DIGESTION RATE OF FOOD PARTICLES
IN THE GUT OF LARVAL HERRING
(*Clupea harengus* L.)

By

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ABSTRACT

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Laboratory experiments with herring larvae *(Clupea harengus* L.) from the local stock in Lindåspollene, north of Bergen, Norway, were performed in the spring of 1978 and 1979. Digestion rates of copepod nauplii and polychaet larvae less than 1.5 hours were found both in first-feeding (8 days post-hatching) and in more advanced (22 days post-hatching) larvae. Bivalve larvae passed undigested through the gut. The rate of passage through the gut varied between 12.5 and 22.5 hours, depending on the type of food organisms. The light conditions in the laboratory seemed to be the most important cause of the observed food selection.

INTRODUCTION

Several studies have been carried out to measure the rate of food passage through the gut of fish larvae. BHATTACHARYYA (1957) dissected the gut of herring larvae during night-time in *in situ* investigations. LAURENCE (1971) fed the larvae coloured microzooplankton. A visual inspection of the continuously feeding larvae gave information of the rate of passage through the larval gut. BLAXTER and HEMPEL (1961) measured the time from the end of feeding to the gut being transparent, and defined this as the rate of passage through the gut of the larvae. WERNER and BLAXTER (1981), using Laurence's method, concluded that the rate of passage is strongly affected by the prey density. Another parameter of importance is the digestion rate of food particles in the gut. If the larvae are continuously feeding, this parameter is dependent on the prey density. WERNER and BLAXTER (1981) observed that some *Artemia* nauplii were still alive after passage through the larval gut, when preyed upon at high prey densities. At lower densities all of the nauplii were digested.

The present experiments were carried out in the spring of 1978 and 1979 in order to measure the digestion rate in the gut of first-feeding (8 days post-hatching) and more advanced (22 days post-hatching) larvae. The rate of food passage and the eventual preference for certain prey organisms were also studied.

MATERIALS AND METHODS

Naturally spawned herring eggs were collected at the spawning grounds of the local herring stock in Lindåspollene (Fig. 1). Eggs were incubated in 8.8 l black glass aquaria with 90 μm mesh size plankton net bottoms. The temperature was kept constant at 9°C. The salinity was a constant 34.5‰, and the light conditions were measured as 10–100 lux during the 1978 experiment, which was performed at the Aquarium in Bergen. After hatching, the yolk sac
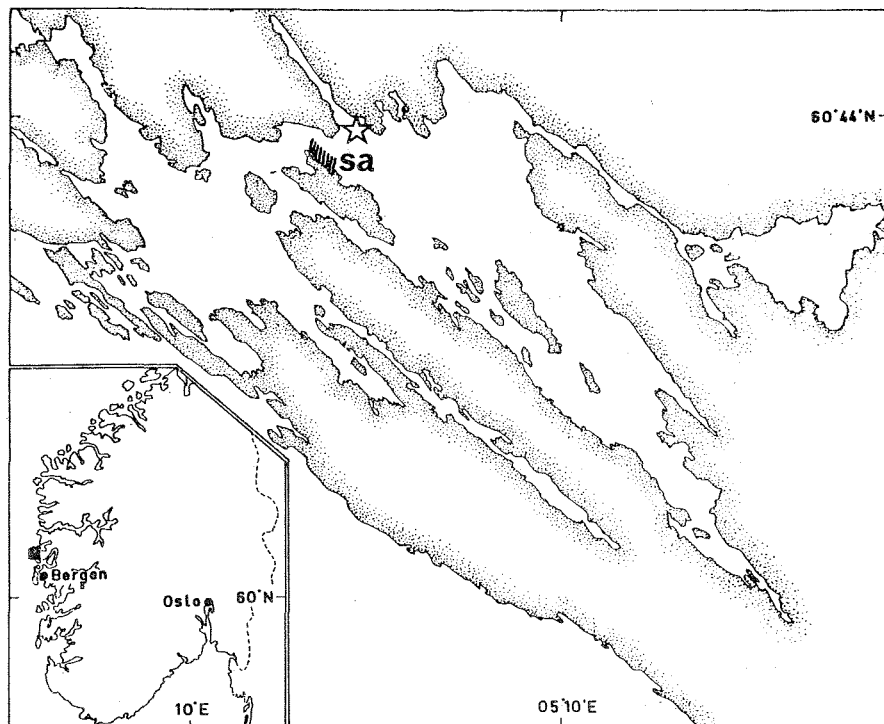

Fig. 1. The location of Lindåspollene with laboratory raft (☆) and spawning area (sa) of the local herring stock.

larvae were put into stock aquaria and fed natural zooplankton to excess from day four after hatching. The larvae were put into the experimental aquaria (Fig. 2) 24 hour prior to the experiment.

In 1979 the experiments were performed on a lab raft at Lindåspollene. The light conditions were the same, while the temperature and salinity, respectively 6°C and 30‰, were lower than in 1978. After hatching, the yolk sac larvae were put into a 400 l stock plastic pen together with natural microzooplankton. To avoid mortality caused by handling, samples of herring larvae in the stock pen were caught with a plastic box during night-time. All the larvae were distributed in the upper 10 cm layer in the plastic pen. They were located with an underwater light. When the plastic box was lowered into the water, the larvae were sucked into it and could be transferred to the

experiment aquarium without being exposed to air or plankton nets. The adaptation time was 14 hours.
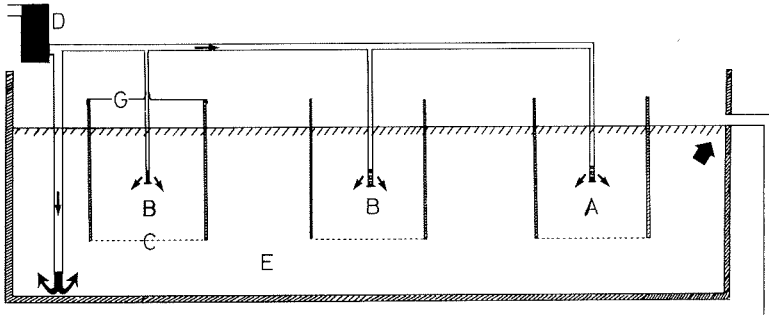

Fig. 2. Experimental equipment. A) Feeding aquarium 8.8 l, B) Digesting aquaria 8.8 l, C) Plankton net bottom, D) Fulflo filter 7 µm, E) Waterbath, G) Black plastic sheet.

During the feeding part of the experiments, the herring larvae were fed copepod eggs and nauplii, copepodites, bivalve larvae and polychaet larvae. The larvae were allowed to feed for one hour. The concentration of microzooplankton was 4–5 per ml both years. After feeding the larvae were transferred to an aquarium with filtered sea water. Ten larvae were preserved each hour, their guts dissected and the digestion rate of the gut content identified (Fig. 3). To avoid the effect of gut clearance, only larvae preserved within 3.5 hours after the end of feeding were used in the feeding incidence (FI%) and selection studies (Prey selection after BERG 1979). The microzooplankton used in the 1978 experiments were collected from 15 meters depth in the Byfjord close to the Institute of Marine Research, Bergen, by the automatic plankton sampler system described in TILSETH, SOLBERG and WESTRHEIM (1981). In 1979 the microzooplankton were collected with the pumping and filtering system shown in Fig. 4.
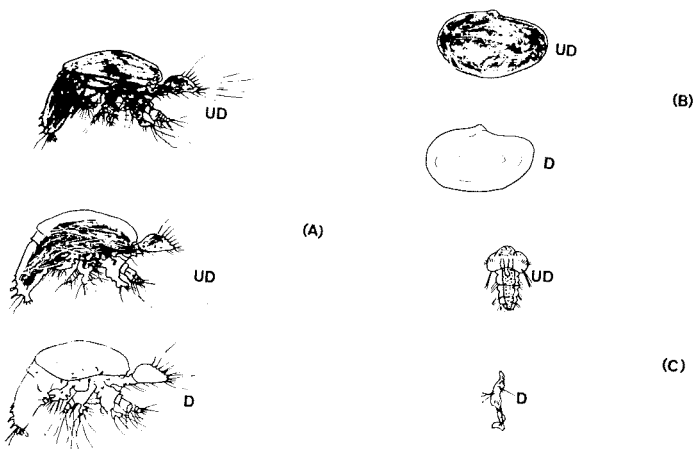

Fig. 3. Rate of digestion: UD) undigested, D) digested. A) Copepod nauplii, B) Bivalve larvae and C) Polychaet larvae.
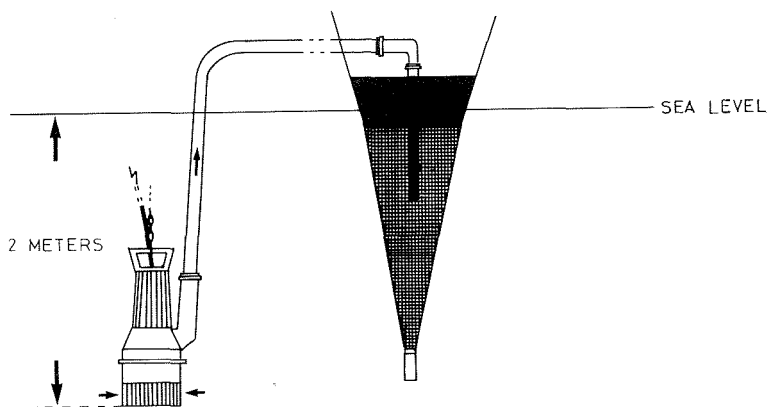
Fig. 4. Pumping and sieving system used in Lindåspollene in 1979. 90 μm plankton net.

RESULTS

The first-feeding larvae reached a standard length of 10.5 mm in 1978 and 10.7 mm in 1979. They weighed 99 and 95 μg, respectively. The more advanced larvae were 12.0 mm long, implying a mean daily growth rate of 0.11 mm from day 8 to day 22 after hatching (Table 1). The gut contents of the larvae preserved before any of the gut content was eliminated, are shown in Table 2. Several food items were found in the guts in 1978. As many as 6 bivalves or 3 copepod nauplii were found in one larvae. The feeding incidence was 63 and 92% in 8 and 22 days old larvae. In 1979 only 9% of the larvae had prey organisms in their guts.

Table 1. Some parameters of the larvae used in the experiments.

Larval age (days after hatching)	Standard length (mm)	Standard deviation (mm)	Dry weight (μg)	Standard deviation (μg)	Numbers of larvae
9 (1979)	10.7	0.60	95	21	160
8 (1978)	10.5	0.45	99	21	152
22 (1978)	12.0	1.06	135	57	130

Table 2. The gut contents of the larvae.

Year	Age (days)	Numbers of larvae	FI (%)	Copepod nauplii 1	2–3	>3	Bivalve larvae 1	2–3	>3	Poly-chaet larvae	Others
1978 ...	8	43	63	14	2	0	2	3	7	1	5
1978 ...	22	38	92	15	4	0	6	7	0	13	3
1979 ...	9	80	9	4	3	0	0	0	0	0	0

The percent distribution of different microzooplankton organisms offered to the larvae in the stock aquaria and in the feeding experiments are shown in Table 3. During the first-feeding period (5–9 days post-hatching) the larvae were given 30–40% copepod eggs, 10–30% copepod nauplii, 20% bivalve larvae and 10–30% polychaet larvae. After the experiment with the first-feeding larvae, the larvae were given an increasing amount of copepod eggs (20–60%), 15–30% copepod nauplii, a decreasing amount of bivalve larvae (20–10%) and variable amounts of polychaet larvae.

Table 3. Frequency of different microzooplankton organisms offered to the larvae (1978).

Days after hatching	4	5	6	7	8	9	10	11	12	13	14	15	16	18	19	20	21	22
Copepod eggs ..	.35	.43	.29	.34	.34	.28	.31	.26	.21	.25	.38	.28	.29	.67	.56	.55	.59	.36
Copepod nauplii	.21	.12	.24	.21	.10	.32	.28	.35	.24	.16	.35	.31	.31	.18	.15	.15	.19	.13
Copepodites ...	.12	.03	.12	.13	.11	.08	.10	.13	.10	.13	.14	.11	.24	.02	.06	.15	.10	.07
Bivalve larvae..	.23	.22	.02	.23	.20	.23	.13	.17	.12	.20	.08	.24	.10	.11	.13	.10	.02	.14
Polychaet larvae	.08	.08	.32	.09	.25	.06	.14	.07	.33	.24	.05	.04	.04	.01	.09	.04	.09	.28
Others	.01	.01	.01			.03	.04	.02		.02		.02	.02	.01	.01		.01	.02

First-feeding larvae digested 50% of the copepod nauplii in 0.5 hours (Fig. 5) in 1978. Of the nauplii, 80% were digested after 1.5 hours. The 1979 results strengthened the impression of a fast dissolution rate in the first feeding
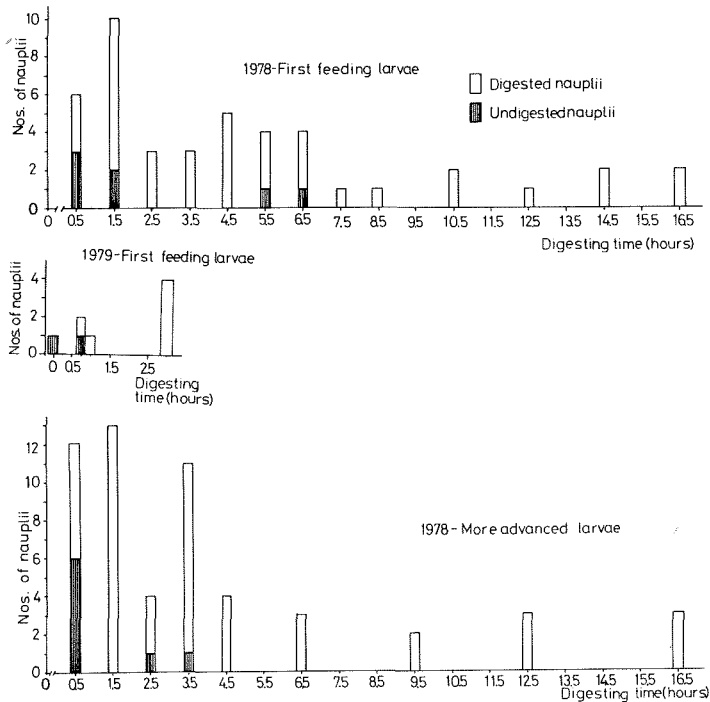

Fig. 5. Digesting rate of copepod nauplii.

larvae in spite of rather scarce material. One undigested copepod nauplii was found in the middle of the feeding period. One out of two nauplii were digested 45 minutes later. At a later time, all of the copepod nauplii were digested.

At 0.5 hours digesting time, 50% of the nauplii in the gut of the more advanced larvae were digested. One hour later all of the copepod nauplii were digested. Still later, two undigested copepod nauplii were found. These were found in guts which contained bivalve larvae.

Most of the bivalve larvae passed undigested through the gut (Fig. 6). A few empty bivalve shells were found after 3–4 hours digesting time in both first-feeding and more advanced larvae in 1978. Polychaet larvae were always found as remains in the larvae gut (Fig. 7).
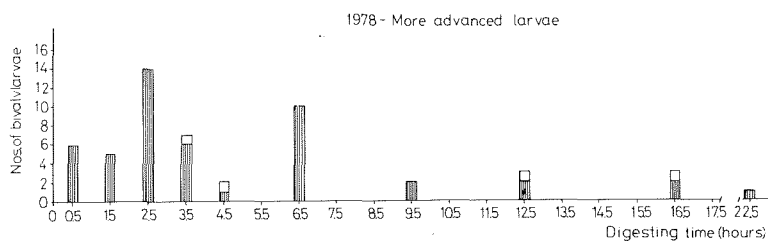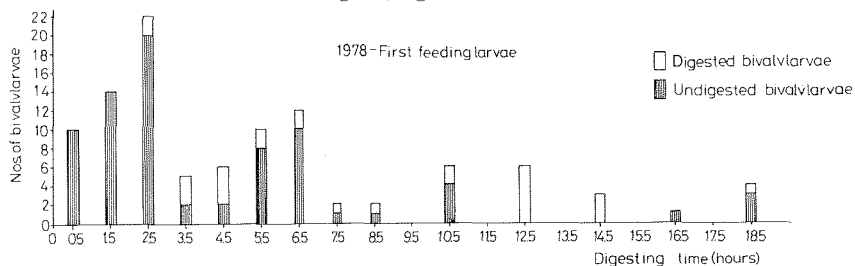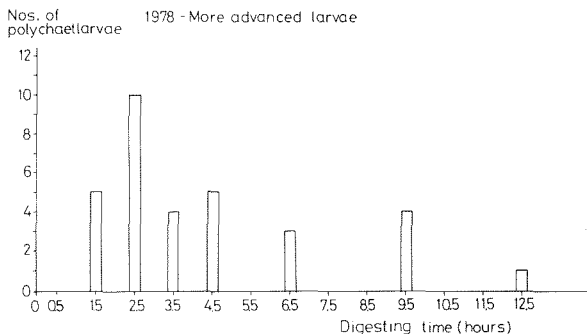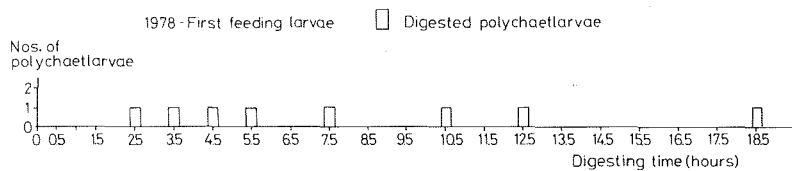
Fig. 6. Digesting rate of bivalve larvae.

Fig. 7. Digesting rate of polychaet larvae.

The larvae showed a positive selection for copepod nauplii and bivalve larvae. But they avoided copepod eggs and copepodites (Figs. 8 and 9). The first-feeding larvae took just small amounts of polychaet larvae, while the more advanced larvae had the same frequency of polychaet larvae in the gut as were present in the food.

The time of passage through the gut was 16.5 hours for copepod nauplii, 22.5 hours for bivalve larvae and 12.5 hours for polychaet larvae. However, most of these particles pass faster through the gut as indicated by the drop in the number of food particles in the gut after 2.5–4.5 hours (Figs. 5, 6 and 7).

DISCUSSION

The larval period is one of fast growth and high mortality. Prey availability is generally considered as the most important regulator of recruitment (CUSHING 1976). Reduced food availability would most probably result in starvation and concequently prolong the larval period during which the larvae are most vulnerable to predation. Copepod nauplii dominate the diet of most fish larvae (HUNTER 1980), so also in herring larvae, but they feed on many other organisms (BLAXTER 1965), and the composition of the diet is another regulatory mechanism. The present material shows that herring larvae have a low digestibility of bivalve larvae. Then high concentrations of this food item can be dangerous or even fatal to the larvae, resulting in starvation or a prolonged larval period.
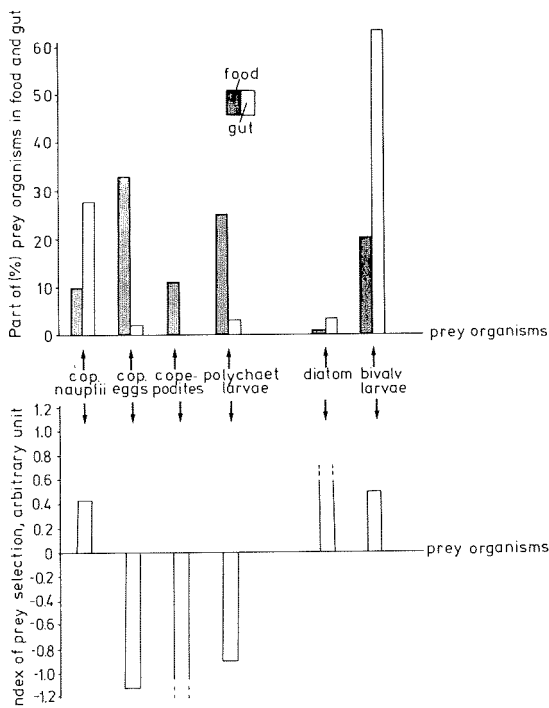

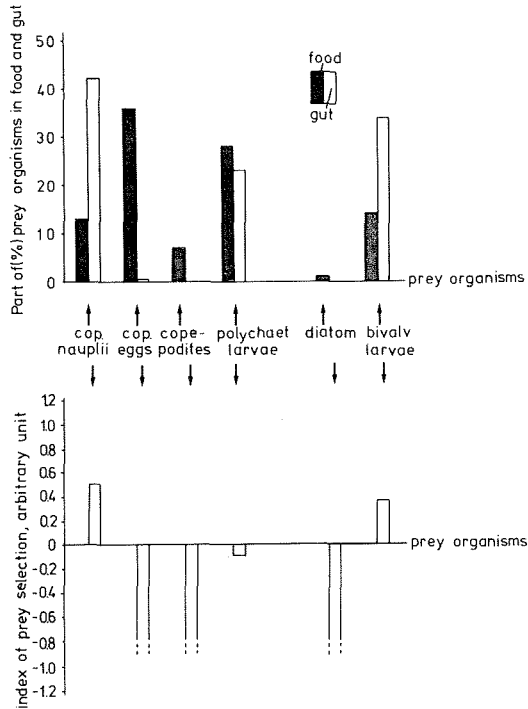Fig. 8. Prey selection in first-feeding larvae (8 days post-hatching).

Fig. 9. Prey selection in more advanced larvae (22 days post-hatching).

The fast digestion rate of copepod nauplii in the gut of herring larvae corresponds with results of TILSETH (pers. comm.) on first-feeding cod larvae. TILSETH stresses that copepod nauplii are completely digested in 0.5 hours. In my material the more advanced larvae digested the copepod nauplii in one hour. The results from the experiments with first-feeding larvae are not as clear, but the 1979 experiment strengthened the impression that also the first-feeding larvae are able to digest the nauplii in one hour.

Polychaet larvae are dissolved in a short time and can be an important food organism of herring larvae from an age of two to three weeks after hatching.

The difference in time of passage through the digestive tract between the present results and results reported by other authors are shown in Table 4.

Table 4. Time of passage of food particles through the digestive tract of two different fish larvae.

Source	Year	Fish	Temperature (°C)	Time (hours)
Kurata	1959	Herring	9	12–20
Blaxter & Hempel	1961	Herring	8–13	4–6
Rosenthal & Hempel	1969	Herring	10	4–10
Werner & Blaxter	1981	Herring	9	3
Present results	1981	Herring	9	12.5–22.5
Laurence	1977	Winter flounder	8	6

The present experiment was primarily designed to measure the digestion rate of food particles in the gut of herring larvae, not the time of passage. The reasons for the extended time of passage observed in the present experiment, compared to others, can be the high impact of bivalve larvae, which are almost indigestible, and the fact that no new food items were ingested during the digesting period. Probably the best method to study the larval gut clearence rate is the one described by LAURENCE (1971). In continuously feeding larvae, newly taken food items can press digested ones out of the gut. This will have a great effect on the passing time. Visual investigations of the gut (BLAXTER and HEMPEL 1961) do not show the empty shells of the prey organisms, and an underestimation of the passing time will be the result.

Herring larvae are generalists, and a wide sprecter of microzooplankton organisms are found in their guts (BLAXTER 1965). The larvae do, however, prefer special food items, illustrated by the positive selection for copepod nauplii and bivalve larvae in the present experiment (Figs. 8 and 9).

The mouth size of the larvae will determine the size of the prey organisms the larvae can take (WIBORG 1948, BLAXTER 1965). In the present experiment the light condition in the laboratory can be the underlying cause of the observed food selection. Although the light conditions are well above the light threshold for feeding of herring larvae, 0.1 lux (BLAXTER 1966), small and transparent plankters like copepod eggs are neglected. ELLERTSEN et al. (1980) observed the highest feeding incidence of cod larvae on Peridinium trochoideum at 1000 lux, while the highest feeding incidence on easily detectable Artemia nauplii was 1.4 lux. SCHNACK (1972) observed a preference for certain size groups, and plankters which showed a contrast against the background. WERNER and BLAXTER (1979) state that herring larvae prefer easily detectable Artemia to transparent natural plankton. Mobile food organisms such as copepodites and copepod nauplii could probably be able to avoid the larvae in good light conditions, but not under lower light intensities. Under such conditions, for example, in the laboratory or at dusk conditions in situ, the larvae with its relatively well developed vision (BLAXTER and HOLLIDAY 1963) will search for easily visible particles, nauplii or coloured bivalve larvae. Under improved light conditions the larvae will take immobile transparent plankters and prey organisms of smaller size and lesser mobility.

Observations of the food selection abilities of herring larvae in situ (BJØRKE 1978) indicate a positive selection for copepod eggs, while the present results show the opposite. The reason might be different light conditions in the field and laboratory investigations.

Of the first-feeding 67% and 92% of the more advanced larvae had food particles in the gut after a one-hour feeding time in high prey concentrations (1978). In 1979 only 9% of the first-feeding larvae had food particles in the gut. The difference in feeding incidence the two subsequent years can be due to the different life history of the two larval cohorts. In 1978 the larvae were stored in

a similar aquarium as the experimental ones. In 1979 the larvae were stored in a plastic pen. They were captured 14 hours before the start of the experiment. There were no signs of capture or handling mortality, but the transfer to a new environment could have stressed the larvae and resulted in a low feeding incidence.

The feeding incidence of 67 and 92% observed in the 1978 experiment is high compared to the maximum of 40% in first-feeding larvae from field investigations at Lindåspollene in the same year (FOSSUM and JOHANNESSEN 1979). ØIESTAD and MOKSNESS (1979) found 63% feeding incidence in 17 days old larvae in a concrete enclosure experiment, and 97% in 24 days old larvae in a plastic pen experiment. The present experiment agrees more closely with these results. Herring larvae may partially or completely void their digestive tract when captured or preserved (ROSENTHAL 1969, HAY 1979). In field studies the larvae are often captured in nets. When the larvae are exposed to the hauling equipment for a long time, they will void their digestive tracts. This will happen to a greater extent in field investigations than in plastic pen and laboratory experiments due to different sampling methods.

The digestion rate in the gut of fish larvae can easily be measured with the present experimental design. The design of the experiment was less satisfying in measuring the time of passage through the gut. Continued feeding will give the most reliable estimates of the gut clearence rate. Food selection abilities can be studied, but the selection is easily influenced by variations in abiotic factors as the light conditions in the laboratory. Additional work where the larvae are fed coloured microzooplankton (LAURENCE 1971) at different food densities and where the gut is dissected according to the present method, can give more informtion about the digestive process in first-feeding larvae.

REFERENCES

BERG, J. 1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). *Mar. Biol., 50*: 263–273.

BHATTACHARYYA, R. N. 1957. The food and feeding habits of larval and postlarval herring in the northern North Sea. *Mar. Res. Scot., 3*: 1–14.

BJØRKE, H. 1978. Food and feeding of young herring larvae of Norwegian spring spawners. *FiskDir. Skr. Ser. HavUnders., 16*: 405–421.

BLAXTER, J. H. S. 1965. The feeding of herring larvae and their ecology in relation to feeding. *Rep. Calif. coop. oceanic. Fish Invest., 10*: 79–88.

— 1966. The effect of light intensity on the feeding ecology of herring. P. 393–409 in BAINBRIDGE, R., EVANS, G. C. and RACKHAM, O. ed. *Light as an ecological factor*. Blacwell Sc. Publ., Oxford.

BLAXTER, J. H. S. and HEMPEL, G. 1961. Biologische Beobachtungen bei der Aufzucht von Heringsbrut. *Helgoländer wiss. Meeresunters., 7*: 260–283.

BLAXTER, J. H. S. and HOLLIDAY, F. G. T. 1963. The behaviour and physiology of the herring and other clupeoids. *Adv. mar. Biol. 1*: 261–393.

CUSHING, D. H. 1976. Biology of fishes in the pelagic community. P. 317–340 in CUSHING, D. H. and WALSH, J. J. *The ecology of the seas*. W. B. Saunders Co., Philadelphia.

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ELLERTSEN, B., SOLEMDAL, P., STRØMME, T., TILSETH, S., WESTGÅRD, T., MOKSNESS, E. and ØIESTAD, V. 1980. Some biological aspects of cod larvae (*Gadus morhua* L.). *FiskDir. Skr. Ser. HavUnders., 17*: 29–47.

FOSSUM, P. and JOHANNESSEN, A. 1979. Field and laboratory studies of herring larvae (*Clupea harengus* L.). *Coun. Meet. int. coun. Explor. Sea, 1979* H:28): 1–17. [Mimeo.]

HAY, D. E. 1979. The effect of capture and fixation on gut contents and body size on Pacific herring larvae. *Int. Coun. Explor. Sea Symp. The Early Life History of Fish, 1979* (PE: Poster 6).

HUNTER, J. 1980. The feeding behaviour and ecology of marine fish larvae. *International Center for Living Aquatic Resources Management Conference Proceedings, 5*: 287–330.

KURATA, H. 1959. Preliminary report on the rearing of herring larvae. *Bull. Hokkaido reg. Fish. Res. Lab., 20*: 117–138.

LAURENCE, G. C. 1971. Digestion rate of larval largemouth bass. *N.Y. Fish game J. 18* (1): 52–56.

––– 1977. A bioenergetic model for the analysis of feeding and survival potential of winter flounder. *Pseudopleuronectes americanus,* larvae during the period from hatching to metamorphosis. *Fishery Bull. Fish Wildl. Serv. U.S. 75*: 529–546.

ROSENTHAL, H. 1969. Verdauungsgeschwindigkeit, Nahrungswahl und Nahrungsbedarf bei den Larven des Herings (*Clupea harengus* L.). *Ber. dt. wiss. Kommn. Meeresforsch., 20* (1): 60–69.

SCHNACK, D. 1972. Nahrungsökologische Untersuchungen an Heringslarven. *Ber. dt. wiss. Kommn. Meeresforsch., 22* (3): 273–343.

TILSETH, S., SOLBERG, T. S. and WESTRHEIM, K. 1981. Sublethal effects of the water-soluble fraction of Ekofisk crude on the early larval strages of cod (*Gadus morhua* L.). *Coun. Meet. int. Coun. Explor. Sea, 1981* (E:52): 1–21. [Mimeo.]

WERNER, R. G. and BLAXTER, J. H. S. 1979. The effect of prey density on mortality, growth and food consumption in larval herring (*Clupea harengus* L.). *Int. Coun. Explor. Sea Symp. The Early Life History of Fish, 1979* (FM:4): 1–11. 6 tab, 4 fig. [Mimeo.]

––– 1981. The effect of prey density on mortality, growth and food consumption in larval herring (*Clupea harengus* L.). *Rapp. P.-v. Réun coun. int. Explor. Mer, 178*: 405–408.

WIBORG, K. F. 1948. Investigations on Cod Larvae in Coastal Waters of Nothern Norway. *FiskDir. Skr. Ser. HavUnders., 9* (3): 1–27.

ØIESTAD, V. and MOKSNESS, E. 1979. Study of growth and survival of herring larvae (*Clupea harngus* L.) using plastic bag and concrete enclosure methods combined. *Int. coun. Explor. Sea Symp. The Early Life History of Fish, 1979* I:2): 1–26. [Mimeo.]