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Rate of digestion, selection of food and daily rations in herring larvae, *Clupea harengus* L.

By Harald Rosenthal

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RATE OF DIGESTION, SELECTION OF FOOD AND DAILY RATIONS IN HERRING LARVAE, Clupea harengus L. [1]

by Harald ROSENTHAL

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Abstract

Rate of digestion, selection of food and daily rations in herring larvae. During rearing experiments with herring larvae digestion time was estimated (total length of the larvae 10 to 14 mm): The average rate of passage of food through the gut is about 0,4 to 0,5 mm per hour when food fills ¼ of the full length of the gut. Larvae of the same size feeding the same plankton are able to select different kinds of food organisms. It seems that *Artemia*-nauplii are not well digested in young herring larvae. On the basis of digestion rate daily food ration was estimated as 30–60 nauplii in 10–11 mm larvae and 80–120 nauplii in larger larvae of 13–14 mm.

INTRODUCTION

/61

The fluctuations in the propagation rate have been traced by most authors to the death of the larvae through starvation shortly after the yolk sac stage. Whether large parts of the larval population of herring must starve to death or can survive, depends on numerous environmental factors (HEMPEL 1963, BLAXTER and HEMPEL 1963, HEMPEL 1965). The density and distribution of the food organisms will have

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1 This report is part of a dissertation, prepared under the direction of Prof. Dr. G. Hempel, for the Department of Mathematics and Natural Sciences of the University of Hamburg.

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as limiting effects as the food requirements and the search performance of the individual herring larva (ROSENTHAL and HEMPEL 1968) have.

A useful measure for estimating the daily food ration required is the digestion rate (i.e., the rate of passage of the food absorbed through the gut). So far only those data are available on this question, which have been either based on estimates according to plankton catches, or have been determined by laboratory experiments in rearing tests by switching lights off or on (feeding interruption) (BLAXTER and HEMPEL 1961). A summary of the observations made so far at sea and in the laboratory are found at BLAXTER (1965).

MATERIAL AND METHODS

The larvae came from artificially fertilized eggs from herrings which had been caught on 18/19 November 1965 in the southern North Sea (near Ijmuiden). They were reared on Helgoland, and the conditions corresponded largely to the technique used by BLAXTER and HEMPEL (1961) for keeping the larvae. The temperature in the rearing basin (about 140 l) amounted to 10 $\pm$ 0.1°C. The basins stood in a constant room (artificial light; max. 1,500 lux at the water surface of the aquaria). The food offered varied and fluctuated with the varying successes of the plankton catches (width of mesh of the nets 75 μ and 150 μ). Artemia nauplii were added to the food (see further details in ROSENTHAL 1967, 1968; ROSENTHAL and HEMPEL 1968).

For the purpose of determing the rate of passage of the gut contents also in dependence of the state of filling of the gut, the measurements have been carried out on individuals.

LILLELUND's method (1957) of feeding varying food organism populations to freshwater fish spawn could not be applied here, because it was impossible to make available food organisms of a certain species in sufficient quantity for the individual feeding periods. Moreover, the larvae would be disturbed in their natural feeding behaviour by short-term changes. Larger losses must be expected through injuries.

The experiments were carried out in the following manner: With a wide-necked pipette, the larvae were caught from the experimental aquarium or basin after feeding, and were carefully transferred with the pipette to a Petri dish. The Petri dish was tilted so that the water was allowed to flow off freely. The herring larva now tried to swim against the water current. By proper tilting of the dish, the flow-off rate could be regulated in such a manner that the larva always remained in the centre of the dish, until only a small water film surrounded the larva in the end. The entire procedure was not allowed to take up more time than only a few seconds - possibly less than five. After the water had flowed out of the pipette with the exception of the water film surrounding the larva, the dish had to be swung around to and fro by 90° several times - at the same moment. The larva became immediately disoriented and remained lying quietly there for some seconds. In this manner the larva was prevented from continuing its swimming movements and from banging its head constantly against the glass of the dish and thereby injuring itself. For the same reason it was necessary to continue to work very quickly. When the larva was quiet, it was photographed under transillumination with the binoculars already prepared for taking the picture. Subsequently, the dish was /62 immersed into a vessel. If the larva swam away undamaged, it could be photographed again after two hours. From the difference of the lengths of the gut fillings of both "photo samples", it was possible to calculate the time of passage of the entire gut contents, unless a compression of the gut contents occurred in the last gut section. Furthermore, it was important that the experimental animal remained exposed to constant temperature conditions throughout the work procedure. To this end, it was necessary to ensure before each experiment that the Petri dishes, the individual basins as well as the pipettes and the glass plate of the binocular serving as a stand had the proper temperature. /63 Slight, short-term temperature fluctuations shocked the larvae and influenced the measurements. In order to avoid lengthy adjustments and searching for the desired picture section, it was recommended to mark off exactly the camera frame size on the microscope stand. Only after numerous preliminary experiments had failed was it possible to achieve a satisfactory manual dexterity. There was only some prospect of success when the entire working procedure took less than 30 seconds. Half of the experimental individuals survived the procedure without any noticeable damage. Damages were immediately noticeable by the changed swimming behaviour of the individual. This method failed in cases of larvae with a total length of more than 14 mm.

RESULTS

1. DIGESTION RATE IN DEPENDENCE OF THE FILLING STATE OF THE GUT

T A B L E 1

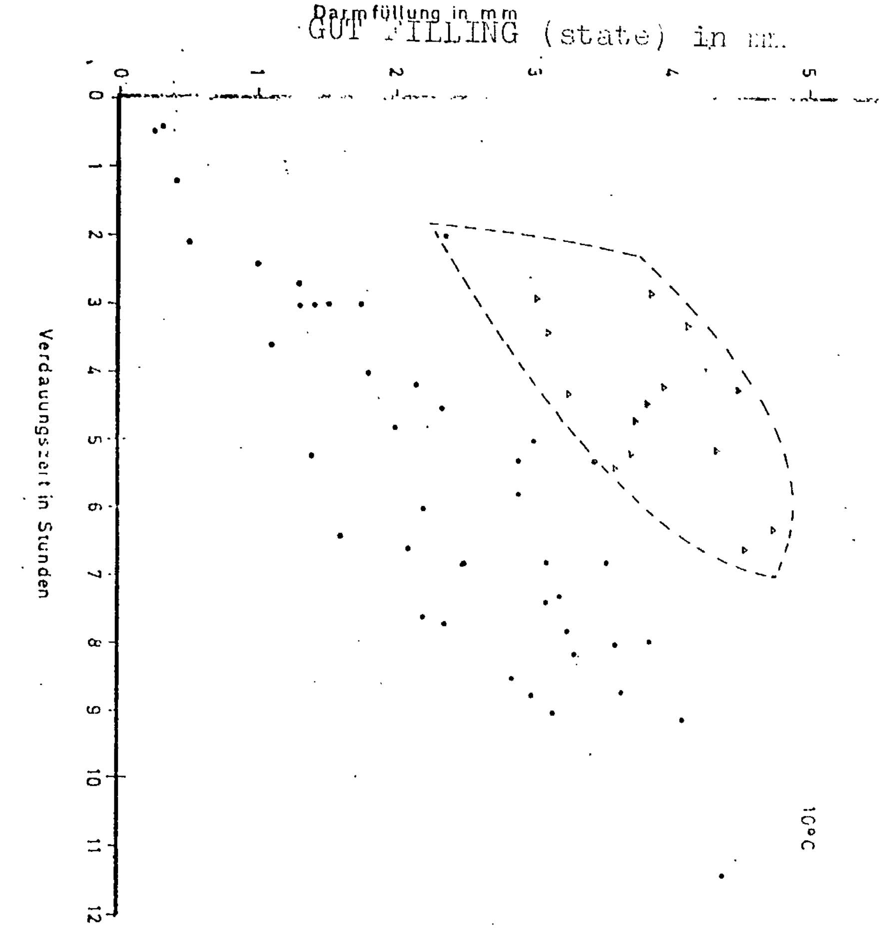
Experiments for the measurement of the rate of passage of the food filling the gut in larvae 11 to 14 mm in length.
Experiment on 20.12.1965. Duration of experiment: 3 hours
(Wild plankton, 70-μ-net)

Total length mm	Number of planktonts in gut and gut filling in mm — Beginning of experiment: Number	Beginning: mm	End: Number	End: mm	Average rate of passage mm/hr.	Estimated time of passage of entire gut contents in hrs.
Total-länge mm	Anzahl der Plankter im Darm und Darmfüllung in mm — Versuchsbeginn: Anzahl	Versuchsbeginn: mm	Versuchsende: Anzahl	Versuchsende: mm	[illegible]	[illegible]
11,5	7	–	1	–	–	–
12,0	3	–	2	–	–	–
13,5	4	–	2	–	–	–
14,0	3	–	1	–		
11,0	7	1,9	2	0,6	0,45	4–6
11,0	4	1,5	0	–	0,50	3
11,0	6	1,9	3	1,4	0,15	9
11,5	11	3,3	3	1,0	0,80	4–5
11,5	3	1,4	1	0,5	0,30	5
11,5	6	3,5	3	1,5	0,67	5
11,5	7	2,7	3	1,7	0,33	5–6
11,5	5	2,2	3	1,0	0,40	5–6
11,5	8	2,4	3	0,8	0,53	4
11,5	6	2,3	4	1,7	0,20	8–9
11,5	9	4,6	6	2,5	0,70	6–7
12,0	?	2,2	[illegible]	0,6	0,62	4
12,0	5	3,1	1	[illegible]	0,47	6–7
12,0	10	4,4	6	3,0	[illegible]	9
12,0	8	3,2	5	2,2	0,33	8–9
12,0	10	3,0	3	1,2	0,60	4
12,0	5	3,1	1	0,4	0,90	3–4
12,0	7	2,6	4	1,7	0,30	8–9
12,0	8	3,6	4	2,2	0,47	7–8
12,0	6	2,9	3	1,7	0,40	7–8
12,0	5	2,9	3	2,2	0,23	10
12,0	10	4,8	5	2,5	0,77	6–7
12,5	4	1,6	0	–	0,53	3
12,5	9	2,1	5	1,6	0,16	10
12,5	?	2,1	4	1,1	0,33	6–7
12,5	?	2,9	3	1,2	0,57	5
12,5	4	2,9	3	1,4	0,50	5–6
12,5	9	4,1	0	–	–	–
12,5	9	4,1	0	–	–	–
12,5	8	2,6	0	–		–
13,0	8	2,8	2	1,7	0,36	7–8
13,0	6	2,5	4	1,4	0,37	6–7
13,0	6	3,1	4	1,8	0,43	6–7
13,0	6	3,0	5	2,0	0,33	9
13,0	8	4,5	2	1,3	1,10	4–5
13,0	6	2,8	3	2,0	0,26	10
13,5	8	3,7	5	2,3	0,47	7–8
13,5	9	3,9	5	2,7	0,40	9
14,0	5	3,8	2	1,4	0,80	4–5
14,0	6	3,2	3	1,8	0,47	6–7

Cont'd: /63

In general, there is a relationship between the time of passage and the gut filling state if the observed values are based on gut fillings occupying between 1/3 and 3/4 of the gut length. In many cases, the observation has been made

GUT FILLING (state) in mm.



Digestion time in hours

FIGURE 1. Digestive rate in dependence of gut filling state. Calculated values for the time of passage of the entire gut contents on the basis of measurements at 2-hr. intervals on herring larvae, 11-14 mm in length. Within broken line: premature defecation observed.

that in cases of considerable gut filling, a much more rapid passage is achieved. This can perhaps be interpreted as a "plug effect" (subsequently closer compression of the food), /64 which might be caused by the intensive intestinal peristalsis. On the other hand, the rate of passage slows down when less than 1/3 of the total length of the gut is filled. This became particularly obvious when the last food fragments were large and closed the anus like a stopper. According to these observations, the rate of passage - with about 1/3 gut filling - reached mean values around 0.4-0.5 mm/hour (compare Table 1).

On the basis of the experimental results one can calculate a digestion time between 4 and 10 hours, in some cases more, with a mean gut filling of 2 to 4 mm (4-9 planktonts). As Figure 1 indicates, the values are considerably dispersed. This should be traced, among other things, to the varying size of the planktonts. The digestion rate of nauplii is higher than that of copepodite stages. There are differences in the digestion rate when the arrangement of the planktonts inside the gut varies in larvae with the same gut filling state. A relatively large planktont at the end of the gut prevents the quicker passage of nauplii fed later (compare Fig. 5), which are then no longer arranged like a string of pearls in the posterior gut section but are situated right next to and on top of each other because of the intensive peristalsis in many cases. The lumen of the gut is therby quite often slightly enlarged.

It was noted in numerous experiments that a premature defecation occurred shortly after the larvae had been caught and transferred, particularly in cases of smaller larvae. After this often spontaneous faeces excretion, the digestion continued at the normal rate for the remainder of the gut contents. The shorter digestion time, which is probably caused by shock reaction or a disturbance, is marked by triangular symbols in Fig. 1 and surrounded by a broken line.

In the experiments, sudden defecation was frequently observable on those larvae which had their gut tightly filled with food organisms. With exclusive feeding with Artemia nauplii, it was observed in one case that one larva, about 17 mm in length which had fed 46 nauplii, suddenly excreted 34 Artemia during photographing. The remaining 12 nauplii followed in the transferral to the vessel.

2. SELECTION OF FOOD

It is surprising that in spite of equal plankton offered with the same "feeding chances" larvae of equal size will, at the same time, prefer different planktonts as food. For this reason, BLAXTER and HEMPEL (1961) ascribe special significance to the greater variety of food organisms in wild plankton as food in rearing experiments. Whereas in these observations, in one experiment only nauplii were snapped (compare Fig. 2a), primarily the copepodite stages were found in other larvae, and both in other larvae. With such an early individual selection capacity, the digestion time may vary. This also favours early growth diversification (fast or poor growth).

Even shortly after the first food intake, the larvae do not show a uniform interest in all the food organisms offered. It would seem as if there were particularly frequent and intensive reaction to those planktonts for which they had snapped successfully previously. This behavious could be regarded as "self-training". It is not known how firmly the predatory scheme is imprinted because individuals could be observed only during one feeding period, but not for several days. However, it was noteworthy that at the beginning of additional Artemia feeding (about 10 days after the first food intake) the artemias were hardly /65 noticed by the larvae. Artemias were snapped only when almost no copepod-nauplii were left in the aquarium. About 3 to 4 days after the first Artemia had been offered, the artemias were noticed just as much as the copepod-nauplii.

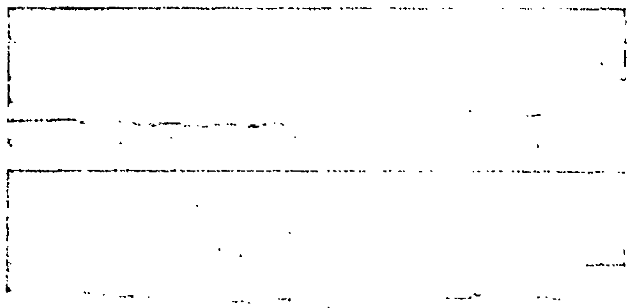


FIGURE 2. Food selection by herring larvae, 13-16 mm in length. Both larvae were caught in the aquarium at the same time after feeding with fine plankton - a (above): only nauplii in the gut (21), b (below): primarily copepodite stages, only 1 nauplius.

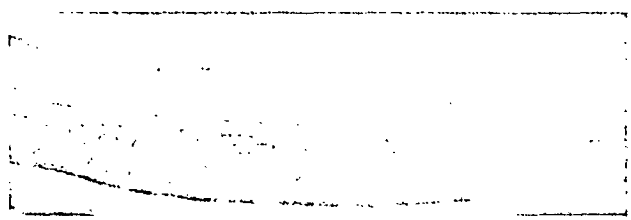


FIGURE 3. Primarily artemia eggs in the gut; three nauplii were fed last (in picture on right side).

However, individual exceptions show that occasionally the most varied things are snapped. Thus, one larva had fed almost exclusively on Artemia eggs (compare Fig. 3) and all the others on nauplii. The Artemia eggs had gotten into the basin by mistake.

During the experiments, a considerable amount of phyto-plankton had been introduced with the wild plankton into the aquaria. However, phytoplankton (so-called green food remains) were never found in the guts of the herring larvae. However, this is not to say that herring larvae in the sea never feed on phyto-planktonts. At the beginning of each feeding period, the zoo-plankton density was large in our basin, and the attention of the larvae was primarily directed to it. When the zooplankton supply was exhausted, the phytoplankton was already dead on the whole, and had sunk to the bottom of the aquarium.

3. DIGESTIBILITY

Only indications of the digestibility of the food offered can be reported. Shortly after the beginning of the food intake, the young larvae are not yet capable of fully digesting the fed planktonts. During the experiments for the measurement of the digestion time, it was noted repeatedly that there were great variations in the state of illumination of the food organisms in the gut. Partly they were still so well preserved in the faeces that they were snapped. This observation had also been made by BLAXTER (1965).

Artemia nauplii would seem to be taken only rarely or not at all by herring larvae (Downs larvae) which are 9-12 mm long. According to investigations by WEISZ (1947), the ratio of the ectodermal to the entodermal mass of artemias during /66 the first nauplius stage is about 3 : 1. Only in the course of the development of the last metanauplius stage will this ratio be reversed. It would seem entirely possible that the larvae are incapable of opening the strong chitin exoskeleton's connecting seams of the freshly hatched nauplii during the relatively short digestion time. As Fig. 4a and 4b show, the _Artemia_-nauplii fed with _Dunaliella_ remained completely dark, whereas the copepods, which had been fed much later, were already strongly illuminated.

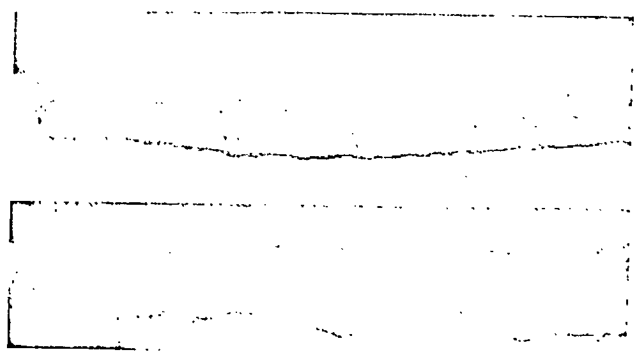


FIG. 4. Digestibility of _Artemia_ nauplii, in larvae 10-12 mm in length. Whereas the copepods are strongly illuminated, the _Artemia_ nauplii remain dark.

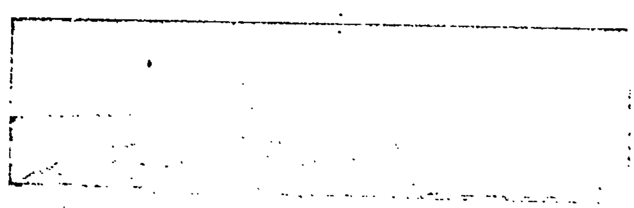


FIG. 5. "Blocking" of the gut passage by a larger planktont. The nauplii which were fed later are piling up in the anterior intestinal section. Immediately prior to this photograph, defecation started (1). The next planktont moves up to the gut lumen which is becoming vacant (2).

Nevertheless, BLAXTER and HEMPEL (1961) succeeded in rearing larvae of up to 20 mm total length only with Artemia-nauplii. However, the possibility is not excluded that small quantities of plankton entered the aquarium with the inflow of unfiltered seawater. DANNEVIG and HANSEN (1952), McMYNN and HOAR (1953) and KURATA (1959) were unsuccessful in Artemia feeding experiments. However, the picture changes completely in rearing experiments with larvae of plaice and sole. In this case, high survival rates have been achieved even with exclusive feeding of Artemia nauplii (compare FLÜCHTER 1965, RILEY 1966). However, an excessive amount of food offered would seem to increase mortality later. RILEY (1966) presumes that the water quality of the aquaria quickly deteriorates in cases of high food quotas and that strong bacteria and ciliate concentrations influence the mortality directly or indirectly. I can support this assumption on the basis of my own observations.

Moreover, one may suspect that (particularly the newly hatched) Artemia nauplii contain substances which may have a detrimental effect in cases of abundant feeding and may promote the mortality. The same effect has been observed also on Hydrozoa cultures (oral report, Dr. WERNER, Helgoland Biological Institute).

4. DAILY FOOD RATION, ESTIMATED ACCORDING TO DIGESTION RATE

If the food digestion rate is known, the approximate food requirement can be calculated. Since the herring larvae continue to feed when the food quantity offered remains the same, it can be assumed that food intake continues until the gut is completely filled. With the possibility of a feeding period of about 12 hours, herring larvae, 10-12 mm in length, fill the gut about two to three times. This applies to water temperatures around 10°C.

The digestion time of the individual planktont is much more rapid with an empty gut than it is with a filled gut. After a longer feeding interruption, the gut can also be filled very 67
quickly. On hungry larvae, about 25 mm in length, I observed 60 successful acts of catching prey within five minutes. BLAXTER and HEMPEL (1961) reported up to 50 planktonts per larva for the same feeding period for larvae, 35 mm in length. This applies also to smaller larvae. It may thus be assumed that the gut is very quickly filled at the beginning of the daily feeding period (shortly after daybreak) with abundant plankton offered, and that the digestion rate can certainly be higher because of a "plugging" effect than the measurements showed on the basis of 1/3 to 3/4 of the gut filled (about 0.5 mm/hour). The number of planktonts which can be fed daily can thus only be rougly estimated by means of the digestion rates determined. It definitely represents a minimum estimate. The mean size of copepod nauplii can be estimated as being 0.2-0.4 mm. If one considers that the nauplii can lie in the gut in the form of a string of pearls, and can also be nested in each other (about 50%) (compare Fig. 2a), the gut may be filled with up to 15 nauplii in larvae, 10 mm in length, and up to 20 nauplii in larvae, 13-14 mm in length. BLAXTER (1962) found up to 10 nauplii in larvae, 10-12 mm in length, up to 40 nauplii in larvae, 14-15 mm in length. Assuming a daily passage of 2 - 3 gut fillings, with a feeding period of 12 hours, the possible food intake is as follows:

10/11 mm-larvae	30 - 60	copepod nauplii or
	25 - 50	*Artemia* nauplii
13/14 mm-larvae	80 -120	copepod nauplii or
	60 - 90	*Artemia* nauplii

With increasing body size, the requirement rises rapidly. From a total length of 20 mm upwards, hungry larvae are capable of snapping a prey of up to 50 planktonts within five minutes. The daily requirement of such larvae was not estimated since it was impossible to offer plankton in sufficient quantity and since there are no observations available on the digestion rate. Moreover, one must count on a daily periodicity in the intensity of the food intake, as RILEY (1966) has found in feeding experiments with plaice larvae. In this case the daily food requirement of 10 *Artemia* nauplii at the time of the first food intake rose to about 240 after two weeks. In our experiments, any possibly existing rhythm was veiled by the frequent variations in the plankton offered daily.

DISCUSSION

On the basis of these observation values, the mean digestion rate can be quoted as 0.4-0.5 mm/hr. for herring larvae, 12-14 mm in length. The calculation of the digestion time for the entire gut contents was made with the assumption that the passage through the gut is continuous. In fact, the faeces excretion occurs in jerks (compare Fig. 5). The calculations of the digestion time may thus include an error of about two hours, if the measurements were made shortly before or shortly after an excretion of faeces.

With the observation of the premature faeces excretion, the suspicion arises that something similar occurs in a catch from the sea. The equipment used for the catch is usually so hard on the larvae, that they will die after a short time. BLAXTER and HOLLIDAY (1963) also expressed the opinion that an ejection of the gut contents through the impact of the catching procedure might be conceivable. BHATTACHARYYA (1957) found only a mean of 4.6 food organisms per larva in North Sea larvae, 14 mm in length. Only one larva had devoured 62 planktonts. /68 In his investigation on herring larvae of the Greifswalder Bodden, WALDMANN (1961) found, on the average, only 2-3 planktonts per larva in larvae, 16-25 mm in length. But also other authors were surprised to notice an always large proportion of empty guts in the young larva specimens (MIELCK 1924, MARSHALL, NICHOLLS and ORR 1937, BOWERS and WILLIAMSON 1951). On the other hand, rearing experiments generally yielded higher values. BLAXTER (1962) reports up to 10 planktonts per larva for larvae, 10-12 mm in length. With an insufficient quantity of plankton supplied, the values were similar in our experiments (compare Table 1). BLAXTER and HEMPEL (1961) found, on the average, 5-10 food organisms per larva in 8-10-mm-larvae. KURATA (1959) reported 5-11 planktonts per larva in rearing experiments on Clupea pallasii.

The early individual food selection would lead us to presume that such behaviour favours growth diversification in a larval population. A rapid diversification of growth can be quite favourable for a larval population. Even if the larvae remain within a restricted area, the possibility of competition for food will be quickly reduced, and a wider use of the plankton will be made possible.

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Summary 68

Larvae of Downs herring were artificially reared in aquaria. Experiments on rate of passage of food through the gut were carried out after the larvae had reached 10–14 mm total length.

Food was provided only intermittently, it consisted of plankton collected off Helgoland by nets of 75 or 150 micron meshes and of *Artemia* nauplii. Rate of passage depends on the state of filling of the gut. If the gut is filled by one third average rate is 0.4–0.5 mm/hour. Nauplii of copepods pass the gut quicker than copepodites. Total time of passage is 4 to 10 hours. "Green food remains" were not observed in the larvae. Experiments showed selection of particular food items by some of the larvae. At early stages larvae might get printed in their preference for some kinds of food. Individual differences in the selection of food might be one of the reasons for the differences in growth rate between larvae of the same age.

At capture larvae frequently defecate part or most of their gut content. That might be the reason for low figures of gut content in sea-caught larvae.

Nauplii of *Artemia* pass the gut of 9–12 mm larvae almost undigested while nauplii of copepods are largely digested, only the exoskeleton being extruded.

The daily ration was estimated under the assumption of 2–3 fillings of the gut. Larvae of 69 10–11 mm might take 30–60 copepod nauplii, larvae of 13–14 mm take 80—120 copepod nauplii. Number of *Artemia* nauplii will be lower by about 25 %.