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FOOD AND FEEDING OF YOUNG HERRING LARVAE OF NORWEGIAN SPRING SPAWNERS

By

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ABSTRACT

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The gut contents of young herring larvae sampled each hour from 3 to 9 April 1967 at three depth intervals around a floating drogue were examined to study their feeding.

Copepod eggs constituted more than 90% of the food items. Feeding started shortly after sunrise within the same hour in the depth intervals 25–5 m, 30–50 m and 75–55 m. Mean length increased with diminishing yolk sac until absorption when mean length decreased. The latter could indicate lack of suitable food.

The mean gut content of feeding larvae did not increase until after absorption of the yolk sac.

Larvae from the deepest strata had less gut contents than the others, probably because a lower percentage of them had absorbed yolk sacs.

A high percentage of larvae feeding during day-time contradicted total defecation due to capture.

No correlation was found between numbers of *Calanus* eggs in the guts and in plankton. Larvae containing *Calanus* nauplii had more assorted gut contents than larvae containing *Calanus* eggs.

The critical period concept is discussed.

INTRODUCTION

Due to the widely held opinion that year-class strength of herring and other fish species is determined during early life, many investigations have dealt with larval stages.

Analyses of food and studies of feeding behaviour have drawn great interest. Several authors have compared the composition of the gut contents of herring larvae with the surrounding plankton, and attempts have been made to estimate the amount of food required for survival (for references see BLAXTER and HOLLIDAY 1963, BLAXTER 1965, SAVILLE 1971, SCHNACK 1972 and MAY 1974).

Most of these investigations, however, dealt with herring larvae from the North Sea and the Baltic and rather little is known about Atlanto-Scandian herring larvae. The plankton at the spawning grounds of this stock is dominated to a much greater degree by *Calanus finmarchicus* than the plankton at the spawning grounds of other stocks. This reduces the diversity of the available food and makes the larvae more or less dependent on one type of food organism.

DRAGESUND (1970) assumes the coincidence in time between occurrence of suitable food and hatching of herring larvae to be the most important environmental factor controlling year-class strength during early larval development of Norwegian spring spawners. The aim of the present investigation was to study a) the food composition of Norwegian spring spawners, b) factors affecting their gut contents, c) selection of food particles, and if possible d) to discover any critical periods.

MATERIALS AND METHODS

The Institute of Marine Research, Bergen, carried out extensive investigations at the spawning grounds of economically important fish as part of the International Biological Programme during the years 1967–1971. The material used in the present work was selected from an experiment to study the drift of herring larvae off the West coast of Norway (DRAGESUND and NAKKEN 1971).

Sampling was carried out 3–9 April 1967 in a larval concentration marked by a floating drogue. The sampling area around the floating drogue covered 1 nautical mile^2. Larval samples were taken almost every hour as oblique hauls with three permanently open Clarke-Bumpus plankton samplers equipped with nylon nets of 500 μ mesh size. Total towing time was 20 minutes, and the samplers were raised in 5 m steps each 4 minutes. The sampling intervals were 25–5 m, 50–30 m and 75–55 m, and the towing speed was 1.5–2 knots. Plankton samples were taken at noon and midnight with Clarke-Bumpus plankton samplers equipped with nylon nets of 90 μ mesh size. The procedure was the same as for larval sampling, except for the use of the closing mechanism of the sampler and a reduction in towing time to 5 minutes.

Larvae from this material were selected for examination as follows (Table 1):

a) Larvae sampled during a 45 hour period from the 25–5 m depth interval to compare feeding intensity with time of day.
b) Larvae sampled during the last 24 hours of the previous period (a) from 50–30 m and 75–55 m to compare feeding intensity in all three depth intervals. Reduction in bottom depth below the floating drogue made this sequence incomplete.
c) Larvae from the plankton samples to compare gut contents and plankton composition, and larvae from the larval hauls nearest in time to these

plankton hauls to increase information when comparing gut contents and plankton composition.

The larvae were examined after six months preservation in 4% formaldehyde.

When present, 50 larvae from each sample were examined. The larvae varied in length from 6.4 to 12.4 mm with an average length of 9.8 mm.

The plankton samples were usually divided into subsamples of a hundredth with a plankton divider (WIBORG 1951), and two of these subsamples were then examined.

Reference to larvae caught at, for example, 1300 hrs., indicates that they were taken between 1230 and 1329. All times referred to are in local Norwegian time. When unspecified eggs and nauplii are mentioned, these are the eggs and nauplii of *Calanus finmarchicus*.

RESULTS AND DISCUSSION

COMPOSITION OF FOOD

Eggs of *Calanus finmarchicus* constituted in number 91.7% of the gut contents, while nauplii of the same species made up 4.6%. Eggs, nauplii and remains of copepod species other than *Calanus* constituted 2.9%.

BLAXTER (1965) reviewed work done on selection of food by herring larvae. He concluded that smaller larvae caught at sea most frequently contain copepod nauplii and eggs, mollusc larvae and some green food. However, a diet consisting of 92% copepod eggs as observed in the present work (Table 2), seems not to have been recorded from larvae of other stocks than Atlanto-Scandian herring. Other authors examining Norwegian spring spawner larvae also report a high percentage of *Calanus* eggs in the diet. SOLEIM (1942) found that *Calanus* eggs constituted the bulk of the larval diet, while RUDAKOVA (1971) found that they constituted 81.7 and 80.9% of the diet in 1966 and 1967 respectively. BJØRKE (1971) observed that *Calanus* eggs constituted in number 93% of the gut contents of young herring larvae.

SCHNACK (1972) examined the gut contents of herring larvae from the North Sea and the western Baltic. Although he found copepod eggs in the guts, no signs of digestion could be seen. This seems to be in contrast to the present investigation where the ratio of 1:2 empty shells to undigested eggs in the guts suggests that *Calanus* eggs are digested by the larvae. The finding of three empty shells and 59 undigested eggs in the foremost part of the guts shows that rather few empty shells are eaten by the larvae. Digestion of copepod eggs is also supported by a rather low percentage (3.3) of undigested eggs in the rectum. However, the findings of higher ratios of undigested to digested *Calanus* eggs as opposed to *Calanus* nauplii suggests that the digestion of eggs is slower than that of nauplii.

The largest food item, a *Balanus* sp. nauplius stage VI, was found in a larva 10.2 mm long.

Table 1. Numbers of examined larvae from the different depth strata.

	90 μ net															
Date, April	3	4		5					6	7		8		9		
Hour	24	15	16	01	02	12	14	24	13	01	12	24	14	01	13	Total
Depth, m																
25–5	7	17	12	21	30	27	35	53	9	–	1	–	5	1	2	220
50–30	–	–	–	–	11	15	–	17	30	5	6	20	5	15	4	128
75–55	–	–	–	–	53	–	7	2	–	23	5	–	–	–	–	90

	500 μ net																					
Date, April	4	5															6					
Hour	13	06	07	08	09	10	11	14	15	16	17	18	19	20	21	22	01	02	03	04	05	07
Depth, m																						
25–5	49	50	50	49	100	50	50	50	100	50	50	98	50	49	50	100	103	–	58	50	50	127
50–30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	169	50	102	–	50	100
75–55	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	117	51	101	47	35	47

	500 μ net continued																				
Date, April	6												7				8		9		
Hour	08	10	12	13	15	16	17	18	19	20	21	22	01	02	10	11	09	12	12	16	Total
Depth, m																					
25–5	52	37	19	32	13	29	17	16	27	49	57	8	6	–	34	24	31	3	27	49	1 913
50–30	50	60	92	–	50	63	–	9	25	37	5	50	26	–	–	–	–	–	–	–	938
75–55	33	29	15	–	–	–	–	–	–	–	–	–	–	37	–	–	–	–	–	–	512

Table 2. Composition of food of 1707 herring larvae.

Undigested food			Digested food		
Types of food	Number	Percentage of total number	Types of food	Number	Percentage of total number
Calanus eggs	2 558	60.42	*Calanus* eggs	1 325	31.30
Calanus nauplii stages I–IV	58	1.37	*Calanus* nauplii stages I–IV	115	2.72
Calanus nauplii stages V–VI	7	.17	*Calanus* nauplii stages V–VI	11	.26
Microcal. nauplii	3	.07	Unidentified nauplii	11	.26
Balanus nauplii	1	.02	*Oithona* nauplii	1	.02
Unidentified nauplii	13	.31	Remains of copepods	67	1.58
Oithona eggs	17	.40	Unidentified objects	34	.81
Metridia eggs	1	.02			
Microsetella	9	.21			
Coscinodiscus	3	.07			

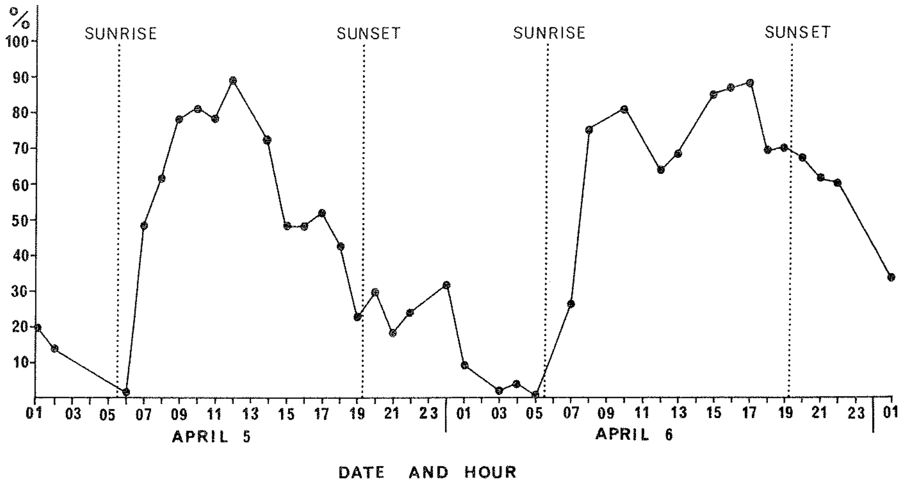

Fig. 1. Percentage of larvae from the 25 – 5 m hauls with undigested gut contents.

FEEDING ACTIVITY

Feeding started shortly after sunrise and declined at nightfall (Fig. 1).

Feeding started within the same hour in all three depth intervals. This activity correlates with observations made by BAINBRIDGE and FORSYTH (1971) on herring larvae in the Clyde. Assuming that the light threshold for feeding is the same at dusk and dawn, feeding activity should have ended at about 1830. Time available for feeding during a 24 hour period would therefore be 13 hours. This differs a little from the 16–18 hours available at 64° N as suggested by BLAXTER (1966). He points out, however, that this is a maximum period based on light measurements taken at the surface; therefore the nearly total cloud coverage of the sky during the 45 hour period of the present investigation may have altered the time available for feeding.

The percentage of larvae with undigested gut contents was rather high at 2000 hrs. in the 25–5 m layer. Therefore, references later in this report to larvae caught during daylight include larvae caught between 0630 and 2029.

YOLK SAC SIZE AND LARVAL LENGTH

The mean length of the larvae increased with decreasing yolk sac size until absorption of the yolk sac, when the mean length decreased. This could indicate insufficiency of suitable food during that period.

The yolk sacs were classified as large, medium, small, absorbed and detatched. Fig. 2 shows the mean length, observed range and 95% confidence limits of 3770 larvae with the various yolk sac sizes. The range

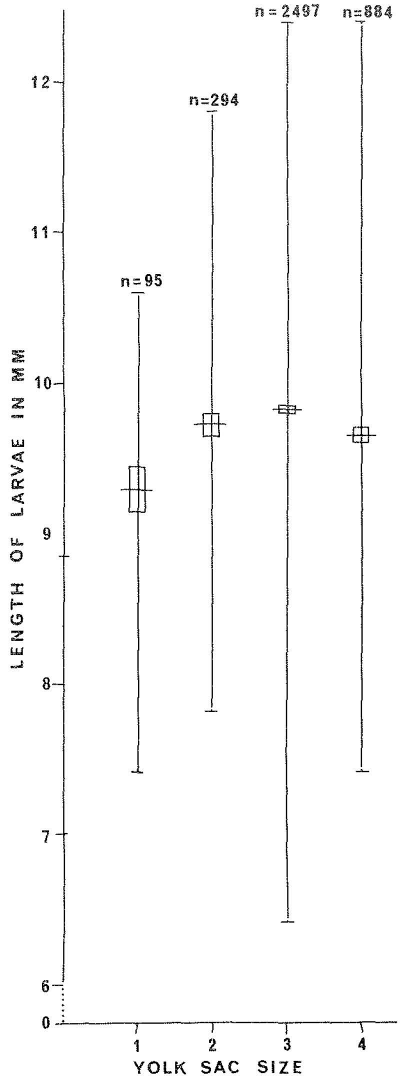

Fig. 2. Mean length, observed range and 95 % confidence limits of the herring larvae examined compared to yolk sac size. 1: large, 2: medium, 3: small, 4: absorbed.

within each stage overlaps to a considerable extent, yet t-tests show significant differences in mean length except for larvae with medium and absorbed yolk sacs. Similar overlapping was found by SOLEIM (1940) and RUDAKOVA (1971) in Norwegian spring spawners, and RUDAKOVA suggests that the overlapping shows differences in composition of the spawners. HEMPEL and BLAXTER (1963) and BLAXTER and HEMPEL (1963) found that herring females with large eggs generally produce larger and presumably stronger larvae with more yolk reserves at hatching. The overlapping in lengh of larvae with different yolk sac sizes might thus indicate differences in composition of the spawners as these authors suggest, but it might also indicate that feeding reduces absorption of the yolk sacs.

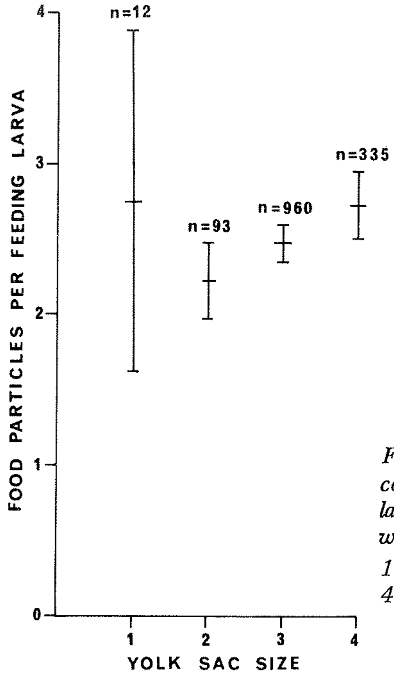

Fig. 3: Mean gut content and 95 % confidence limits of feeding larvae caught during daylight compared with yolk sac size.
1: large, 2: medium, 3: small, 4: absorbed.

Reduction in mean length with absorption of yolk sac, combined with the fact that the same larvae had the largest gut contents, (see later) could indicate insufficiency of suitable food for the larvae after absorpion of the yolk sac. BLAXTER and HEMPEL (1963) report shrinkage in body length of larvae starved under laboratory conditions.

FACTORS AFFECTING AMOUNT OF FOOD IN THE GUT

1. Yolk sac size

The percentage of larvae feeding increased with decreasing yolk sac size, but the mean gut content of feeding larvae did not increase significantly until absorption of the yolk sac.

Almost all authors who have studied feeding of herring larvae, report feeding before the yolk sac is absorbed. Of the 2150 larvae caught during daylight in the present work, 27% of those with large yolk sacs contained food, as did 61, 65 and 70% with medium, small and absorbed yolk sacs, respectively. When omitting the larvae without food, only larvae with absorbed yolk sacs had significantly greater gut contents than larvae with medium and small yolk sacs (Fig. 3).

This observation corresponds with that of ROSENTHAL and HEMPEL (1971) who found that herring larvae with yolk sacs were not successful in catching food items. The high mean gut content of the 12 larvae with large yolk sacs (Fig. 3) has to be disregarded because of few observations.

2. Depth

The highest mean gut content and the largest proportion of feeding larvae were found in the 50–30 m layer.

When studying the amount of gut contents in larvae from different depth intervals, only those caught during a short daylight period were examined to reduce the influence of changes in plankton. Therefore, only larvae caught between 0630 and 1229 on 6 April could be examined from the present material. The mean gut content per larva from the upper to the lowest depth strata was 1.1, 1.6 and 0.7 organisms, and the proportion of larvae with gut contents was 55, 56 and 39% respectively. All the differences between mean gut content were significant at the 5% level.

In the 25–5 m and 50–30 m plankton hauls taken at 1300 hrs. the numbers of *Calanus* eggs and nauplii were 4000 and 5600 organisms per m^3 respectively. Due to insufficient depth the 75–55 m plankton hauls had to be omitted that day. However, on the preceeding and following nights the densities of eggs added to nauplii were 1500 and 3200 per m^3 respectively.

It is questionable as to whether the number of food items in the different depth layers caused the differences found in mean gut content, since the variation coefficient of a single plankton sample is known to be high (CASSIE 1963). Larvae from the deepest layer had the lowest mean gut contents and the lowest percentage of feeders. It was concluded earlier that larvae without yolk sacs had higher mean gut contents than the others. The percentage of larvae at this stage was 18 in the deep layer as opposed to 53 in the two upper ones; therefore it is conceivable that the low mean gut content and low proportion of larvae feeding were due to the low percentage of larvae with absorbed yolk sacs found in this layer.

3. Defecation

Evidence for recent defecation was not found in this material. The high ratio of larvae with gut contents indicates that total defecation took place only to a lesser degree during capture and fixation.

HØGLUND (1968) observed a difference in the condition of the intestine between larvae that had apparently not contained any food for rather a long time and those that had emptied their guts shortly before capture. In the former the whole alimentary canal was transversely contracted with no hollowness visible, while in the latter the hindermost part of the gut immediately before the anus was more or less wide open. He also found a connection between time of feeding and ratio of larvae with distended guts. The condition of the intestine was recorded during the present investigation. After examination of larvae from the 25–5 m hauls no diurnal pattern could be seen in the ratio of larvae with distended guts. Eighty-eight per cent of 1371 larvae caught during daylight had distended guts, as had 90% of 625 larvae caught at night.

Some authors have observed partial or total defecation by stressed larvae (HARDY 1924, BLAXTER 1965, ROSENTHAL and HEMPEL 1971). It is thus conceivable that larvae from hauls of short duration would contain more food than those from longer ones. The number of food particles from 108 larvae caught during daylight in the upper 25 m in six 5 minute hauls was compared with that of 235 larvae caught in 20 minute hauls immediately before or after the 5 minute hauls. No significant difference in number of food particles was found when applying a t-test. This does not indicate that no defecation occurred, it might just as well show that the degree of defecation at capture and fixation is the same in both types of hauls. However, the high ratio of larvae with gut contents (Fig. 1) indicates that total defecation only took place to a lesser degree during capture and fixation.

4. Selection of food particles. Food densities

The two dominant organisms in the zooplankton, *Calanus* eggs and nauplii, were also the two dominant food items. No correlation was found between the number of *Calanus* eggs in plankton and in guts.

Larvae consuming *Calanus* eggs had a less assorted diet than those eating *Calanus* nauplii.

When studying selection of food particles, only larvae caught together with the food, in this case only larvae from the daylight plankton hauls, should be examined. Unfortunately some of the plankton hauls had rather few herring larvae (Table1). When the number of larvae from these hauls was less than 15, all larvae from the previous or following larval hauls were included. If the total number thus reached was still less than 15, the data were not used. A total of eight camparisons between plankton composition and gut contents could thus be made (Table 3). The ratio of *Calanus* eggs was usually higher in the larval guts than in plankton, while that of *Calanus* nauplii was lower, except when the density of nauplii exceeded ca. 5000 per m^3. Disregarding one observation, the percentage of *Microsetella* spp. and of other copepods was always higher in plankton than in the guts. Cyclopoid nauplii were not found in the guts of these larve although they constituted up to 25% of the plankton.

BLAXTER (1965) stated that herring larvae 8 mm long could take food items up to 1.3 mm in length, and this would normally include stage II copepodites of *Calanus finmarchicus* (WIBORG 1948). This implies that most of the organisms present in plankton could have been ingested by the herring larvae (Table 3), but obviously *Calanus* eggs and nauplii were preferred.

Serveral authors report discrepancies between composition of gut contents of herring larvae and surrounding plankton. HARDY (1924) found that *Pseudocalanus* was preferred to *Acartia* even when both were present in equal numbers. BHATTACHARYYA (1957), on examining plankton from the same hauls as larvae, found that many more planktonic organisms were available

Table 3. Composition of zooplankton and gut contens of herring larvae caught concurrently.

Sample	4 April, 15 hrs.				5 April, 12 hrs.				5 April, 14 hrs.				6 April, 13 hrs.			
Depth interval	25–5 m				25–5 m				25–5 m				25–5 m			
No. of larvae from plankton hauls	17				27				35				9			
No. of larvae from larval hauls	0				0				0				32			
Food items	In plankton		In diet		In plankton		In diet		In plankton		In diet		In plankton		In diet	
	No./m^3	%	No.	%	No./m^3	%	No.	%	No./m^3	%	No.	%	No./m^3	%	No.	%
Calanus eggs	2 200	63.6	40	97.6	500	38.2	61	96.8	420	42.9	54	100	3 660	85.7	80	96.4
Calanus nauplii	300	9.5	0	0	60	4.6	0	0	110	11.2	0	0	340	8.0	2	2.4
Cyclopoid nauplii	450	13.0	0	0	330	25.0	0	0	20	2.0	0	0	90	2.1	0	0
Microsetella spp.	40	1.2	0	0	10	0.8	0	0	100	1.2	0	0	0	0	0	0
Other copepods	430	12.0	0	0	400	30,5	0	0	330	33.7	0	0	110	2.3	1	1.2
Other items	10	0.3	1	2.4	10	0.8	2	3.2	0	0	0	0	70	1.6	0	0

Continued:

Samples	4 April, 12 hrs.				6 April, 13 hrs.				7 April, 11 and 12 hrs.				9 April, 12 and 13 hrs.			
Depth interval	50–30 m				50–30 m				25–5 m				25–5 m			
No. of larvae from plankton hauls	15				30				1				2			
No. of larvae from larval hauls	0				0				24				27			
Food items	In plankton		In diet		In plankton		In diet		In plankton		In diet		In plankton		In diet	
	No./m^3	%	No.	%	No./m^3	%	No.	%	No./m^3	%	No.	%	No./m^3	%	No.	%
Calanus eggs	990	37.5	40	97.6	2 960	45.2	113	92.6	11 000	58.3	15	60.0	14 390	64.5	17	53.1
Calanus nauplii	550	20.3	0	0	2 680	40.9	6	4.9	5 320	28.2	8	32.0	5 240	23.5	11	34.4
Cyclopoid nauplii	620	23.9	0	0	150	2.3	0	0	350	1.9	0	0	260	1.2	0	0
Microsetella spp.	140	5.3	1	2.4	220	3.4	0	0	170	0.9	1	4.0	0	0	0	0
Other copepods	280	10.6	0	0	470	7.2	0	0	1 070	5.7	1	4.0	1 870	8.4	4	12.5
Other items	50	1.9	0	0	70	1.1	3	2.5	970	5.1	0	0	550	2.5	0	0

Table 4. Frequency of different kinds of gut content compared with yolk size.
A χ^2 test for *k*-independent samples.
E = Expected frequency. O = Observed frequency.

Gut Contents	Yolk sac size			Total
	Absorbed	Small	Medium and large	
Copepod eggs	E 281.8	807.5	88.6	
	O 276	820	82	1 178
Copepod eggs and other objects	E 33.5	96.0	10.5	
	O 35	89	16	140
Other objects	E 18.7	53.5	5.9	
	O 23	48	7	78
Total	334	957	105	1 396

$\chi^2 = 6.022$ df = 4 $p > 0.05$

than were eaten by the larvae. HENTSCHEL (1950) found that copepod nauplii were not eaten although they constituted up to 50% of the plankton, and that copepodites and adults were preferred instead although they constituted only 6%. WALDMANN (1961) found that copepods were by far preferred and the *Eurytemora* prevailed in the food in spite of its rare occurrence in the plankton.

A t-test for k independent samples (SIEGEL 1956) was applied to find out if a decrease in yolk sac size led to a change in the larval diet (Table 4). The test, comprising 1396 larvae containing food caught during daylight, did not show any significant change in composition of yolk sac size with different diets. Student t-tests on the same material did not reveal significant changes in mean length with different diets. This means that, within the size groups represented in this investigation, selection of food is not dependent on the age of the larva. This correlates with observations made by other authors (LEBOUR 1921, HARDY 1924, BOWERS and WILLIAMSON 1951) who found that changes in diet did not occur until after the yolk sac stage.

Table 3 shows a considerable increase in number of both *Calanus* eggs and nauplii on 7 and 9 April. In order to find any correlation between food items in the plankton and in the guts, the numbers of *Calanus* eggs and nauplii in plankton were rounded off to the nearest thousand and compared to the mean number of the same items per larva by the Spearman rank correlation coefficient (SIEGEL 1956) (Data from Table 3). Significant correlation was found with *Calanus* nauplii, but not with eggs.

To eliminate any possible influence of larvae too weak to feed, the mean numbers of eggs and nauplii per larva containing food were compared to the numbers of those items in the plankton. Again, significant correlation was found with nauplii, but not with eggs. Also the number of eggs and nauplii per larva containing food caught during daylight was correlated with the number of the same items in the plankton. The results were the same; significant correlation was found only between nauplii ingested and in plankton. A possible explanation for the above observations could be that the larvae had developed the habit of catching specific food items. After laboratory experiments ROSENTHAL (1969) suggested that herring larvae might gain preferece for certain kinds of food items during the early life stages, depending on their success in catching the first food particle. He also found that a change in diet from copepod nauplii to *Artemia* did not occur until 3-4 days after the other kind of food particle was added to the original ones. Thus the eight comparisons of diet and plankton composition in Table 3 might represent different larval populations, each population containing larvae searching for food items which they have been successful in catching previously. The increase in number of both eggs and nauplii on 7 and 9 April was obviously due to the fact that the floating drogue became surrounded by a different watermass. This increase in eggs would not lead to an increase in the number of eggs in the larval diet if the new watermass also contained larvae used to catching nauplii. This might also be the reason for the observed correlation between nauplii in plankton and diet. In the samples taken before 7 April the number of nauplii in plankton was low, and the larvae present were in the habit of catching eggs. The samples from 7 and 9 April had higher numbers of nauplii both in plankton and in the diet, and this made the correlation significant.

Of 1256 larvae containing *Calanus* eggs, 5% contained other food items; and of 40 larvae containing *Calanus* nauplii, 28% contained other food items. Larvae containing both eggs and nauplii are not included in these figures. Thus it seems that larvae eating nauplii have an increased ability to catch other food items compared to larvae eating eggs

BLAXTER (1965) refers to investigations where food concentrations required by herring larvae varied from between 300 to 22 000 organisms/m^3. In the present investigation the densities of eggs added to nauplii varied from 530 to 18 990, with an average of 6 300 food praticles per m^3, *Calanus* eggs constituting 71% of these. However, since *Calanus* eggs constituted more than 90% of the gut contents and the nutritional value of one egg is low compared to that of the usually larger organisms reported to be eaten by herring larvae, the observed densities of food in the present work were probably still too low to maintain survival and growth. Also, the decrease in mean length of larvae without yolk sacs (Fig. 2) could indicate deficiency of suitable food after absorption of the yolk sac. DRAGESUND and

NAKKEN (1971) investigated mortality among larvae from the same larval patch as was studied in the present work. They found a reduction of about 95% of the larval population at a length which corresponded to the period of completion of yolk absorption.

THE CRITICAL PERIOD

The critical period concept suggested by HJORT (1914), maintains that the strength of a year-class is determined by the availability of planktonic food shortly after the larval yolk supply has been exhausted. MAY (1974) reviewed this concept in the light of ecological and experimental data. He stated that although other factors also undoubtedly influence larval survival at sea, field and laboratory data suggest that starvation may be an important cause of larval mortality at the end of the yolk sac stage.

Attempts have been made to compare the amount of gut contents of herring larvae with the abundance of available food. LISHEV, RANNAK and LISIVNENKO (1961) report a relationship between the abundance of herring and fry and the number of food organisms in the Bay of Riga from 1955 to 1961. (Quoted from BLAXTER and HOLLIDAY 1963). BAINBRIDGE and FORSYTH (1971) found high feeding intensities associated with high biomass of available prey organisms in the Clyde. SCHNACK (1972) found correlation between biomass in guts and in plankton. Several authors, however, report discrepancies between composition of gut contents and surrounding plankton. HARDY (1924) found that *Pseudocalanus* was preferred to *Acartia* even when present in equal numbers. BHATTACHARYYA (1957), on examining plankton from the same haul as the larvae, found that more planktonic organisms were available than were eaten by the fish. HENTSCHEL (1950) found that copepod nauplii were not eaten although they constituted up to 50% of the plankton, and that copepodites and adults were preferred instead, although they constituted only 6%. WALDMANN (1961) found that copepods were by far preferred and that *Eurytemora* prevailed in the food in spite of its rare occurrence in plankton. SCHNACK(1972) found it difficult to correlate the ingestion of copepod nauplii and gastropod larvae to their quantitative presence in plankton. LEBOUR (1924) found that herring larvae contained mainly molluscs, copepods and unicellular matter (green food remains). Disregarding the latter, as it is not clear whether this is eaten by the copepods before they themselves are ingested, her data shows that only 15% of the larvae containing molluscs and 14% of those containing copepods had other gut contents. DUKA(1968) characterised clupeoid larvae as stenophagous; i.e. the qualitative food components of the larvae are restricted to two or three species of organisms. This is probably the explanation of the findings mentioned previously. The different larval populations become accustomed to catching certain food items and continue to search for these despite greater abundance of other food organisms.

Herring larvae are known to start feeding while they still have large yolk sacs, most probably in order to be able to catch food items when the yolk sac is eventually absorbed and they become dependent on external food.

As food objects *Calanus* eggs are non-motile and without spines, and should thus be easy to catch from any direction. However, they hatch within 24 hours, while development through the nauplius stages lasts for at least 20 days (JONES and HALL 1974). Even if single *Calanus* females are observed to spawn over several weeks (MARSHALL and ORR 1955) and eggs are thus to be found over a long period, nauplii are available over a much longer period. So, if a larva gains preference for *Calanus* eggs because of a temporarily high percentage in the plankton, it will still be searching for them when it becomes dependent on external food. At this stage the surrounding food items might consist mainly of nauplii hatched from the eggs. ROSENTHAL (1969) found that herring larvae needed 3–4 days to change from ingesting copepod nauplii to taking *Artemia*, in other words, from one motile organism to another. The time needed to change from non-motile *Calanus* eggs to nauplii as diet might be longer and thus exceed the time required to reach the «point of no return» as indicated by BLAXTER and EHRLICH (1974). This describes the point at which 50% of a larval population are too weak to feed if food becomes available. For herring larvae this was found to occur six days after absorption of the yolk sac. Difficulties in changing from non-motile to motile food items may also account for the rather low percentage of larvae observed containing *Calanus* eggs together with other food items in this investigation.

On the other hand, larvae starting to feed in a watermass where *Calanus* nauplii are the dominant food items have a lesser likelihood of entering watermasses containing unfamiliar food organisms, as nauplii are present in plankton for a much longer period than eggs and are thus more dispersed. It also seems from the present investigation that the ability to catch nauplii increases the ability to catch other motile food items, since the percentage of larvae containing both nauplii and other food organisms was rather high. This could increase the chance for survival due to the wider food range available to the larvae.

DRAGESUND (1970) stressed the importance of coincidence in time between hatching of herring larvae and the occurrence of suitable food when considering the survival of the larvae. It appears that this coincidence must be emphasized; not only must suitable food be present when the larvae start to feed, but if they gain preference for certain kinds of food at this stage, as suggested by ROSENTHAL (1969), it is of importance for the survival that the same kind of food is available and abundant when they become dependent on external food. This implies that larvae starting to feed when *Calanus* eggs are predominant in plankton have less chance of surviving than those starting to feed when nauplii are abundant.

CONCLUSION

The kind of food particles eaten by smaller larvae of Norwegian spring spawners was similar to that of herring larvae of other races. The proportion of copepod eggs in the diet however, was different, constituting more than 90% of the food items.

Feeding seemed to start shortly after sunrise within the same hour in the depth intervals 25–5 m, 30–50 m and 75–55 m.

The length range of larvae with different yolk sac sizes overlapped considerably, yet t-tests showed an increase in mean length with decreasing yolk sac size, except for larvae with absorbed yolk sacs which were shorter than those with small yolk sacs. This could indicate lack of suitable food after the yolk sac stage.

The percentage of larvae feeding increased with decreasing yolk sac size, but the mean gut content of feeding larvae did not increase until after absorption.

Larvae from the deepest strata, 75–55 m, had less gut contents than the others, probably because of a lower percentage of larvae with absorbed yolk sacs in this depth layer.

Some authors report larvae defecating partially or totally when stressed. Larvae from hauls of short duration did not have greater gut contents than larvae from longer ones. Total defecation was contradicted by the high ratio of feeding larvae caught during daylight.

No correlation was found between the number of *Calanus* eggs in the guts and in plankton. Larvae containing nauplii had more assorted gut contents than larvae containing eggs.

A «critical period» could arise when larvae having learned to feed on *Calanus* eggs have to change to motile objects when nauplii hatch.

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