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On the Biology of Herring Larvae in Schlei Fjord, Western Baltic

by

D. Schnack+)

+)Institut für Meereskunde
an der Universität Kiel
23 Kiel
Niemannsweg 11

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Introduction

Feeding conditions during the larval stage are often considered as the most important factor determining recruitment at least in herring of the North Sea and the North Atlantic. The larvae of spring spawning herring in the Baltic live in rich coastal waters, and food seems not to be a restrictive factor to them. But in fact, very little is known about the relations between feeding of herring larvae and the amount or composition of food or the behaviour of the larvae caused by abiotic factors. The work done on feeding of herring larvae was summerised by BLAXTER & HOLLIDAY (1963) and BLAXTER (1965). Some new aspects were given on the ICES-Symposium "On the Biology of the Early Stages and Recruitment Mechanisms of Herring" (1968). It is obvious that the more distinct ideas about the necessary food supply for herring larvae are mainly based on experimental studies. Results, however, found in tanks under special conditions, can not be directly transferred on herring larvae living under natural conditions. For this reason studies on these problems were started in the Schlei fjord, an important nursery area for larvae of spring spawning herring of the Western Baltic (fig. 1).

The Schlei fjord is a narrow and shallow water path, reaching about 25 miles in the land, it is fairly well separated against the open sea. In general its plankton production is high, but considerable differences were found in the amount and composition of the plankton with time and region. Those fluctuations provide a most favourable basis for quantitative studies on the feeding ecology of herring larvae.

In spring, 1969, three surveys were made in the Schlei: at the end of April, the end of May, and the beginning of June. At 9 stations, herring larvae and their food were caught in different depth layers. As sampling gear a modified Gulf V, called "Nackthai" (mesh size 3oo μ) and a socalled "Baby Hai" (mesh size 55 μ) were lashed together (fig. 2). At the end of May additionally a neuston sampler after DAVID (1965) with tow nets, one above the other, (3oo μ mesh size) was used for sampling the upper few centimetres of the water column.

At the end of April only a small number of very young larvae was found. For detailed studies the older larvae, caught during the following two surveys in great numbers, were used only.

Vertical Distribution of the Herring Larvae

During the main surveys, at the end of May and the beginning of June, the herring larvae were caught in 6 and 4 depth layers respectively. Between the two surveys, a considerable difference in the distribution was observed, depending on the weather conditions:
The situation in June is given in figure 3. On two sampling days with bright sunshine the larvae were more or less equally distributed. Only on station 6 and 7 the abundance increased towards the surface. On these stations, however, the larvae were caught at dusk and dawn respectively. The mean length of larvae, also given in figure 3, does not show a uniform change with depth.

At the end of May, sampling was carried out on a dark day with heavy overcast and rain. The larvae were extremely concentrated in a small depth range from the surface to 2o or 8o cms below. The mean length decreased with increasing depth (fig. 4).

A larval population being closer to the surface on an overcast day than on a bright day was found by several workers (e.g. WOOD 1968) and agrees well with the experimental findings of WOODHEAD & WOODHEAD (1955): Looking at the swimming direction of the larvae, the authors noticed a predominant horizontal component at high light intensities, while at low intensities the vertical component dominated showing a positive phototaxis.

Figure 4 demonstrates the extreme effect of this behaviour in turbid coastal waters. The decrease of mean length with depth, as shown in the same figure, demonstrates that the intensity of reaction to light depends on length or age of the larvae, the larger larvae showing a greater preference for the surface.

In the June survey, were light had little effect, an influence of temperature on the vertical distribution of the larvae was obvious. The distribution of temperature is given in figure 5. It may be compared with the isolines of the most frequent length groups of larvae in figure 6. In spite of the uncomplete picture, due to only few data available, the similarity in the contures is obvious, expecially around station 2. Taking all data the negative correlation between length and temperature is statistically significant ($r = o{,}8/\alpha < o{,}o1$). The vertical distribution which is governed by light and temperature may have a direct influence on feeding, as the distribution of larvae does not necessarily correspond with the distribution of their food organisms, and the high concentration of larvae (up to 5oo per m^3) in certain narrow strata may result in competition for food.

Food Supply

To get an impression of the plankton situation at the end of May, the settlement volume of invertebrates (without coelenterates) is given in figure 7. In contrast to herring larvae, the invertebrate plankton was not concentrated in the surface layers but was almost equally distributed in the sampled depth range. From the inner part of the Schlei (station 9) to the outer region(station 1) the volume decreased sharply.

The samples mainly consisted of the copepod Eurytemora affinis and its young stages. Nauplii were the most numerous. Several other groups which were found in increasing numbers towards the outer region are given in table 1. A considerable change in the plankton composition between the May and June survey is obvious by comparing table 1 and table 2. Moreover figure 8 allows a comparison of the composition of biomass in μg dry weight between all three surveys.

At the end of April the high portion of nauplii even in weight has to be emphasized. This is of some importance in connection with the appareance of only very young herring larvae at that time. At the end of May adult Eurytemora and their copepodit stages were most important. In June a surprising small amount of food was available, consisting mainly of nauplii in the inner part of the Schlei and of mollusc larvae in the outer region. A study of the gut contents showed that these molluscs were not digested by the herring larvae at all. They were therefore not considered in the calculations of the biomass supply shown in figure 8. The situation in June is moreover characterised by distinct changes, from station to station, in the relative importance of the various taxonomic groups (tab. 2). For this reason, the June material provides good indications on selection and utilization of food depending on the composition of plankton.

Relation between Feeding and Food Supply

The gut contents of herring larvae in the Schlei are given in the tables 3 (May) and 4 (June) for different length groups, several stations, and two layers. In spite of the extreme concentration of larvae below the surface in May, there are no distinct difference in the gut contents between the investigated depth layers (tab. 3). This corresponds to the rather even distribution of invertebrate plankton. The guts of larvae from the surface layer, caught by a neuston net, have not yet been examined in detail, but it was noticed that they were all filled up. This means, that the very high larval concentration in a small depth range at the end of May did not lead to a shortage of food by direct competition.

At the beginning of June, at most stations the larvae of the upper depth range had a smaller amount of organisms in their guts than larvae from the deeper range (tab. 4). This tallies quite well with the plankton distribution (tab. 2).

Selection of food by herring larvae becomes evident from figure 9. The average of both investigated depth layers is taken and the relative abundance of the main groups of organsims in the guts is compared with their relative abundance in the plankton. Three groups of relatively large organisms were very much preferred. Even if they provide only a small part of the plankton, a considerable amount was found in the guts. The small mollusc larvae were not taken in a higher proportion until the amount of bigger organisms became very low.

As herring larvae are snapping for each single prey organism, they normally make use of their food supply in a very economic way by preferring the bigger organisms. On the other hand, gastropode larvae were preferred to nauplii, although both have a similar size. This may be due to the gastropods, being less transparent and therefore being easier recognizable. It should be pointed out, that none of the molluscs in the guts was digested. In this case the selecting behaviour of the larvae was obviously unfavourable for their nutrition.

In spite of the very different groups of organisms available in June, only a selection depending on size or visibility of the prey was found. This type of selection was found in the May material too.

The influence of the concentration of food on the feeding activity becomes evident when comparing the amount of organisms taken by herring larvae with the corresponding plankton supply at the end of May (fig. 1o). One should expect, that the gut contents increase assymptotically to a maximum value with increasing food supply. This was shown for several species of fish by IVLEV (1961) and LEBRASSEUR et al. (1969) a.o. In our case, however, the gut content decreased again if the food supply exceeded an optimal concentration. This is not an effect of different size-composition in the plankton. In figure 1o B only the prey organisms of preferred size were considered. The relations between gut contents and food supply is very similar to figure 1o A, where the whole biomass was taken into account. From figure 1o B we may conclude that the optimal concentration of food for herring larvae, 14-19 mm in length, amounts to about 2oo prey organisms of preferred size per litre.

It may be suggested that herring larvae, which have to fix each single prey organism, get confused by a too large number of food organisms as it is known in general for predatious animals.

Conclusions

While at the end of May the herring larvae partially had optimal feeding conditions in the Schlei, in the inner part of the fjord, an excessive supply of food made the conditions unfavourable again. At the end of April the great supply of nauplii certainly was a good source of food for the very young larvae appearing at that time. At the beginning of June there was a great supply of nauplii and, in the outer part, a very high number of mollusc larvae. But at this time a shortage of suitable food for the herring larvae, which were larger now, was obvious.

It is impossible to get a complete picture of the Schlei as a nursery area for herring larvae from three surveys only. These surveys, however, do already point out, that this fjord with a generally high plankton supply does not always offer optimal conditions. Moreover, they show that the amount of invertebrate plankton does not yet permit for a competent assessment of feeding conditions. Extreme concentrations of larvae in narrow depth strata, governed by light and temperature, have to be taken into account as well as the composition of plankton in connection with the size-depending selection by larvae, especially in view of the different digestive utilization of prey organsims. In the case of heavy feeding on undigestable mullusc-larvae, the possible unfavourable effect of the selecting behaviour became evident. Further studies will have to deal with the nutritive values of the prey organisms in detail.

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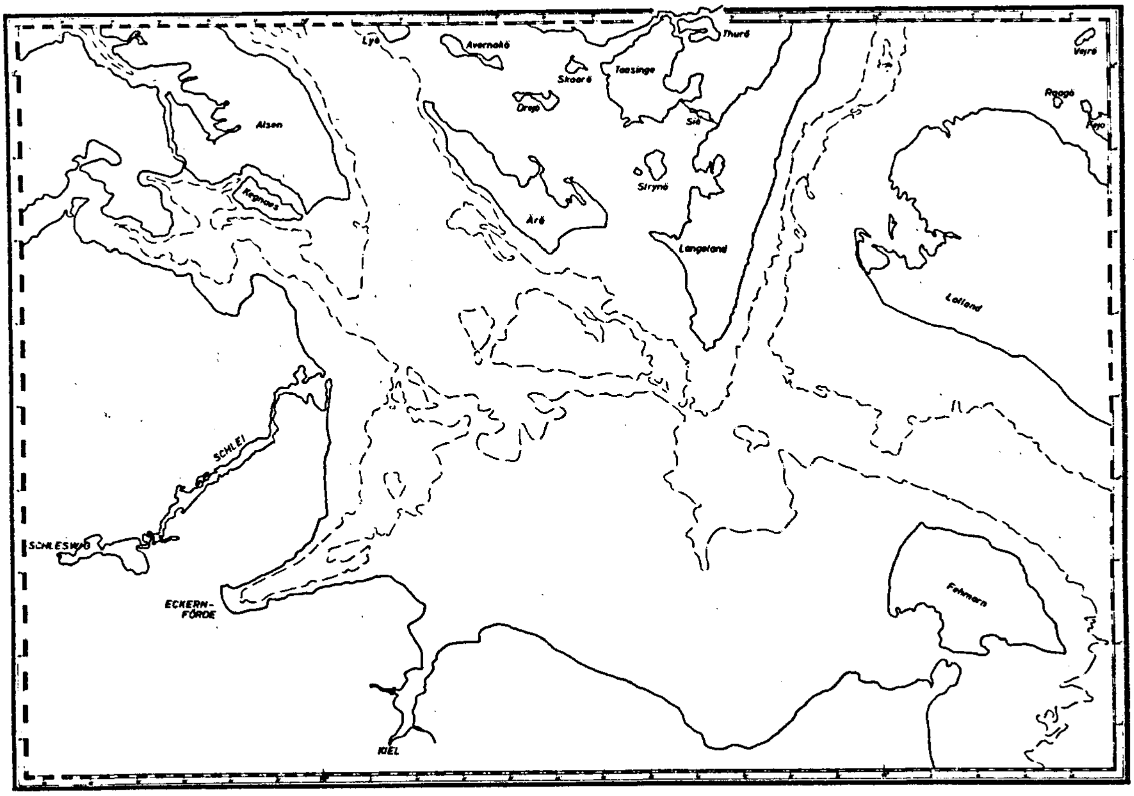

Figure 1A: Position of the Schlei fjord in the Western Baltic

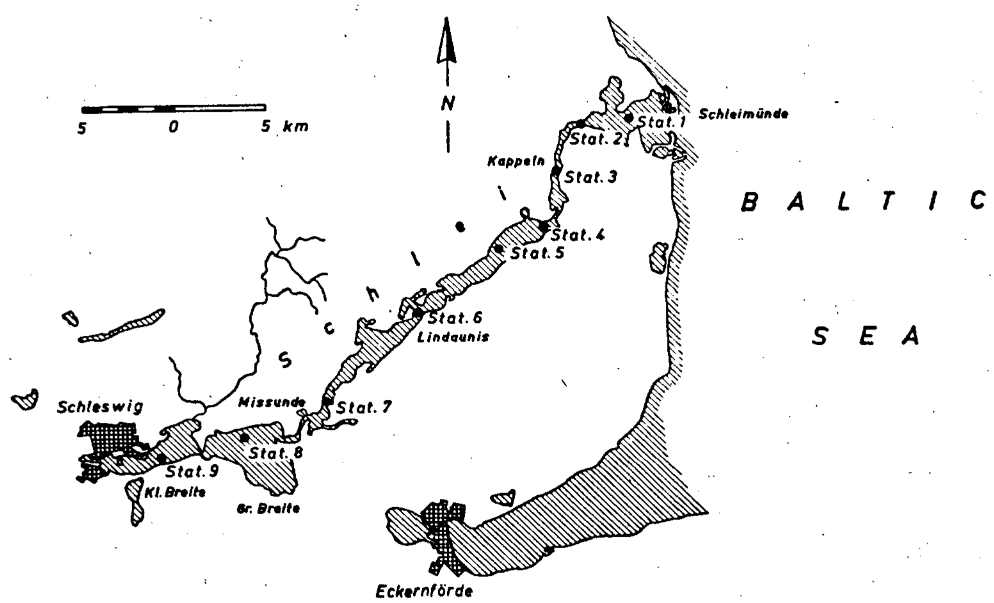

Figure 1B: Sampling stations in the Schlei fjord

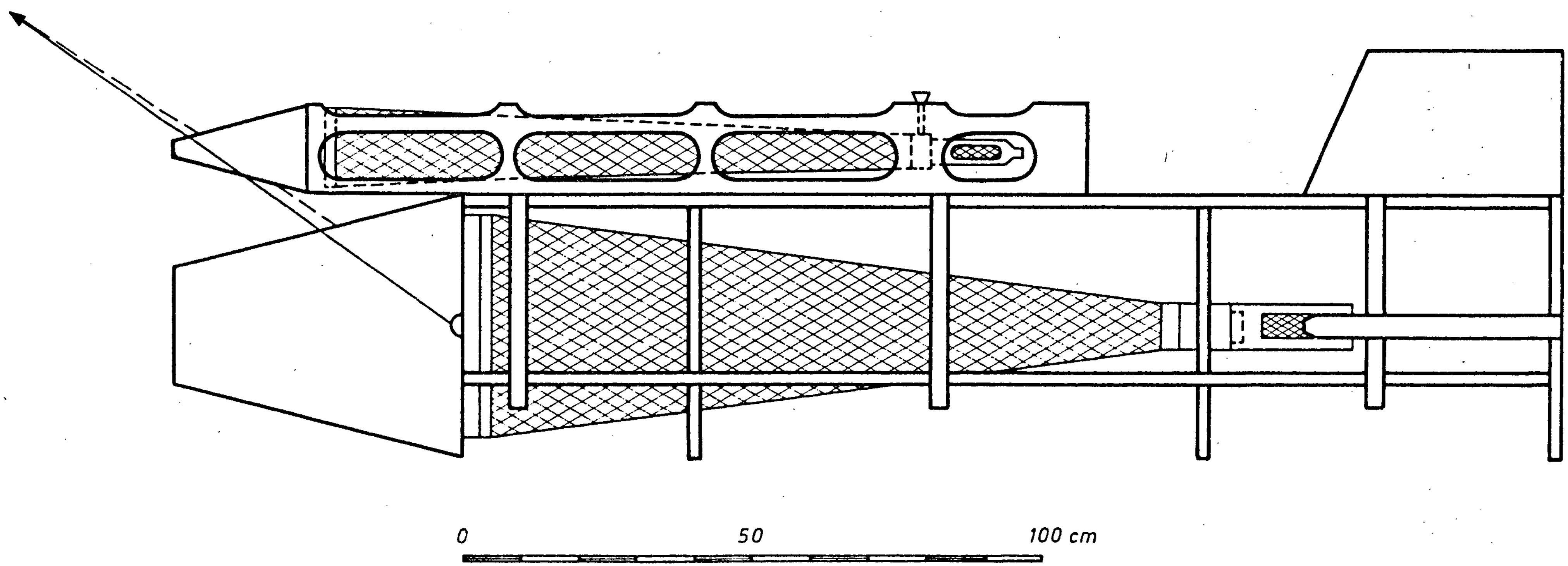

Figure 2: Sampling gear: "Nackthai" and "Baby Hai"

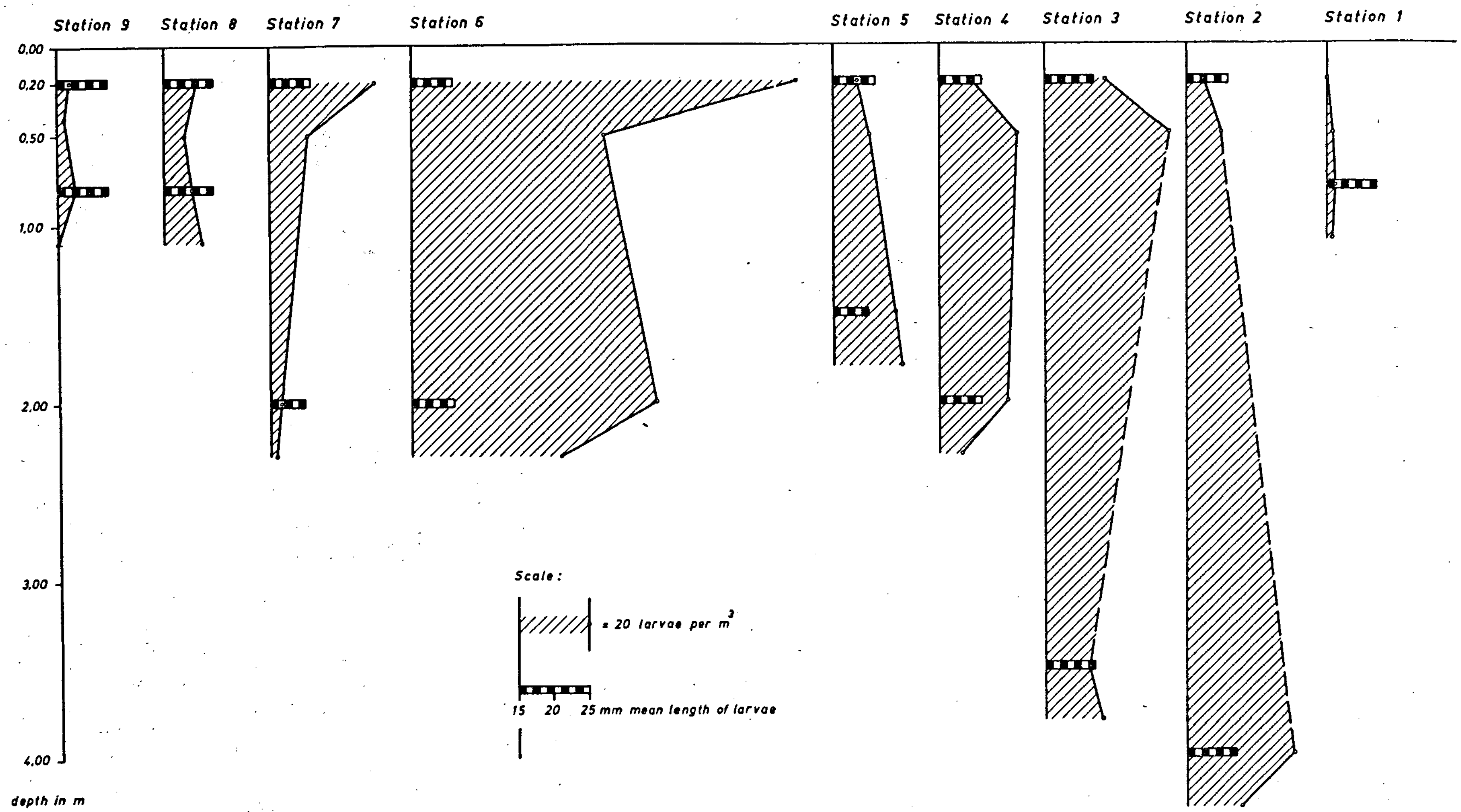

Figure 3: Vertical distribution of herring larvae in the Schlei on 11/12.6.1969 (bright sunshine)

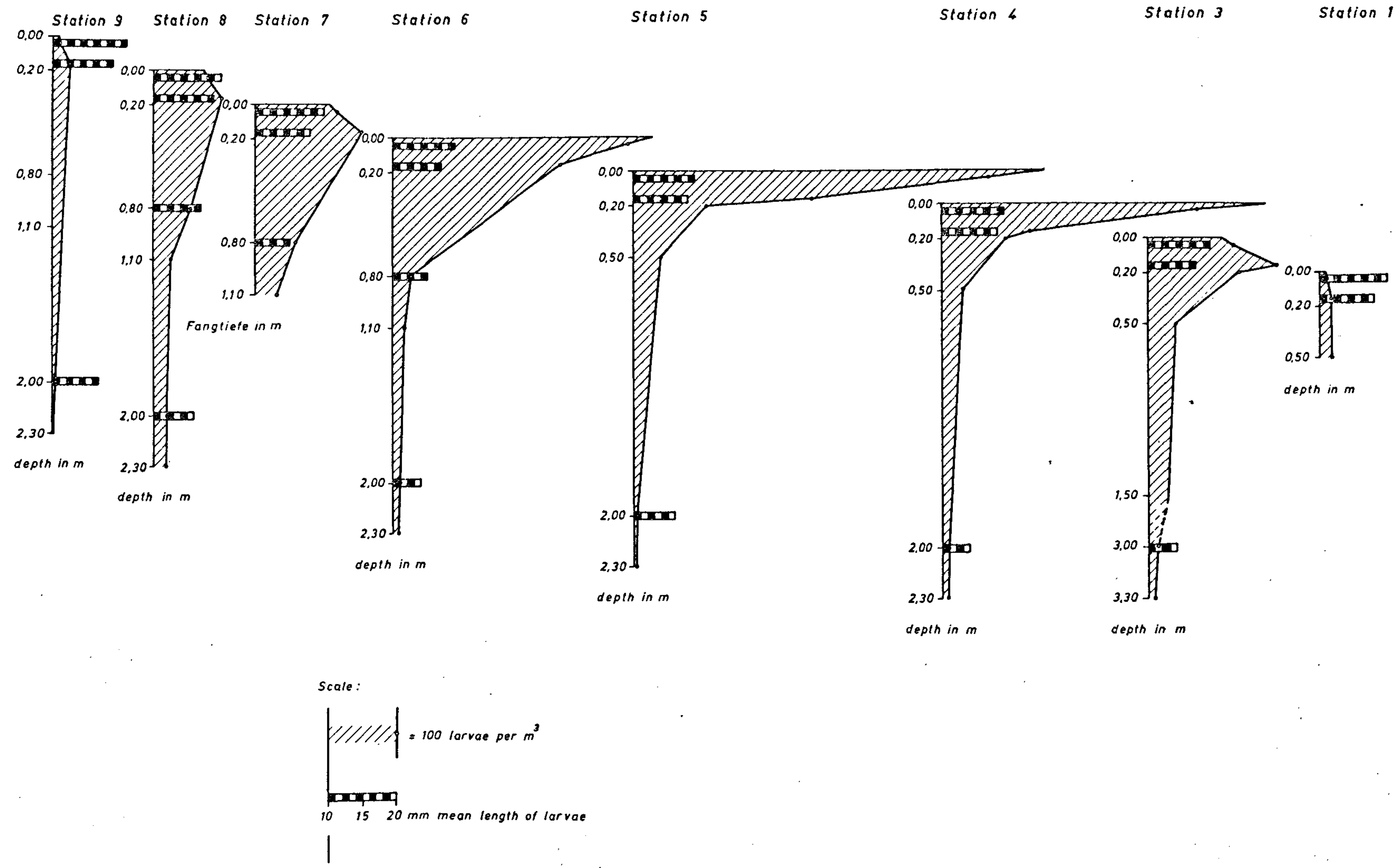

Figure 4: Vertical distribution of herring larvae in the Schlei on 28.5.1969
(overcast sky)

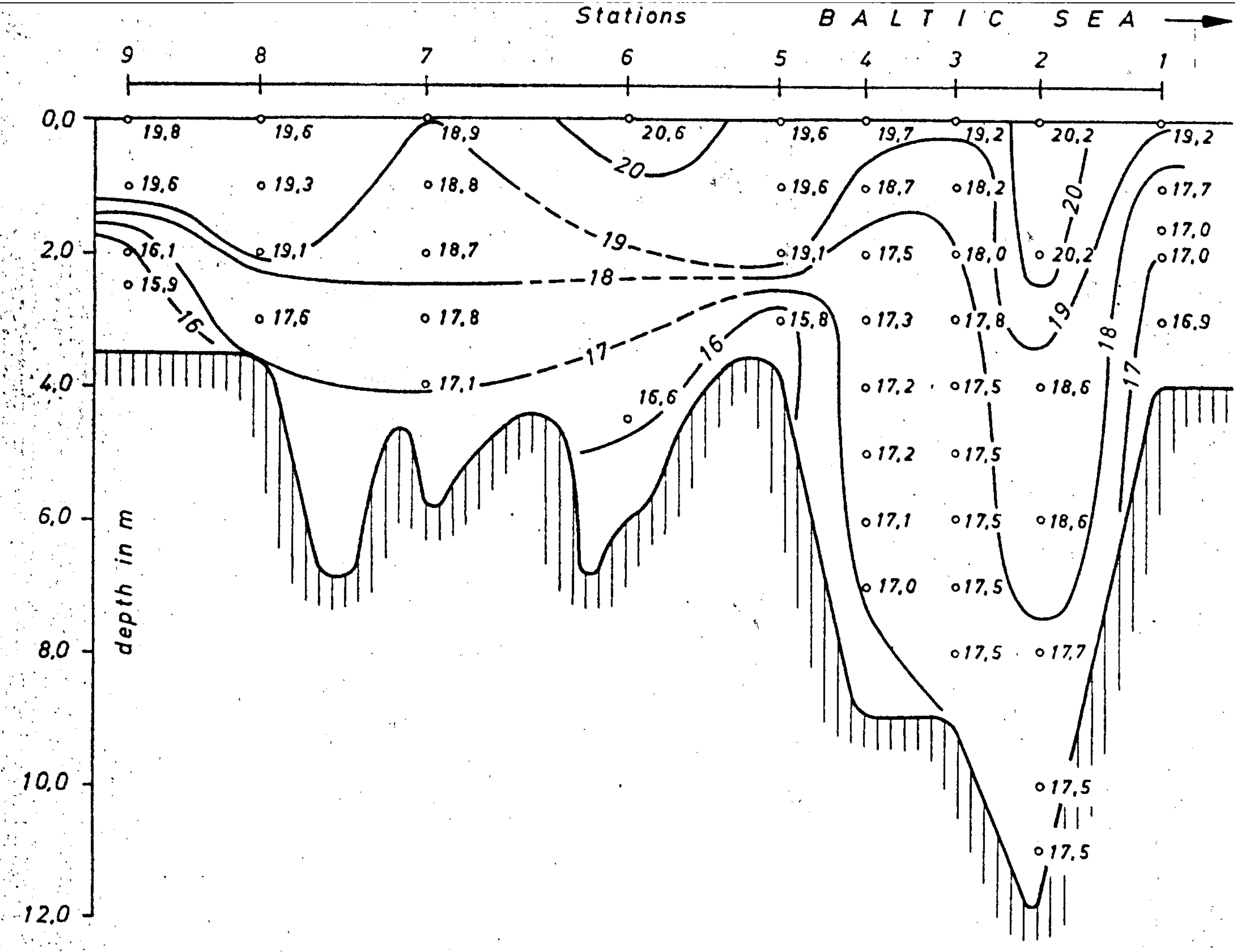

Figure 5: Vertical distribution of temperature (°C) in the Schlei on 11/12.6.69.

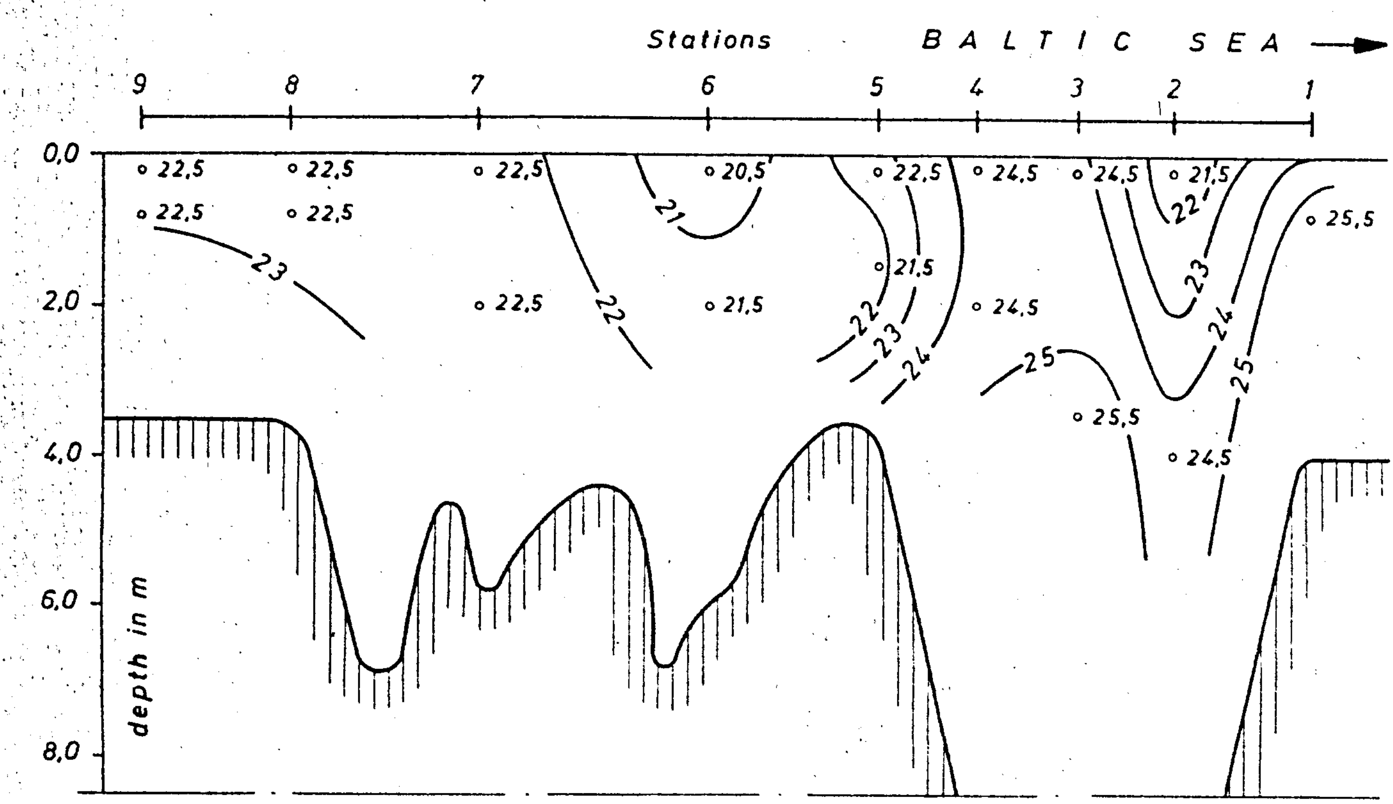

Figure 6: Isolines showing the distribution of the most frequent length groups of herring larvae (mm) in the Schlei on 11/12.6.69.

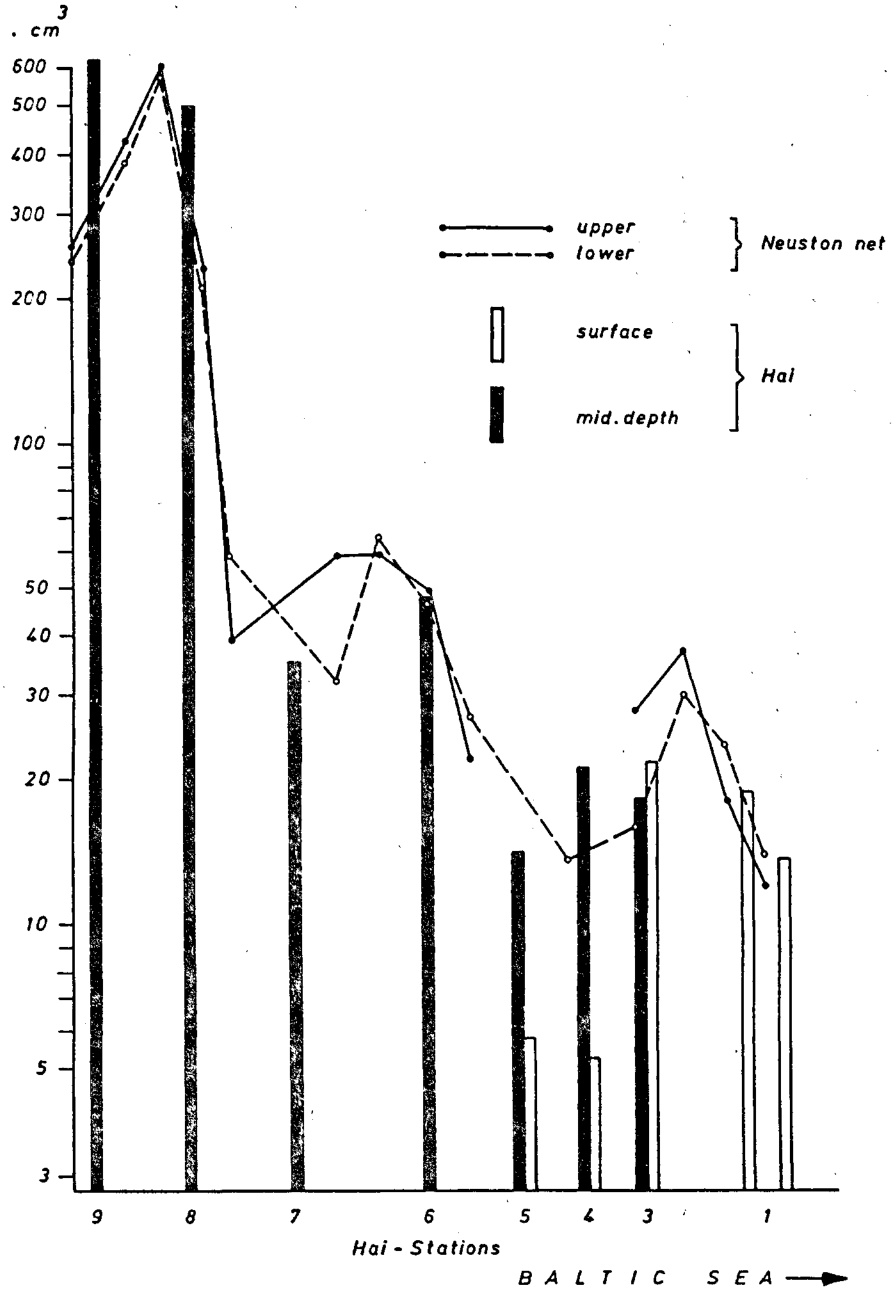

Figure 7: Settlementvolume of the invertebrate plankton (without coelenterata) from about 38 m³ water in the Schlei fjord on 28.5.1969.

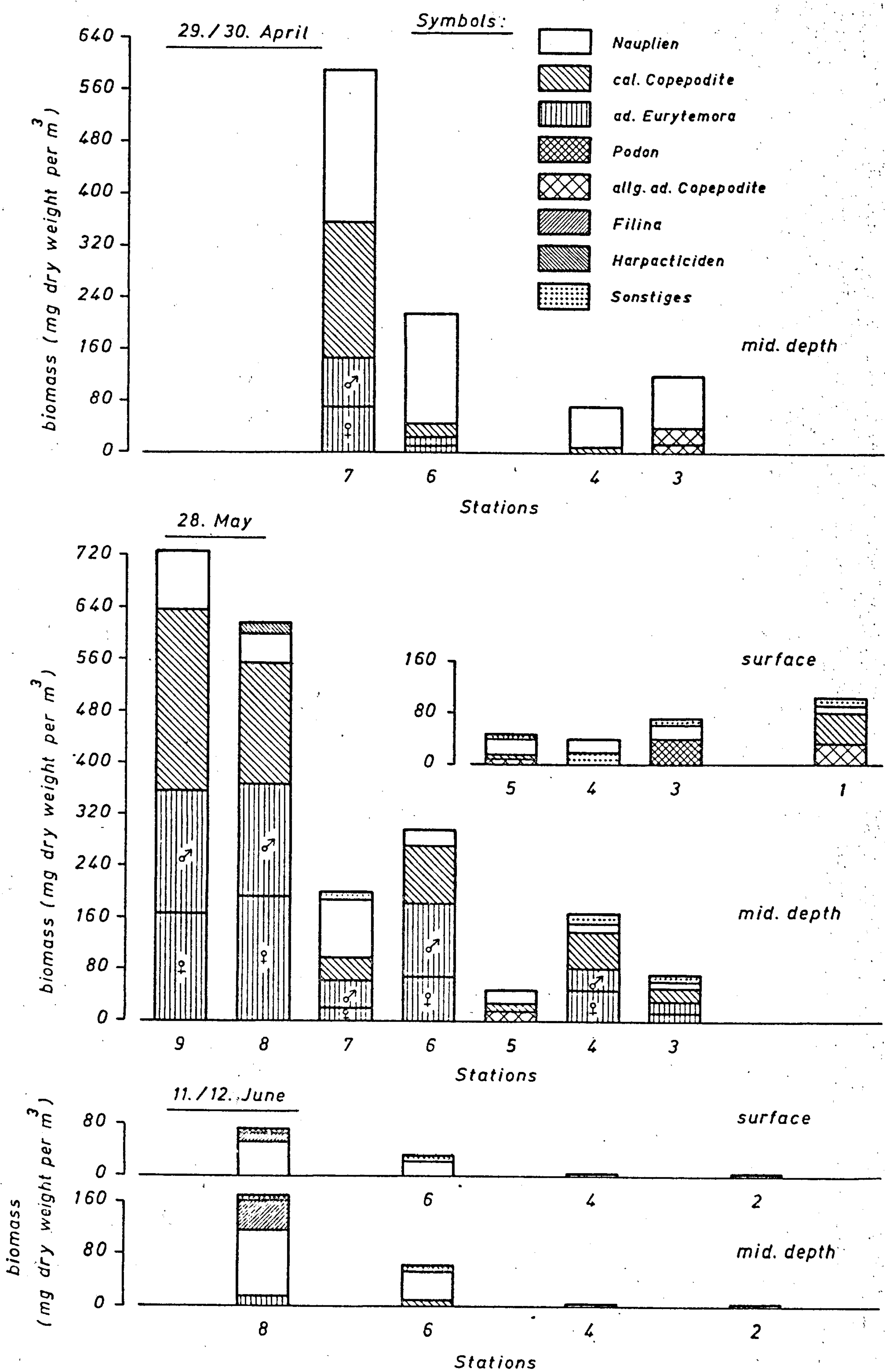

Figure 8: Distribution and composition of biomass of invertebrate plankton during three surveys in the Schlei fjord.

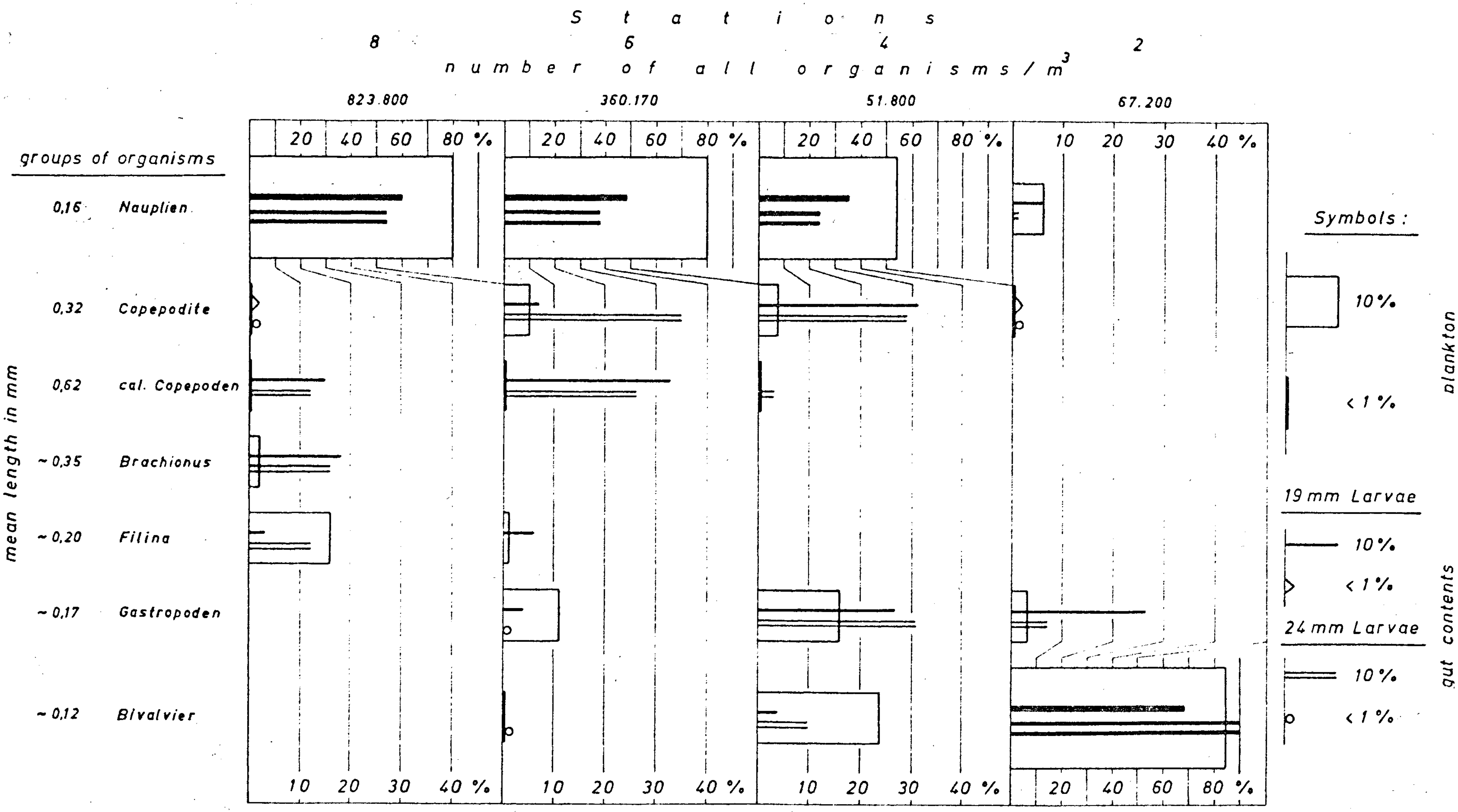

Figure 9: Relative abundance of the more important groups of invertebrate organisms in the plankton and in the guts of herring larvae in the Schlei on 11/12.6.69.

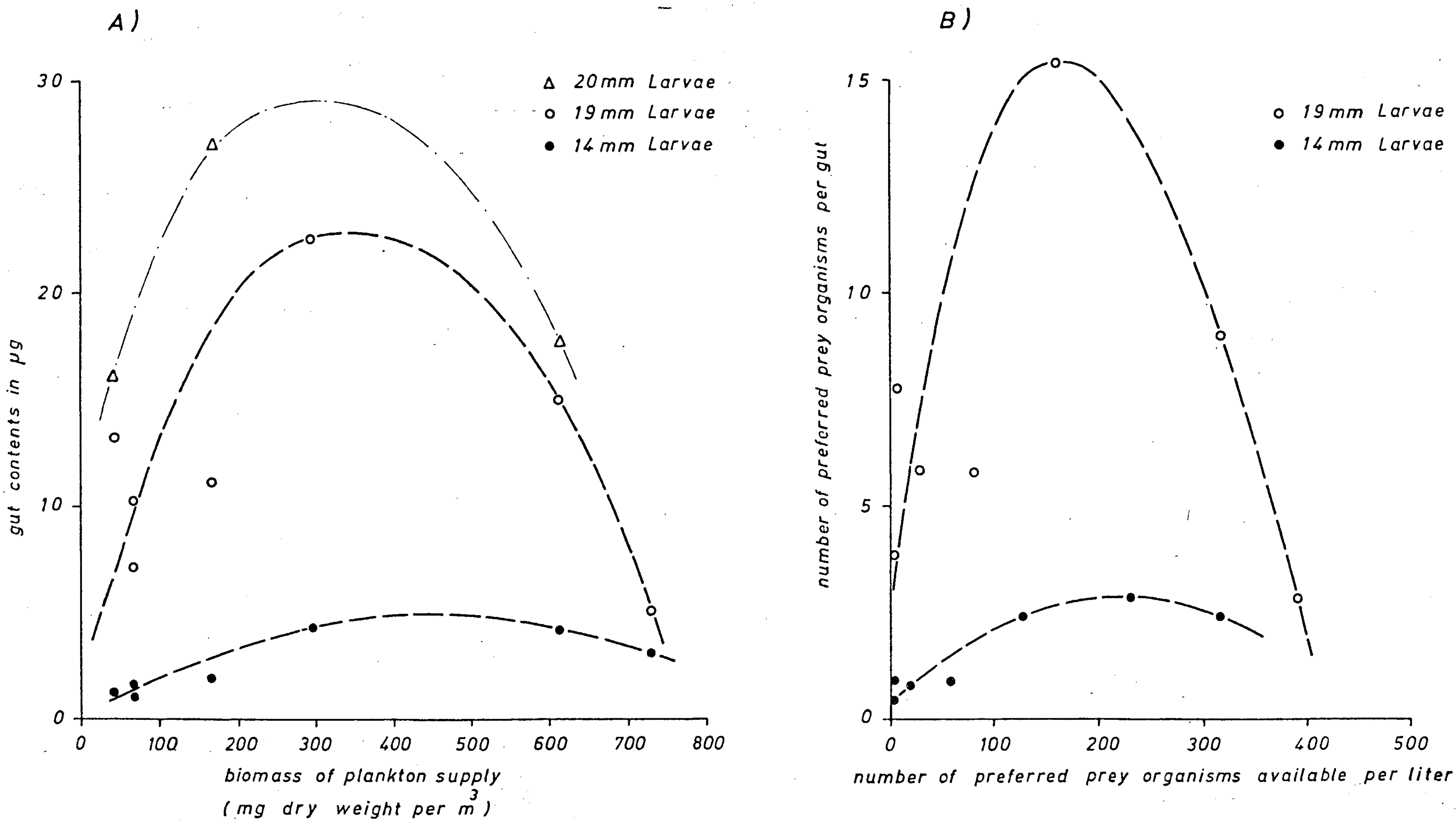

Figure 10: Relation between feeding and food supply (gut contents = biomass of prey organisms in ug dry weight).

Table 1 : Distribution of invertebrate plankton in the Schlei fjord on 28,5.1969

– number of organisms per m^3 –

Station	9	8	7	6	5	5	4	4	3	3	1
depth of haul (m)	2,30	2,30	1,10	2,30	2,30	0,50	2,30	0,50	3,30	0,50	0,50
calanoid Copepods											
Centropages											75
Pseudo- ♀					20		300		100		290
calanus ♂							100		15		260
Acartia					20	+	400		450		620
Eurytemora ♀	75.600	88.000	7.400	31.200	1.600	1.200	22.300	1.300	5.900	310	5.500
♂	102.000	92.000	23.900	61.000	6.000	2.400	17.900	1.200	9.300	560	7.300
Copepodites											
Eurytemora	217.000	140.000	26.600	68.400	8.700	3.600	40.700	4.000	13.900	1.100	25.500
other calan.							3.000	920	980	500	7.400
other Copepods											
Oithona							790	470	270	310	3.100
Harpacticoids		8.100	1.900	740	290	310	200	330	300	350	600
Copepod nauplii	872.000	515.000	917.000	205.000	192.000	273.000	142.000	227.000	88.900	235.000	99.000
Cirripede nauplii				740	380	160	200	40	+	100	75
Cladocera											
Podon			1.600		650	1.400	690	670	650	7.100	1.000
Evadne						+				+	+
Polychaete larvae				1.500	290	310	30.800	18.700	14.900	6.800	5.100
Mollusc larvae											
Gastropods							4.400	2.200	5.000	2.100	4.900
Bivalves								2.900	5.000	1.100	13.400
Rotifers											
Brachionus	46.000	7.400	2.700				+				+
others	170	1.100	+								
Tintinnids											+
Ceratia											510
Diatoms								+		+	+
Total	1 312.770	851.600	981.100	368.580	209.950	282.380	263.780	259.730	145.665	255.330	174.630

Table 2 : Distribution of invertebrate plankton in the Schlei fjord on 11/12. 6. 1969

– number of organisms per m^3 –

Station	8	8	6	6	4	4	2	2
depth of haul (m)	0,50	1,10	0,50	2,30	0,50	2,30	0,50	4,30
calanoid Copepods								
Acartia				+		+		
Eurytemora ♀	980	4.100	50	480				
♂	1.200	4.900	100	1.250				
calanoid Copepodites								
Eurytemora	+	4.600	4.600	39.000	750	2.500	60	100
others				+		+		+
other Copepods								
Harpacticoids	1.900	4.600	180	480	+	+	190	30
Copepod nauplii	463.000	825.000	201.000	390.000	20.000	20.000	3.300	3.500
Cirripede nauplii			+	+	+	400	170	140
Cladocera								
Podon	+	+		+				
Polychaete larvae		+	4.400	9.500	14.500	13.500	3.900	2.100
Rotifers								
Filina	53.000	247.000	4.400	1.500				
Brachionus	19.800	17.600	+	+				
Mollusc larvae								
Gastropods			52.800	7.800	5.800	6.000	2.000	1.550
Bivalves	+	+	+	3.100	7.300	10.300	48.800	57.500
Tintinnids					+	350	4.500	2.700
Ceratia		+					580	480
Diatoms			+	+	2.200	+	1.400	750
Total	539.800	1107.800	267.530	452.810	50.550	53.050	64.900	68.850

Table 3 : Composition of gut contents of herring larvae in the Schlei fjord on 28. 5. 1969

- number of organisms per 10 larvae -

length of larvae	20 mm				19 mm									14 mm									8 mm
station	8	4	4	mean	9	8	6	6	4	4	3	3	mean	9	8	6	6	4	4	3	3	mean	4
depth of haul (m)	2,0	2,0	0,2		2,0	2,0	2,0	0,2	2,0	0,2	3,0	0,2		2,0	2,0	2,0	0,2	2,0	0,2	3,0	0,2		2,0
calanoid Copepods																							
Acartia (adult)		1,0		0,3																			
Pseudo- ♀		2,0	2,7	1,6					1,7	0,8			0,3										
calanus ♂		9,0	1,8	3,6					3,3	1,7	0,9		0,7										
Eurytemora ♀	19,0	30,0	11,0	20,0	7,0	11,0	19,0	20,0	10,0	14,0	10,0	4,5	11,9			4,0	1,8					0,7	
♂	43,0	29,0	9,0	27,0	15,0	39,0	48,0	69,0	12,5	10,0	11,0	14,5	27,4	5,7	9,0	10,0	5,5	1,0	0,9	1,7	1,0	4,4	
calanoid Copepodites																							
Eurytemora	43,0	75,0	51,0	56,3	15,0	40,0	88,0	89,0	35,0	49,0	37,0	19,0	46,5	18,6	19,0	14,0	21,0	8,0	8,0	5,8	3,0	12,2	2,0
others			5,0	1,7						4,2	1,8		0,8										
Nauplii								3,0		0,8	43,0	13,6	7,6			21,0	29,0	55,0	32,0	36,0	63,0	29,5	9,0
not calanoid Copepods		4,0	2,7	2,2					9,0	1,7	0,9		1,5					3,0				0,4	
Podon			0,9	0,3					0,8			0,9	0,2										
T o t a l	105,0	150,0	84,1	113,0	37,0	90,0	155,0	181,0	72,3	82,2	104,6	52,5	96,9	24,3	28,0	49,0	57,3	67,0	40,9	43,5	67,0	47,2	11,0

Table 4 : Composition of gut contents of herring larvae in the Schlei fjord on 11/12. 6. 1969

- number of organisms per 10 larvae -

length of larvae	19 mm									24 mm								
station	8	8	6	6	4	4	2	2	mean	8	8	6	6	4	4	2	2	mean
depth of haul (m)	0,2	0,8	0,2	2,0	0,2	2,0	0,2	4,0		0,2	0,8	0,2	2,0	0,2	2,0	0,2	4,0	
calanoid Copepods																		
Eurytemora ♀	15	10	1	19					5,6	10	69	10	142		5			29,5
♂	9	18	1	18					5,8	18	113	12	98	6	6			31,6
others								1	0,1						2			0,3
Copepodites		1	2	4	4	9	1		2,6	3	2	92	242	89	157	6	3	74,3
other Copepods	1				2			2	0,6	26	4	1	3	12	11	5	22	10,5
Copepod nauplii	40	327	17	20	12	6	17	3	55,3	511	378	256	38	97	105	15	44	180,5
Cirripede nauplii			1						0,1		1			5	2	2	4	1,8
Cladocera (Podon)		6							0,8	4	4							1,0
Polychaete larvae					(2)				(0,3)					(3)	(8)	(2)	(1)	(1,8)
Rotifers																		
Brachionus	25	44							8,6	184	76							32,5
Filina	4	10	3	1					2,3	16	201							27,1
Keratella	1	1							0,3	2	2	2					1	0,9
Mollusc larvae																		
Gastropods			2		15	1,8	53	84	19,5			5	3	111	146	216	190	83,9
Bivalves					1	0,9	88	371	57,6			3		39	39	4080	1942	762,9
Tintinnids											2					7	19	3,5
Total	95	417	27	62	36	18	159	461	159,4	774	852	381	526	362	481	4333	2226	1242

( ) : only fresh polychaete larvae counted