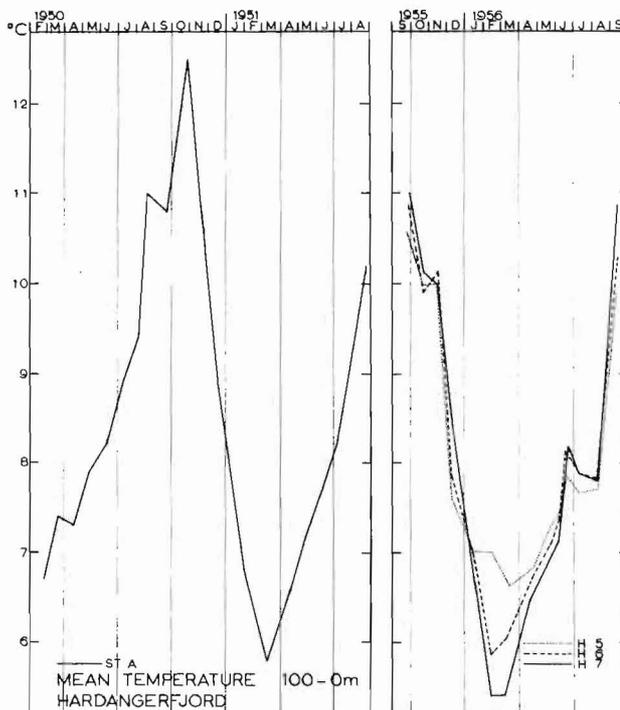


Fig. 5. Salinity isopleths for Stns H5, H6, and H7 in Hardangerfjorden, during 1955-1956. Based on data from Saelen (1962).

In Hardangerfjorden an exchange of deep water occurs in a similar manner to that found in Trondheimsfjorden. Deep inflows of Atlantic water occurred in March, May, June, August, and during November-December in 1950, and during June-July in 1951. The inflows in August and November-December in 1950 were characterized by high salinities ( $> 35.1^{\circ}/\text{oo}$ ), but no such inflow had started by the end of August 1951. A significant difference between these two years is thus indicated.

Deep inflows also seem to have taken place during September-October and in December in 1955 and in February, June, July, and September in 1956. In 1955, the inflows seemed to become progressively reduced towards the inner parts of the fjord. The salinity sections given by Saelen (1962) indicate that the saline water is found at deeper levels at the inner stations, but the water is too homogeneous to allow further interpretation. In 1956, however, the inflow seems to have led to the formation of an intermediate layer of saline water, which was easily recognizable far into the fjord. The frontal border of this influx was situated at Stns H7 in July, H6 in August, and H5 in August-September.

Lie (1967) did not separate the various species of plankton found below the 100 m level, but according to his observations and those of Gundersen (1953), the fluctuations in volume of the zooplankton during the autumn are mainly due to *C. finmarchicus*, copepodites stage V. Zooplankton volumes were large in the 100-300 m layer at Stn H7 in September and during November-December 1955 (Lie 1967, fig. 6). A lesser, but still distinct, maximum was recorded at Stn H6 during November-December, a little later than that recorded at the outer stations, while no corresponding maximum was found at Stn H5. This sequence of maxima corresponded to the nature of the inflow in 1955, which first occurred at H7, later at H6, and was perhaps depressed below the sampling depth at H5. In 1956, a progressive time lag in the maximal zooplankton volumes was found, from July at H7 to August at H6 and after September at H5, corresponding to a simultaneous intermediate inflow.

At the 300-800 m level at H5, where deep samples were taken only during 1955-1956, *C. finmarchicus* was less dominant, but the small peak during October-November 1955 and the large peak in September 1956 corresponded with the weak influx recorded below the

300 m level during October-November in 1955 and with the more pronounced influx in September 1956. At Stn A, Gundersen (1953) recorded small maxima below 400 m in early August and during October-November 1950. The August stock may have been derived from the autochthonous maximum at 0-50 m in early July, but deep inflows in July-August may also have brought in more. Another small maximum in late October may also have been related to the simultaneous deep inflow. The stocks of *C. finmarchicus* in Hardangerfjorden were generally smaller than those in Trondheimsfjorden.

Large quantities of *C. finmarchicus* have been recorded along the edge of the coastal banks (Sars 1886, Ruud 1929). Wiborg (1954) suggested that the plankton in the coastal edge area could originate from 1) the deeper waters immediately offshore, 2) from the Norwegian Sea and the stocks in the North Atlantic current, or 3) from the coastal areas further south. The presence of these large pre-spawning accumulations along the continental slope must be important for the development of the huge masses of *C. finmarchicus* found in summer on the coastal banks of Northern Norway.

In the Møre area, both Ruud (1929) and Wiborg (1955) recorded an abundance of *C. finmarchicus*. Ruud assumed that *C. finmarchicus* might spawn off Shetland, and even further westward, and complete their development to copepodite stages IV-V and adults on their way to Møre, where they accumulate. Wiborg (1954) found summer maxima of copepodite stages (IV-V) at Ona, which he could not easily trace back to local stocks; their length frequencies indicated that the northern stock might be recruited to some extent from the southern coastal or offshore areas and be carried in with the coastal current.

Copepodite stages IV-V which enter Trondheimsfjorden in summer may therefore originate from several sources, but the rich coastal concentrations present to the south-west of the fjord may form an important source of supply.

Although deep inflows regularly occur in Hardangerfjorden, the autumn stock of *C. finmarchicus* found there generally seems to be smaller than in Trondheimsfjorden. The records of Wiborg (1954, 1955) and Lie (1965, 1966) indicate that *C. finmarchicus* is less abundant in the southern parts of the west coast, and thus both summer and autumn inflows may contain lower concentrations of *C. finmarchicus*.

The mechanisms that regulate the stock of *C. finmarchicus* in a fjord are dependent on several parameters, involving the biology of the species, the physical characteristics of a particular fjord, as well as the history of the water masses on the coast. The combination of these variables must be expected to give rise to large annual variations within the fjords, as well as to differences in abundance between fjords.

#### TEMPERATE AUTOCHTHONOUS SPECIES AND THE HYDROGRAPY IN SUMMER AND AUTUMN

A number of temperate autochthonous species (*Pseudocalanus elongatus*, *Temora longicornis*, *Centropages hamatus*, *Acartia longiremis*, *Acartia clausi*, *Oithona similis*, *Limacina retroversa*, *Podon polyphemoides*, *Evadne nordmanni*) have their main maxima in Trondheimsfjorden during the summer and autumn (Strömngren 1973 a, b). Such specimens are taken in the upper 100 m water layer, and the bulk of them probably keeps quite close to the surface. These species also show considerable annual variations in abundance, as well as significant differences in number between the outer and the inner fjord.

Several species show a significant decrease in number towards the inner part of the fjord. In Table 5 the average numbers of different species found during June-October are ranked according to the position of the stations within the fjord and the respective rank correlations are tabulated. The correlation between abundance and the horizontal distribution of stations is highly significant for *E. nordmanni*, *T. longicornis*, *L. retroversa*, and *O. similis* ( $P < 0.007$ ). For *P. elongatus*, *C. hamatus*, and *A. clausi* the correlation is significant at the 0.03 level. For *P. polyphemoides* and particularly for *A. longiremis* no such relationship was found.

The mean temperature for the 0-100 m ( $\bar{t}_{0-100}$ ) and 0-5 m ( $\bar{t}_{0-5}$ ) water layers have been interpolated by means of second degree polynomials. Table 5 shows the overall mean water temperature for the 0-100 m ( $\bar{t}_{0-100}$ ) and 0-5 m ( $\bar{t}_{0-5}$ ) layers during June-October. Overall mean temperature for 0-100 m decreases towards the inner part of the fjord, while that for the 0-5 m layer shows almost the opposite trend. Since complete agreement exists between the horizontal

Table 5. Average numbers of the various temperate autochthonous copepod species found at each station in Trondheimsfjorden during June-October each year, correlated with station position and the overall mean temperature of the upper 0-5 m water layer ( $\bar{t}_{0-5}$ ). The overall mean water temperatures of the upper 0-100 m ( $\bar{t}_{0-100}$ ) are shown. Standardized variables ( $\alpha$ ) and significance levels indicated

	1963				1964			1965			1968		1969		number station $\alpha = \frac{x - \bar{Ex}}{\sqrt{\text{var } x}} P(x \leq \alpha)$		number $\bar{t}_{0-5}$ $= \frac{x - \bar{Ex}}{\sqrt{\text{var } x}} P(x \leq \alpha)$	
	18	15	6	1	18	15	6	1	15	6	15	6	15	6				
<i>E. nordmanni</i>	685	102	0.8	0.2	6400	1204	312	164	720	300	2470	1020	4000	2940	- 3.33	0.0004	+ 1.55	0.07
<i>T. longicornis</i>	874	1530	48	1.2	1664	1373	937	20	2011	1370	3760	3040	8364	11840	- 2.89	0.002	+ 1.11	0.14
<i>L. retroversa</i>	370	112	20	0.4	360	580	15	13	350	30	20	120	268	460	- 2.44	0.007	+ 0.67	0.26
<i>O. similis</i>	740	314	354	75	7808	4756	2518	1217	3875	3030	3230	2670	10416	10650	- 2.44	0.007	+ 0.22	0.42
<i>C. hamatus</i>	255	202	7	0.2	300	102	23	1	700	920	770	1480	760	4280	- 2.00	0.02	+ 1.11	0.14
<i>P. elongatus</i>	702	694	130	84	7018	7888	1653	170	1431	2006	3590	1250	1702	2670	- 2.00	0.02	+ 0.22	0.42
<i>A. clausi</i>	78	28	12	5	177	261	45	7	20	30	0	20	60	0	- 2.00	0.02	+ 1.11	0.14
<i>P. polyphemoides</i>	85	25	0.2	0.2	1784	2916	7150	514	170	570	910	1740	772	1180	- 1.11	0.14	- 0.22	0.42
<i>A. longiremis</i>	189	26	13	5	64	39	216	95	300	440	1110	1450	500	1830	- 0.22	0.43	- 0.67	0.26
$\bar{t}_{0-100}$	9.16	9.07	8.71	8.38	8.87	8.76	8.44	8.23	8.84	8.69	7.94	7.57	8.51	8.50				
$\bar{t}_{0-5}$	11.39	12.60	12.64	12.28	10.65	11.23	11.67	11.54	10.77	10.82	11.85	11.51	12.56	12.91				

distribution of the stations, then the abundance  $\bar{t}_{0-100}$ -correlation will be equal to the abundance/station -correlation shown in Table 5. On the other hand, the number/ $\bar{t}_{0-5}$  -correlation for the same period was not significant. This may indicate that temperature level itself is not decisive for the number of specimens of those species which prefer the uppermost layers.

The rapid increase in mean temperature in 0-100 m found several years from August and onwards (Fig. 6), may not be explained by solar radiation only, and an advective supply of heat must be assumed. A similar temperature effect in Hardangerfjorden (Fig. 7) was explained by Saelen (1967) to be due to influxes of warm coastal water.

The order of size of the increase in mean temperature in the 0-100 m layer and of the corresponding horizontal gradient towards the inner part of the fjord may roughly give an idea about the relative strength and the timing of the August and September influxes.

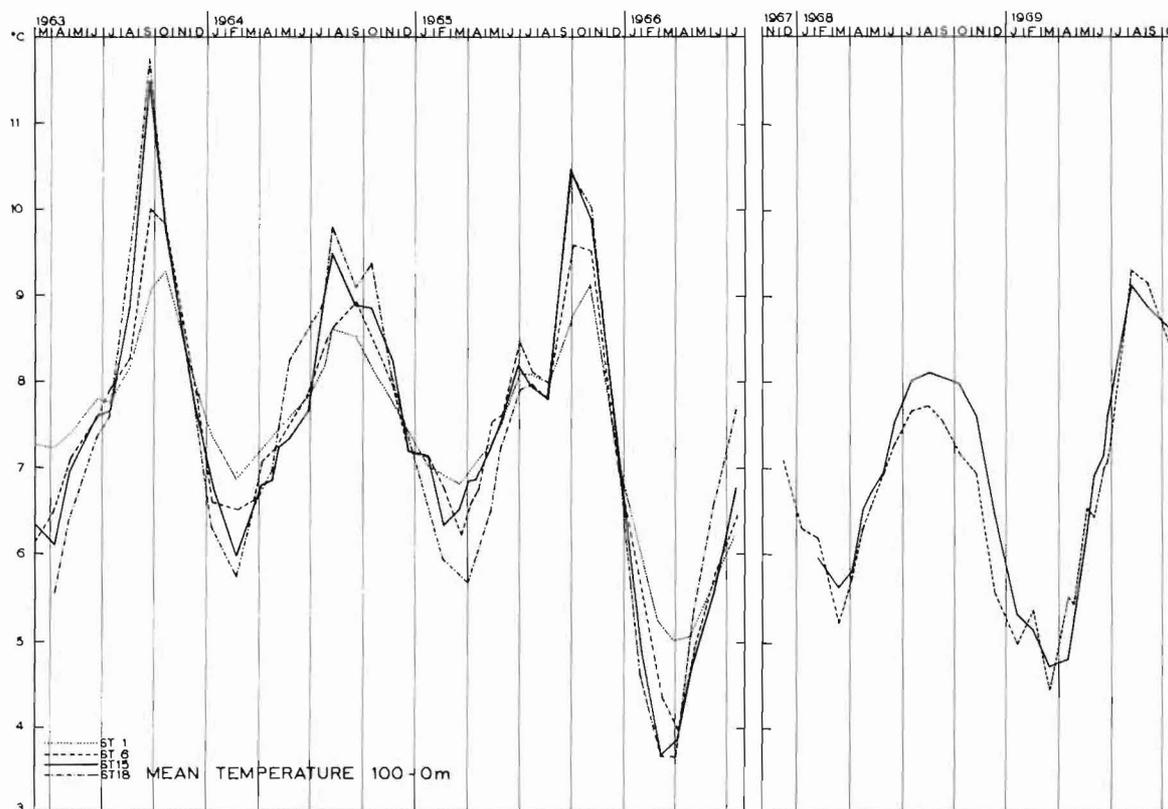


Fig. 6. Mean temperature of the upper 100 m ( $\bar{t}_{0-100}$ ) at the various stations in Trondheimsfjorden during 1963-1966 and 1967-1969.

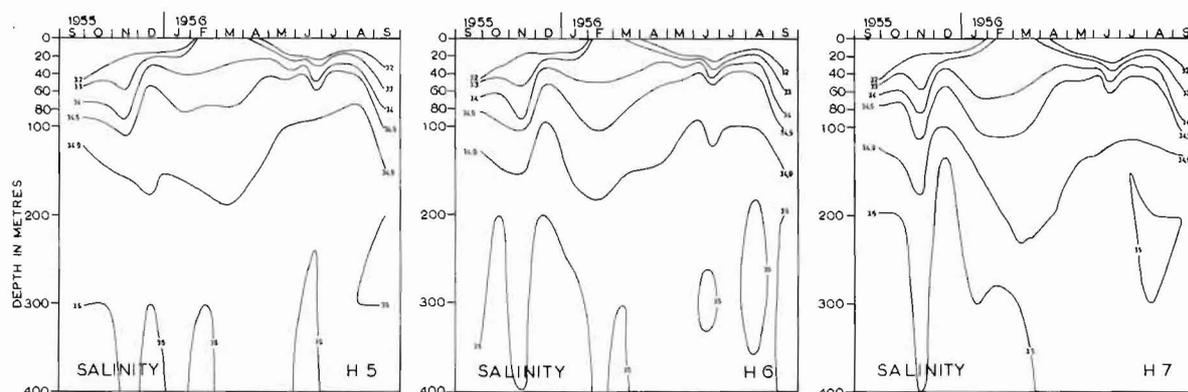


Fig. 7. Mean temperature of the upper 100 m ( $\bar{t}_{0-100}$ ) at the various stations in Hardangerfjorden during 1950-1951 and 1955-1956. Based on unpublished data (Institute of Marine Research, Bergen) and data from Saelen (1962).

1963 seems to have been a year in which a very strong influx into Trondheimsfjorden occurred (Fig. 6), while in 1968 very low mean temperatures were recorded at 0-100 m, indicating a much smaller supply of warm water. In Hardangerfjorden a stronger influx was indicated in 1950 than in 1956 (Fig. 7).

Most of the species mentioned above are known to be abundant on the coast (Wiborg 1954) and the warm water influxes may bring with them immigrants which contribute to the local stocks. The highly significant correlation found in Trondheimsfjorden between station and abundance may thus be explained by immigration. *A. longiremis* in fact, which is relatively scarce in coastal waters, showed no gradient along the fjord. Variations in the coastal stocks may influence the immigration effect.

Large stocks of several temperate species may develop in landlocked areas within the fjord, probably induced by the high temperatures there, and these, too, may represent local sources of supply (Strömgren 1973 b), but are probably of minor importance for the

fjords as a whole.

The summer-autumn immigration and the maintenance of the stocks of copepod species which normally keep to the uppermost water layers is also influenced by the run-off in summer and autumn. In Trondheimsfjorden the spring run-off is mainly due to the snow-melt; it reaches its maximum in May and decreases gradually throughout June. During summer supplies of freshwater and the consequent brackish water run-off are small. The rivers flowing into Hardangerfjorden, however, are fed by large glaciers and there the water supply reaches its maximum during June and July and may still be at a high level during August-October (Jorde & Klavestad 1963). This indicates that the brackish water run-off may remain important in Hardangerfjorden until the late summer. Temporary changes of discharge may also be of some significance. In Trondheimsfjorden the large volume of freshwater discharge recorded in September 1964 and October 1965 probably reduced the influxes to some extent. The temporary drop in mean temperature in Hardangerfjorden during June-July 1965 coincided with a maximum discharge of freshwater (Jorde & Klavestad 1963).

The wind effect on transport is more obscure, but, however, in September 1963 a strong western wind improved the inward transport of surface water.

*E. nordmanni*, *P. polyphemoides*, and *L. retroversa* all showed rapid increases in all years in Trondheimsfjorden during June-July. For *E. nordmanni* and *L. retroversa*, the horizontal gradients in Trondheimsfjorden indicate that immigration plays an important role during the early summer. *P. polyphemoides* showed a more irregular horizontal distribution pattern and is known to be variable in its occurrence on the coast (Wiborg 1954). All three species achieve their main maxima on the coast during June-July. *L. retroversa* showed a second maximum in the autumn, particularly in the outer fjord, coinciding with the warm water influxes. In Hardangerfjorden the recorded stocks of *E. nordmanni* were small (Gundersen 1953, Lie 1967), although large stocks were normally present in June in the southwestern coastal areas (Wiborg 1954). *L. retroversa* was absent from Hardangerfjorden in 1955 and 1956 (Lie 1967). Gundersen (1953) explained a sudden occurrence of this species in July 1950 as a result of immigration. The general pattern for these three species may

indicate that the prolonged brackish water outflow from Hardangerfjorden reduces the chances of immigration following their early summer maxima on the coast.

*O. similis*, *P. elongatus*, *T. longicornis*, and *C. hamatus* are frequent in Trondheimsfjorden, but the horizontal gradients shown in Table 4 indicate a supply of these copepods from coastal waters. Large stocks of *O. similis*, *P. elongatus*, and *T. longicornis*, in particular, may be present early on in the summer, which may be related to preceding water influxes. The maxima later on in the summer also seem to coincide closely with such influxes and are due to both the local and the introduced populations. *C. hamatus* occurs in smaller numbers in the main fjord, although it is very abundant in Borgenfjorden, a landlocked basin in the inner Trondheimsfjord (Strömngren 1973 b). This species is generally known to attain its largest numbers in such basins (Colebrook et al. 1961) or near the shore (Bigelow 1926). Shallow waters in the archipelago bordering the coast might form favourable breeding places, although Wiborg (1954) reported *C. hamatus* to be relatively scarce at stations on the open coast. Large numbers of *P. elongatus* are reported to occur on the coast of Möre, a little south of Trondheimsfjorden (Ruud 1929, Wiborg 1954) and *T. longicornis* may be very numerous in the same area, although its occurrence is variable and may be dependent on renewed supply from the south (Ruud 1929).

In Hardangerfjorden *O. similis* and *P. elongatus* were numerous, but decreased towards the inner part of the fjord (Lie 1967). *T. longicornis* was more variable, but the large maximum recorded in July 1950 may have been related to better conditions for immigration at that time than in 1956. *C. hamatus* was not observed in Hardangerfjorden by either Gundersen or Lie (op.cit.). All these four species may suffer from the effects of surface drift out of the fjord. The absence of *C. hamatus*, in particular, may be supposed to be due to the brackish water run-off, as this species is known to stay in or above the discontinuity layer (Hansen 1951, Strömngren 1973 c).

*A. clausi* showed no clear correlation with the warm water influxes, although the horizontal gradients for this species in Trondheimsfjorden indicated some relationship between immigration and such influxes. In Hardangerfjorden the occurrence of *A. clausi* in 1950 coincided with a strong influx of warm water. Wiborg (1940)



The large numbers of *Salpa fusiformis* (Table 6) recorded during August and September 1963 also indicate a warm water influx at that time.

The isolated occurrence of *C. typicus* in 1964 may indicate that this species is better able to penetrate into the fjord, perhaps due to its slightly deeper vertical distribution than *C. armata* and *A. patersoni*. Immigration of *C. typicus* may thus be less dependent on run-off and wind conditions. This assumption is supported by the fact that neither Gundersen (1953) nor Lie (1967) recorded *C. armata* or *A. patersoni* in Hardangerfjorden, perhaps connected with the marked run-off which occurs there throughout the summer and autumn. *C. typicus*, on the other hand, was found in Hardangerfjorden in autumn by both Gundersen and Lie (op.cit.); Gundersen recorded a small stock from June to September 1950, simultaneously with a strong warm water influx. Lie found *C. typicus*, in the fjord proper, only in September 1956.

Table 7. Occurrence of *Paracalanus parvus* in the annual plankton hauls made during the autumn period

Stn	<i>Paracalanus parvus</i>						
	1963	1964	1965	1968	1969	1970	1972
18	460	101	-	-	-	-	260
15	638	0	600	950	3300	50	1160
6	67	0	1650	0	0	240	720
1	0	0	-	-	-	-	110

*Paracalanus parvus* (Table 7) suddenly occurs in Trondheimsfjorden sometime in September nearly every year, but declines after October. Its distribution in time and space seems to be well correlated with the warm water influxes. For Oslofjorden, Wiborg (1940) suggested that *P. parvus* was transported in the surface by wind drift. Its distribution in Trondheimsfjorden, however, indicates that the conditions in the surface layer are less important for *P. parvus* than for the more exclusively surface species, *C. armata* and *A. patersoni*. This may be due to the relatively deeper vertical distribution of *P. parvus* (Strömngren 1973 c). This may favour the

more or less permanent occurrence of *P. parvus* in Hardangerfjorden since its maxima there coincide with the maxima for the coastal stocks in September (Gundersen 1953, Wiborg 1954), by which time surface run-off has declined.

The number of *P. parvus* in Norwegian coastal areas varies greatly from year to year (Wiborg 1954). The relatively large stock found in Hardangerfjorden in 1954, compared with 1955 and 1956, may have been related to the larger size of the coastal stock in August 1950, observed by Wiborg (1954), as well as to a stronger warm water influx.

Two other allochthonous species, *Metridia lucens* (Table 8) and *Rhincaalanus nasutus*, are mainly found below the 50 m level in Trondheimsfjorden (Strömngren 1973 a). Both species are found in relatively deep layers in Atlantic waters (Östvedt 1955, Rees 1957) and are probably brought into the fjord by deep inflows, although local stocks from the southern part of the coast may form a further source of supply (Wiborg 1954). *R. nasutus* has only been recorded twice, at Stn 15 in December 1963 and in February 1964. *M. lucens* was more numerous during the autumn and small stocks persisted throughout the winter. Both the spatial and temporal distribution of *M. lucens*, as well its abundance, may be related to inflows of Atlantic water.

Table 8. Presence or absence of *Metridia lucens* in the annual plankton hauls made during the autumn period

Stn	<i>Metridia lucens</i>				
	1963	1964	1965	1969	1972
18	+	0	-	-	+
15	+	+	+	+	0
6	0	+	+	0	0
1	0	+	-	-	0

ASPECTS OF THE DYNAMICS OF THE ZOOPLANKTON  
IN TRONDHEIMSFJORDEN

As discussed in the preceding chapters, current transport in both surface and deep layers is probably of major importance for the establishment and success of several zooplankton species in Trondheimsfjorden. The transport effect, furthermore, is influenced by both biological (reproduction, vertical migration) and hydrological-climatological factors. Several of these parameters vary independently, so a description of the species dynamics in the fjord is necessarily very complicated. Some of the main features, however, may be outlined on a basis of the investigations carried-out in Trondheimsfjorden (Strömngren 1973 a, b, c).

For those autochthonous species which show spring maxima, spawning in Trondheimsfjorden takes place during March and April. The adult *C. finmarchicus* migrate to the surface during February and March and large numbers of nauplii and young copepodite stages are found in the uppermost water layers during March-May. Numerous larvae of bottom invertebrates are also found near the surface during the same period and several autochthonous species which have their main maxima in summer and autumn also propagate to some degree in spring and produce small stocks. The spring maxima for all these spring spawners, whose larvae stay in the uppermost layers, show great annual variations (Strömngren 1973 a).

Any zooplankton species which remains near the surface during the early spring, before the spring flood sets in, is exposed to a small but significant brackish water run-off and some of the stock will be carried away out of the fjord. The great annual variation in numbers of the spring generations of *C. finmarchicus* were evidently due to this effect.

Several other autochthonous species, which also spawn during spring, show a far greater stability from year to year (*Metridia longa*, *Pareuchaeta norvegica*, *Chiridius armatus*, *Scolecithricella minor*, *Microcalanus pusillus*, *Heterohabdus norvegicus*, *Oncaea borealis*, *Oithona spinirostris*, *Sagitta elegans*, *Tomopteris helgolandica*). These species spawn in deeper water and their juvenile stages tend to keep below the discontinuity layer. This vertical distribution prevents significant losses occurring at the surface. Simultaneously, any tendency toward prolonged or continuous spawning

will also reduce the annual variation due to short-term environmental influences.

Species which have a very restricted reproductive period (e.g. *Calanus hyperboreus*), or species whose reproductive capacity is reduced in cold water (e.g. *Pseudocalanus elongatus*, *Temora longicornis*, *Centropages hamatus*, *Oithona similis*, *Evadne nordmanni*, *Podon polyphemoides*, *Limacina retroversa*) produce only small spring stocks. This may be due to loss by run-off, combined with the limited possibility of replacement by local production.

In May, river discharge is greatly increased by snow melt water. At this time, however, the larvae of *C. finmarchicus* have reached a developmental stage at which they stay deeper in the sea and further dispersal is thereby reduced. Several species, however, must be expected to lose a significant part of the stocks in the annual run-off.

During the summer and autumn warm water is introduced into the fjord. This water carries with it autochthonous summer and autumn species from the coast, which complement or replenish the local stocks (e.g. *P. elongatus*, *O. similis*, *L. retroversa*, *C. hamatus*, *T. longicornis*, *A. longiremis*, *A. clausi*, *E. nordmanni*, *P. polyphemoides*). The size of the introduced stocks depends upon the breeding successes of the coastal ones, on the previous history of the coastal water masses and on the strength of the influx.

High water temperatures accelerate the development of both the local populations and of the immigrants. Losses by run-off probably take place throughout most of the summer, but immigration and reproduction together generally result in a net surplus.

During June and July the spring generation of *C. finmarchicus* has developed into copepodite stages IV and V. The summer generation of *C. finmarchicus* then spawns and these summer larvae are generally distributed at deeper levels than those produced in spring. Occasionally, older copepodites from the spring generation, or larvae from the summer generation, may be carried into the fjord, but normally both outward and inward transport takes place in different water layers.

Later on in the autumn, allochthonous warm-water species may be introduced into Trondheimsfjorden (e.g. *Metridia lucens*, *Paracalanus parvus*, *Centropages typicus*, *Candacea armata*, *Rhincalanus nasutus*, *Anomalocera patersoni*, *Salpa fusiformis*). This immigration

mainly depends on the strength of the influxes and on the previous history of the coastal water masses.

Deep inflows of saline water take place in autumn, when the summer stock of *C. finmarchicus* on the coast has developed into copepodite stages IV and V. These stages are brought into the fjord in the deep inflow. In the fjord they remain in deep water and overwinter in the fjord basins. This supply is dependent upon both the size of the summer and autumn stocks on the coast and on the strength of the inflow.

This autumnal net supply into the fjord compensates for the vernal loss of the larvae of *C. finmarchicus*. The stock of *C. hyperboreus*, on the other hand, which may also suffer from losses during the spring, is not re-augmented in this way, because the coastal waters are poor in this species and the stock in the fjord therefore remains at a low level.

As discussed above, the interchange of zooplankton between the fjord and the coast seems to be dependent on several factors: precipitation and river discharge, water influxes at deep and at intermediate levels at all seasons, the history of the coastal water masses, and the vertical distribution and reproductive cycle of the different species. These factors can all vary more or less independently and this complex situation naturally causes large temporal and spatial variations in the recorded abundance of many of the more important species.

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