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RECRUITMENT STUDIES OF HERRING (*Clupea harengus* L.) IN LINDAASPOLLENE, WESTERN NORWAY, 1–3

By

ARNE JOHANNESSEN
Department of fisheries biology, University of Bergen,
P.O.Box 1839, N-5011 Bergen, Norway

ABSTRACT

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This study was conducted between 1977 and 1980 on the herring stock of a landlocked fjord, Lindaaspollene in western Norway. It describes the early life history from time of spawning to about two months after hatching.

Paper 1 deals with the major spawning grounds, Bjørnøy and Syslakvåg. A general study of the spawning areas and the distribution of eggs in relation to substrate and depth, as well as mortality of eggs at different stages of development, is presented. The spawn was primarily deposited on hard bottom substrates from high-tide water level down to about 10 m depth. Little spawn was observed on fine sand or mud. The mortality was generally low during the pre-hatching period, averaging less than 10%. Egg densities of more than one million eggs per square meter were accompanied by reduced survival rates. Diving ducks (*Somateria mollissima*) were estimated to have a predator potential of 1/3 of the total herring egg production in 1977. Fish predators were estimated to remove up to 2/3 of the total egg production in years with light spawn (1978), but this was considered negligible in years of heavy spawning. On the basis of egg abundance, seasonal estimates of spawning stock size were obtained.

Paper 2 describes hatching, distribution and mortality of herring larvae. A method for estimating larval production based on the abundance of larvae at an early stage of development and the rate at which the larval numbers decline, is presented. Different metods to estimate larval production were compared and discussed in relation to sampling, environmental and biotic factors. Hatching begins during the latter half of April and the early part of May, and the hatching season lasts for some 3–4 weeks. Hatching success fluctuated widely in relation to estimates of egg production with an average of 50%. Dispersal of larvae from the hatching centres was traced by intensive sampling aied by information about the surface water circulation. Vertical distribution of herring larvae was examined in relation to stage of development, time of the day, and surface illumination. Newly hatched larvae rose to surface waters shortly after hatching and showed small variations in amplitude of migration. The vertical migration seemed to increase with increasing age. Density-dependent mortality between hatching and an age of about 2.5 months was found to have mean rates of 8 to 16% per day. The impact of predation by planktonic invertebrates on the mortality of newly hatched herring larvae is discussed in relation to *in situ* observations.

Paper 3 describes growth, condition and feeding characteristics in relation to abundance and mortality of herring larvae. Growth and survival were better in 1977 and 1979 than in 1978 and 1980. Mean growth in 1978 was observed to be comparatively slow (0.13 mm/day in lenght and specific growth rate of 1.1%/day) during the first two weeks after hatching, coinciding with the first-feeding stage. This was consistent with high mortality which probably was linked with environmental conditions. Only prey items of less nutritive value to fish larvae, such as bivalve larvae, were available at the feeding stage. Only a small fraction of herring larvae survived the first-feeding stage. Their growth recovered when the feeding conditions improved in May and June with a new peak production of zooplankton, but their numbers were not sufficient to support a good year-class. Beyond 20 mm in standard length, corresponding to an age of 50 days after hatching, net avoidance influenced the size distribution of herring larvae. A feeding period approximately 18 hours, with peak feeding incidence between 0500–1200 hrs, and 1500–2100 hrs, was recorded over a wide range of larval stages. Mean feeding incidence was observed to be low in herring larvae younger than two weeks (19%), increasing to 65% in 4–7 weeks old larvae. The diet of herring larvae consisted primarily of copepod nauplii, while copepodites constituted the main food of larger larvae.

1. ASPECTS OF SPAWNING AND EGG DEVELOPMENT

INTRODUCTION

During recent years an increasing number of fish stocks have been overexploited, and several of these are in danger of extinction. Assessment studies of fish populations are therefore urgently needed. These can be obtained in several ways. Data on catch and effort from the commercial fishery has frequently been applied for this pupose. To assess resources not exposed to a commercial fishery, a direct estimation of stock size can be obtained by acoustic surveying combined with fishing experiments or, alternatively, by quantitative sampling of the spawning products in time and space combined with fishing experiments to obtain estimates for length frequency distribution, gonadal maturity, fecundity and sex ratio of the spawning stock.

Location of the spawning grounds may be indicated by commercial catches or experimental fishing for spawning and spent herring, by herring spawn in the stomachs of other fish, by the presence of newly hatched herring larvae in plankton catches, or by direct observations, e.g. scuba diving. The spawning products of herring are characterized by their great adhesiveness. When deposited on the sea bed, they resemble white carpets. The use of bottom grabs, a common quantitative method for sampling demersal spawn, is not feasible for many herring stocks due to the substrates of the spawning sites and the limited area of many spawning beds. The spawning grounds for Atlanto-Scandian herring are usually located at 80–200 m depth (Runnstrøm 1941). In shallow waters (0–30 m), alternative methods for quantitative sampling of eggs are available.

For Pacific herring and several coastal populations of North Sea and Baltic herring which spawn in the littoral and sub-littoral regions, scuba diving surveys have proved their legitimacy as a tool for spawn assessment studies (e.g Tibbo *et.al.* 1963, Hemmings 1965, Haegele *et.al.* 1976, Aneer 1979). Due to the shallow distribution of herring spawn in Lindaaspollene, Furevik (1976) found scuba diving techniques suitable for spawning-ground investigations, and such were therefore selected as the primary survey method during this study. The life history of the local herring stock in Lindaaspollene, western Norway (Fig. 1.1), is described by Lie *et.al.* (1978). During 1973–74 Furevik

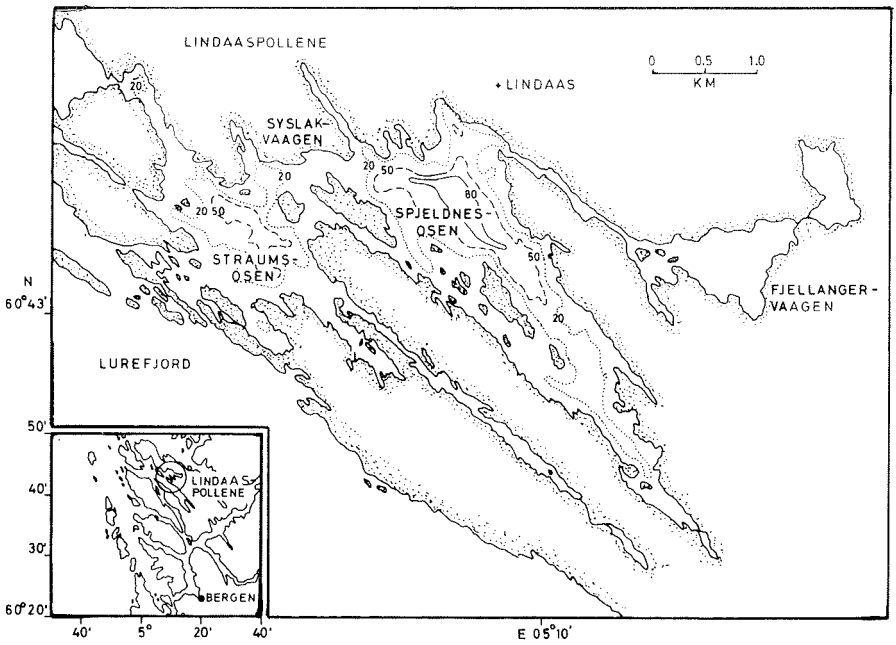

Fig. 1.1. Lindaaspollene with isobaths in meters indicated.

(1976) studied spawning behaviour and early life history of the Lindaas herring stock. Acoustic investigations of the spawning stock were conducted during 1978–1980 by Aksland (1983).

The present study is a continuation of those investigations initiated by Lie *et. al.* (1978) in an effort to improve the predictions of annual variations of herring, with particular emphasis on aspects of spawning and mortality.

The investigations began in 1977 and were carried out each spring until 1980. Detailed investigations of the functional significance of different substratum types for spawn deposition, as well as studies on mortality in relation to egg density, substratum type and depth, have been incorporated. Studies to evaluate the validity and reliability of the methods used in the investigation have been an integral part of the spawning ground surveys.

MATERIAL AND METHODS

PILOT SURVEYS

When gonadal conditions in the herring indicated the approach of spawning, the daily gill netting was supplemented by visual surveys along the shore to determine spawning time and place. Ropes with gill net stones were dropped haphazardly in areas where previous herring spawns had occured, to be used as markers for spawn depositions.

After locating the spawning grounds, scuba divers surveyed the spawning areas and their surroundings to determine the boundaries, substrate types, and

depths and to estimate spawning intensity. The latter was measured on a subjective scale of 0–4:

0 – no spawn
1 – very light spawning, with scattered spots of spawn
2 – medium spawning, covering a thin continuous layer
3 – dense spawning, covering a dense continuous carpet of up to two egg layers
4 – very dense spawning, with more than two layers of thickness

Ropes marked at one metre intervals were stretched out along the sea bed perpendicular to selected sites on the shoreline. Divers obtained detailed descriptions of the bottom substrates and spawn intensities of the spawning area along these transects. Based on the pilot estimate of the spawning intensity and bottom substrates the spawning area was divided into separate regions.

FIELD SAMPLING

Egg samples for estimation of total spawn were taken within five days of spawning. For egg mortality studies, repetitive sampling with intervals of a few days was conducted in the same areas. Dead eggs were distinguished from living ones by their opacity.

Two scuba divers collected samples of spawning-area substrates, i.e., pieces of vegetation, stones, and mollusc shells within the grid, handing these over to the surface personnel for preservation in 4% formaldehyde. The divers carried out subsampling as necessary. Bias due to non-random sampling was difficult to omit because of the nature of the bottom substrates and the employed sampling techniques.

Rocky bottom sampling in 1979 and 1980 was carried out by an underwater camera (Nikonos Calypso camera). The subject fields with 80 mm and 35 mm lenses were 41.9 cm^2 and 178.8 cm^2 respectively. The photographic equipment was calibrated by counting eggs on selected objects after *in situ* photographing. To compare changes in egg densities over time, frames and metal tags were placed on specific sites of the sea bed.

In mud or sand, open-ended Perspex cylinders with detachable end-pieces, were driven into the bottom substrate, and samples were collected by «air-lift» (Bjørke, Gjøsæter and Sætre 1972).

Prior to 1980 the number of egg layers was not recorded because only one layer was usually found over most of the area. A total of 1002 substrate samples and photographs were collected during 1977–1980, of which 589 are from 1980.

Cod and haddock were caught near the herring spawning grounds with entangling nets. These fish were measured for total length, and the stomach was put into a 4% seawater-formaldehyde solution for examination in the laboratory.

Temperature and salinity on the spawning grounds were recorded with a T/S-recorder to the nearest 0.1°C and $0.5‰$.

SAMPLE PROCESSING

In the laboratory each preserved substrate sample was examined for total number of eggs and number of dead eggs. Horizontal area of stones, shell fragments and seaweeds exposed for spawning products was calculated. If the number of eggs in any sample was high, a volumetric plankton splitter was used for subsampling. The number of viable eggs per square meter in each sample was then determined.

Underwater photograps taken from the spawning area were magnified 10x under a DURST photo-magnifier, and two or more randomly selected subareas of fixed size were used to estimate the number of eggs per square meter. The variance imposed by subsampling procedures was considered small compared with the major field sampling variance.

Each predator fish stomach was measured for volume. For those stomachs containing herring eggs, a subsample of eggs was collected from the anterior-, mid-, and posterior regions and sorted into the following groups, modified after HEMPEL and HEMPEL (1971):

I: eggs hyaline with embryo clearly visible.
II: eggs containing an opaque mass in which the embryo is still discernible. These eggs may have been alive at ingestion, but are in a more advanced stage of digestion.
III: eggs damaged, parts of the embryo visible.
IV: eggs containing a more or less homogeneous opaque mass. In these eggs fertilization probably failed.
V: eggs damaged, no embryo recognizable.

DATA ANALYSIS

The estimated number of eggs per square meter from each sample was matched to location, substrate type, depth and date. The mean number of eggs per unit area, weighed by its proportion of the total area, was used to calculate the mean per square meter for the entire spawning ground. The sampling variance was calculated as the variability between samples within each region. Missing data from any region were simulated by the mean number of eggs and its variance from the same region at a different time or from similar regions at the same time of sampling.

SAMPLING EFFICIENCY

During 1980, as a result of improved training, underwater photography was preferred to substrate sampling, thus allowing a more efficient use of time. The results of underwater photography versus direct sampling of substrate objects were compared in 1979 and 1980. In four out of the six sites examined, no

difference in egg density was found between the methods ($p>0.05$, Mann-Whitney). In the remaining two, substrate sampling showed 51% and 47% higher egg density ($0.01<p<0.05$, Mann-Whitney). These differences may be due to biased sample selection by divers. Since neither of the two methods was considered more reliable, data were pooled.

RESULTS

HYDROGRAPHY

During 1977–1980 spawning in Lindaaspollene normally took place at temperatures of 4–6°C when the ice cover had left the area. During the incubation period, the water temperature rose to between 5 and 8°C (Table 1.1). During the same period, salinity at the spawning grounds fluctuated between 26 and 29‰ with snowmelting and precipitation.

Tidal forces are the main circulators of water over the shallow and protected spawning grounds. Tidal amplitude in Lindaaspollene is normally 35–50 cm (Dahl *et al.* 1973) with a velocity on the Bjørnøy spawning ground of about 0.5 knots (0.25 m/s) at the mean between low and high tide.

Table 1.1. Temperature conditions at the herring spawning grounds during spawning and 50%-hatching (1977–1980).

Year	Spawning date	Water temp. (°C)	50% hatching date	Water temp. (°C)
1977	25 March	4.2	20 April	5.1
1978	6 April	5.0	30 April	7.6
1979	12 April	5.7	9 May	6.6
1980	13 April	6.0	7 May	8.5

SPAWNING – TIME AND LOCATION

Time of spawning

Spawning of herring in Lindaaspollene normally takes place in late March or early April, varying by several weeks from year to year (Table 1.2). During 1977 the date of spawning was not accurately determined, but gill net catches on 22 March confirmed that spawning was underway and on 26 March spawn was recorded by scuba divers, indicating approximately one-day old spawn.

Main spawning was usually recorded not later than in the first half of April. Gonad sampling of adult herring in 1978 and 1979 indicated that a second spawn would take place a few weeks later. Cod and haddock replete with herring spawn and the appearance of herring larvae some weeks later confirmed this in May 1979.

On 12 April 1979, the spawning act was observed between 1000 and 1100 hours at 0–2 m depth on the western side of Gølna Island (Figs. 1.2 and 1.3). The water was characteristically milky, as described by HOURSTON and ROSENTHAL (1976a). It appears that a spawning herring deposits all the eggs within a single day. The presence of a small boat drifting along the spawning ground did not seem to affect the spawning process.

Table 1.2. Date of spawning during 1977–1980 at Bjørnøy and Gølna (B) and Syslakvåg and Grunnavik (S) spawning grounds.

	March	April		April	
Year	22–26	4	6	12	13
1977	B				
1978		S	B		
1979				B	
1980					S

Spawning area

Two main spawning grounds of herring in Lindaaspollene have attracted particular attention for scientific studies since 1977. In the past, the Syslakvaag area was the only known spawning ground for the herring stock in Lindaaspollene (Figs 1.1 and 1.2). During the present study spawning occurred in this area in 1978 and 1980. The other main spawning ground, Bjørnøy, was discovered by scuba diving in 1977, and it was also occupied in 1978 and 1979. Other spawning grounds are considered to be of minor importance and are not dealt with in this paper.

Bjørnøy

The Bjørnøy spawning ground is located northeast of Bjørnøy island (Figs 1.1 and 1.2) where the shoreline is predominantly bedrock and boulders. From the shoreline the bottom slopes steeply down to 5–15 m. A shallow sandy bottom with a light distribution of boulders, gravel, and shell fragments lies between Bjørnøya and Gølna (Fig. 1.2).

The eastern shore of Gølna is similar to that of Bjørnøy with bedrock sloping sharply with depth, interrupted only by narrow ledges in that rock. On the northern shore of Gølna the bottom is shallow and rocky, with an area of about 200 m^2, and covered with red calcareous algae (*Lithothamnion* sp.), which seems adequate for spawn deposition. The western shoreline of Gølna, consisting mainly of rocks, slopes gently towards the sandy bottom at 5 m depth.

The spawning area around Bjørnøy and Gølna was estimated to 8500 m^2, bounded by the sea surface and about 10 m depth.

The vegetation in the spawning area is, in general, sparse. Several species

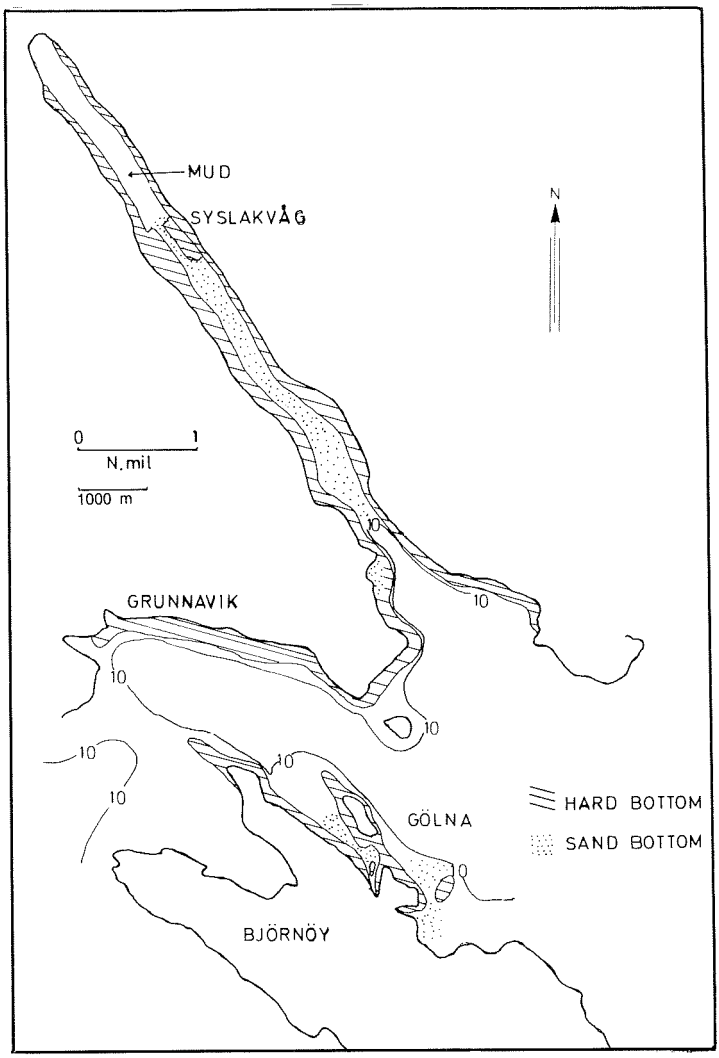

Fig. 1.2. The spawning grounds of herring in Lindaaspollene with bottom type and 10 meter isobath indicated.

occur with *Fucus* sp., *Codium fragile*, *Cladophora* sp., and *Enteromorpha* sp. being the most common.

The pelagic fauna in the spawning area is predominantly fish, such as *Gadus morhua*, *Melanogrammus aeglefinus*, and *Pollachius pollachius*. The sedentary fauna was dominated by tunicate species (e.g., *Ciona intestinalis*), bryozoa, tube-building polychaetes (e.g., *Spirorbis* sp., *Pomatoceros triqueter*), mussels (e.g. *Mytilus edulis)*, sea anemones, and echinoderms.

The light conditions along the spawning ground are variable. Spawn deposited along the eastern shorelines receive direct sunlight during the first

few hours of the morning; thereafter they are shaded by the land in the south and west. The northern and western parts of Gølna receive direct sunlight most of the day.

Syslakvaag

The other major spawning ground, Syslakvaagen, is located in a bay about 1 km north of the Bjørnøy area (Fig. 1.2). The bay points NW-SE with bedrock rising steeply on both sides. The bottom depth varies from about 60 m at the mouth of the inlet to about 2 m in the region where sand and rocks are replaced by mud. Several skerries are found in the area where there is a distinct transition from rocks and coarse sand to mud. The region described above, including the skerries and a narrow region of about 200 m^2 along the shorelines, covers an area of about 2500 m^2, and was previously considered to be the main spawning ground in Syslakvaag (FUREVIK 1976).

As a rule, the eastern shorelines along the entire spawning area in Lindaaspollene consist of steeply sloped bedrock, stretching from the surface to about 10 m depth, in some places even deeper. Northwest of the outer Syslakvaag area, the bottom substrate is similar to the eastern shores all the way up to the Grunnavik area, though the rocks slope more gently with depth. No eggs were deposited on the southern shores. Along the western shores, spawn was deposited at a depth range of 2–4 m. In the inner part of the Grunnavik area, the eggs were deposited on rocks at depths ranging from 0–4 m (bottom).

During 1980, spawning occurred in the areas Syslakvaag and Grunnavik, covering an area of 7280 m^2 with eggs (Figs 1.2 and 1.3).

The Grunnavik area was more exposed to sunlight, wind, and wave action than most of the Syslakvaag area. This seemed to influence the period of embryonic development, which is inversely proportional to temperature.

CHARACTERISTICS OF SPAWN

Classification of spawn intensity

A pilot survey over the spawning ground was made by scuba divers shortly after spawning. The entire spawning ground was divided into a grid and classified according to intensity of egg deposition and bottom substrates (Fig. 1.3). Such a procedure allocates more sampling effort to areas with high egg density, and thus reduces the total variance of the abundance estimates. Table 1.3 indicates the relative intensity of spawn deposition by area during the period of investigation. It shows that in years with large egg numbers (1977 and 1980) the spawning area is effectively utilized for spawn deposition.

Extremely high densities of spawn were observed only in a few sites in 1980, and low spawn intensiy (less than 100 000 eggs/m^2) covers only a small portion of the entire region. In years with light spawn, as in 1978 and 1979, it seems that spawn deposition occupies the lower and medium categories.

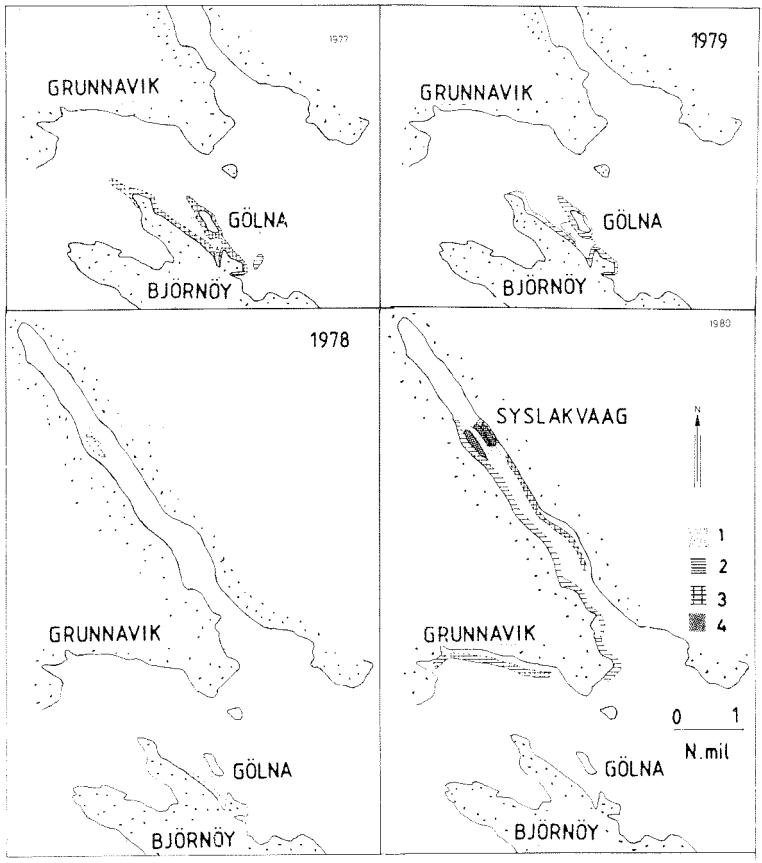

Fig. 1.3. Intensity of spawn deposition on different spawning grounds in Lindaaspollene during each of the years 1977–1980. See text for further explanation.

Table 1.3. Distribution of herring spawning by area (% of total spawning ground) per category of spawn intensity.

Category	Egg no. per m^2	1977 (%)	1978 (%)	1979 (%)	1980 (%)
1	1– 100 000	8	36	23	10
2	100 000– 500 000	10	64	77	58
3	500 000–1 000 000	82	<1	<1	22
4	> 1 000 000	<1	<1	<1	10

Annual variations in spawn deposition

In appendix Table I.1–I.4 mean egg density and total number of eggs for each year are given in relation to location, depth interval, and substratum for spawn attachment.

There is great variation in egg density and regional extension of the spawning grounds between years. The smallest spawning area observed during

the investigation period was about 1000 m^2 in 1978. The greatest spawning ground recorded by area was nearly 8450 m^2 in 1977, while in 1980 it was 7280 m^2 and in 1979, 3745 m^2. It should be remembered that the areas mentioned are «effective areas», i.e., areas excluding zero distribution of eggs.

The greatest overall egg densities were recorded in 1977 and 1980 with respective means of 614 000 and 554 000 eggs/m^2. The total number of eggs were estimated to be 5.2×10^9 and 4.0×10^9 in the respective years. The lowest number of eggs per square meter was observed in 1978 with a mean of 147 000 eggs/m^2 and a total of about 1.4×10^8 eggs (3% of total spawn in 1977 or 1980).

There seems to be an increase in spawning ground area with increasing number of eggs per unit area, perhaps to avoid too dense concentrations of spawn, and thus improve the survival rate of the eggs.

For 1977 two estimates of egg abundance one week apart are given in Appendix Table I.1 and I.2. The first estimate was mainly based on samples of eggs deposited on seaweeds, which in recent years has been found to hold substantially greater numbers of eggs per unit area than most other substrate types. The second estimate, one third the value of the first, is partly due to predation from other animals, e.g., diving ducks, ophiuroids, and fish. The relatively small number of samples, particularly in the first survey, and the great diversity observed in many surveys, indicate that the estimates were not reliable. More sampling from high-egg-density areas, which frequently coincided with those of great extension, was therefore carried out in the subsequent years.

From 1978 onwards the precision of egg abundance estimates was therefore considerably improved, as is indicated by the ratio of standard error to mean number of eggs per unit area (Appendix Table I.2–I.4). Average values of about 10% were considered adequate although values up to 100% might occur within some regions. Areas which were inadequately sampled were assigned estimates of egg density *i*, based on the subjective classification of spawn intensity during the pilot survey, or *ii*, by the estimates of egg density from areas with similar substrate, depth and geographical location.

Substrate preference

It is assumed that the number of eggs spawned per unit area on any kind of bottom substrate reflects the degree of preference for that substrate type. Table 1.4 presents the data from 1978 to 1980 on the number of eggs deposited per square meter according to substratum type.

As mentioned earlier, the vegetation on the spawning grounds was sparse. Seaweeds was therefore considered to be of little importance as a spawning substratum, although high egg densities might be recorded on it (Table 1.4). Spawning herring seemed to prefer hard bottom covered by sedentary

Table 1.4. Number of eggs per square meter (Mean $\pm\sigma_{\bar{x}}$) · 10^3 recorded on different substrata shortly after spawning (1978–1980).

Yar date	1978 7–8 April	1979 15 April	1980 15–18 April
Days after spawning	1–4	3	2–5
Substratum types			
Rocks	481±241	251±18	418±43
Boulders	389±105	199±30	797±443
Shells, Echinoderms	248± 59	202±55	870±146
Red algae (calcareous)	208± 81	33	568±103
Seaweeds	246±104	2690±1874	3073±2355
Sand (with boulders)		133±64	
Fine sand	10± 4	22	
Mud	1± 1		

tube-building polychaetes and calcareous red algae (*Lithothamnion* sp.). Spawn also covered steep rocks. The transition from a site covered with spawn to one without was usually abrupt, indicating that the spawning herring was in close contact with the substrate. Eggs were seldom found on sand or mud, but high densities of eggs were observed on boulders dispersed on a sandy bottom.

Vertical distribution of eggs

Spawn was generally distributed from the sea surface down to approximately 10 m depth. In 1977 eggs were deposited up to 10 cm above low tide level indicating that spawning took place during high tide. During more recent years, eggs were deposited from mean low tide level or 10–15 cm below this level.

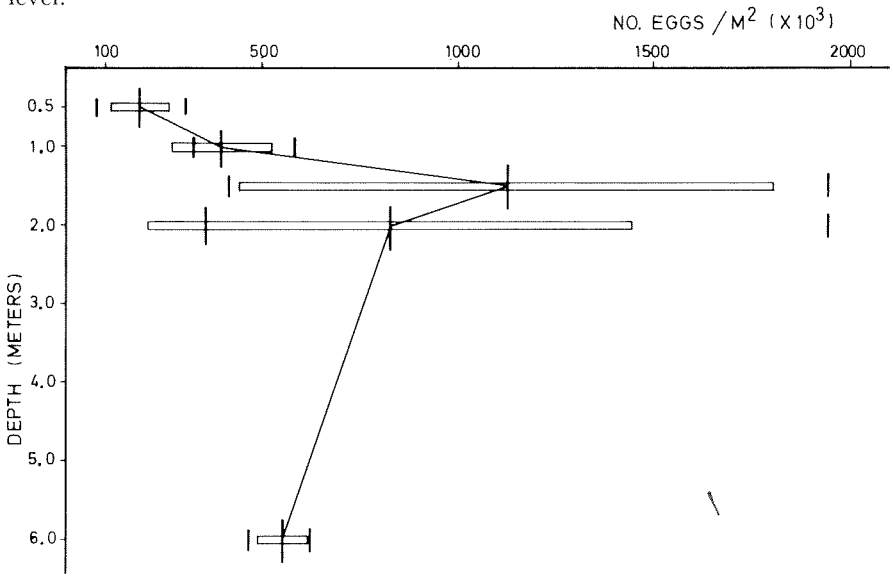

Fig. 1.4. Egg density (mean ± standard deviation and range) versus depth.

During 1980, underwater photography was used in Syslakvaagen to examine depth-related egg density (Fig. 1.4). The density of eggs was low close to the surface, but increased just below the wave action zone. Mean egg density seemed to decrease again with increasing depth, although no significant difference in egg density was observed between 1.5 m and 6 m depth ($P>0.05$).

EGG MORTALITY

A. Natural mortality

Mortality at different egg densities

In 1980 egg mortality was studied in relation to egg densities at different times after spawning. The proportion of dead eggs increased with increasing age of the spawn (Table 1.5). A mean mortality of about 1–2% shortly after spawning (less than 5 days) increased to approximately 8% just before hatching (20–25 days after spawning). Mortality increased close to hatching, particularly at egg densities exceeding one million eggs per square meter. However, since the data refer mainly to eggs distributed on hard bottom substrates and since the number of samples was low, it is not possible to draw any unambiguous conclusions.

Mortality and substratum

Mean mortality of eggs recorded on hard-bottom substrates was usually low during the first two weeks after spawning (less than 10%) and increased with time although the proportion of dead eggs prior to hatching was usually below 20% (Table 1.6). The proportion of dead eggs in the uppermost egg layer was less than average and did not seem to increase prior to hatching regardless of density.

Samples from soft-bottom substrates were not included in this investigation. Observations from previous years indicate that mortality of eggs distributed on sand and mud is substantially higher than on the other kinds of substrates

Table 1.5. Mean mortality (%), age of spawn (days) and egg density in 1980.

Date	15–18 April		29–30 April		3–8 May	
Days after spawning	2–5		16–17		20–25	
No. eggs per m^2	N	Mortality % mean range	N	Mortality % mean range	N	Mortality % mean range
<250 000	15	4.8 (0–5.5	1	0	30	9.8 (0–34.3)
250 000– 500 000	32	1.2 (0–7.4)	5	1.2 (0.4–4.5)	15	6.4 (0–28.6)
500 000–1 000 000	23	1.5 (0–4.3)	10	1.3 (0.7–3.4)	6	5.2 (0.3–13.7)
>1 000 000	15	1.4 (0.5–8.1)	11	2.0 (0.5–8.1)	4	18.6 (10.8–28.8)
Pooled	85	1.6 (0–8.1)	27	1.2 (0.4–8.1)	55	7.8 (0–34.3)

Table 1.6. Mean egg mortality (%) on different substratum types and specific sampling sites on the rocky bottom (skerries) from data obtained in 1980. (1) designates mortality in the uppermost egg layer.

Days after spawning	2–5			16–17			20–25		
Date	15–18 April			29–30 April			3–8 May		
		Mortality (%)			Mortality (%)			Mortality (%)	
Substratum	N	Mean	Range	N	Mean	Range	N	Mean	Range
Pooled data									
Rocks	44	1.1	(0 –7.4)	13	5.6	(0 –19.4)	10	17.0	(0 –28.8)
Boulders	2	1.1	(0.8–1.6)		–	–	13	15.4	(0 –24.3)
Red Algae *(Lithothamnion sp)*	2	1.7	(1.6–1.8)	11	1.2	(0 – 2.4)	6	7.0	(0.3–13.7)
Shells/ Echinoderms	18	1.4	(0 –3.2)	4	1.1	(0.4–1.9)	1	12.0	–
Seaweeds	7	2.2	(0 –5.5)	1	1.1	–	9	5.1	(1.5–34.3)
Specific sites:									
Gillnet stone	2	3.3	(1.7–4.8)	6	2.1	(0.7–4.5)	1	7.9	–
Gillnet stone (black)	4	1.9(1)	(0 –4.3)	3	6.5	(2.7–8.1)		–	–
Gillnet stone (red)		2.2	(1.7–4.8)		–	–	3	3.7	(3.0– 4.2)
Rocks	12	0.7(1)	(0 –2.6)		–	–	4	20.3	(15.5–28.6)
							4	6.5(1)	(2.7–11.4)
Rocks	4	0 (1)		6	1.5(1)	(0 – 8.8)	4	5.2(1)	(0 –13.9)
Rocks	2	0 (1)	(0 –0)	14	8.3(1)	(0 –39.6)		–	–
Rocks	4	0 (1)	(0 –0)	10	2.6(1)	(0 – 6.3)		–	–
Rocks	10	1.8(1)	(0 –8.0)	6	2.1(1)	(0 – 5.3)	3	6.3(1)	(6.1– 6.7)
Rocks	6	1.1(1)	(0 –2.6)	8	2.9(1)	(0 –10.0)	4	2.8(1)	(0 – 5.9)
Rocks	4	0 (1)	(0 –0)	17	18.1(1)	(0 –81.1)		–	–
Rocks	6	0.5(1)	(0 –3.2)	14	1.3(1)	(0 – 8.3)		–	–
Rocks		–	–	6	1.7(1)	(0 – 6.9)	4	3.1(1)	(0 – 6.9)
Rocks	6	2.8	(0 –5.7)	6	8.2(1)	(0 –19.4)	4	8.6	(5.3–12.5)
							9	5.7(1)	(0 –21.4)
Rocks	1	35.0(1)	–	6	1.0(1)	(0 – 7.7)		–	–

investigated. The proportion of dead eggs on sandy bottom and mud in 1978 was of the order of 36% (range 25–50%) and 67%, respectively, 1–2 days after spawning.

Relative frequency of dead eggs in fish stomachs

An indirect measure of the natural mortality of herring eggs on the spawning grounds was obtained by examination of the stomach contents of demersal fish which feed on herring spawn. Stomach content analysis showed that the

majority of eggs were found in the mid and posterior regions of the predator fish stomachs.

Eggs in the stages of digestion I (recently ingested), II, and III are assumed to be alive at ingestion, while IV and V are assumed to be dead. Stage I-eggs generally dominate the anterior stomach region of both cod and haddock.

The mean proportion of living eggs in the anterior region of cod stomachs (80%) did not decrease significantly with time (Fig 1.5). In haddock, however,

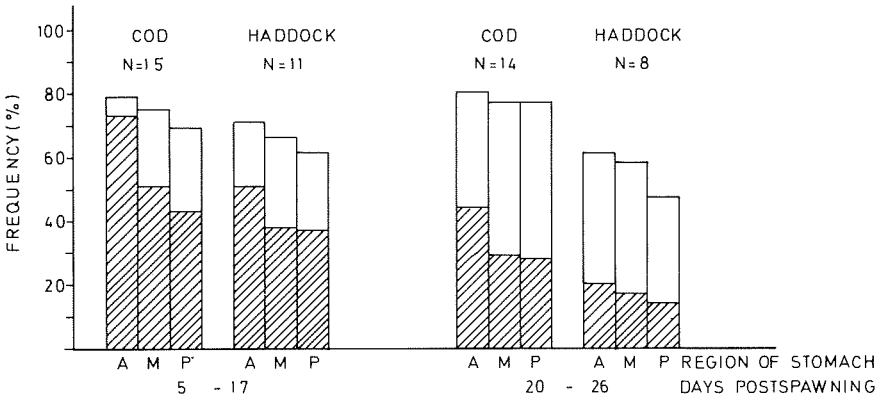

Fig. 1.5. Mean relative proportion of herring eggs alive (%) in different regions of the predator fish stomachs. The cross-hatched part of the column refers to eggs in stage I of digestion. A, M and P refer to the anterior-, mid-, and posterior regions of the stomach.

the proportion was reduced from approximately 70 to 60% during the trial period. The smaller proportion of live herring eggs in haddock indicates that some selection or differences in feeding habits exist between the two species. Because of progressive digestion, the proportion of dead to live eggs in the posterior regions is presumably overestimated (HEMPEL and HEMPEL 1971). Thus estimates of egg mortality were made from the anterior region only, yielding an average of 75.8% living eggs. The great range in mortality (0–100%) may be due to heterogeneous substrata, differences in sampling time relative to the feeding time of the fish, or species-specific feeding strategies, which makes this method doubtful for the estimation of mortality of herring eggs.

B. Mortality due to other causes

Egg loss

A reduction in number of eggs per square meter with time is mainly attributed to predation by fish, invertebrates and diving ducks. Removal of spawn by means of wind, or wave action and strong currents is assumed to be negligible

as the eggs are firmly attached to most substrate types. Frames covering selected sites were used for comparative tests of loss of herring spawn.

During 1977 there was a marked reduction in the number of eggs on the spawning ground in the course of one week. Sample estimates (Appendix Table I.1–I.4) and diver surveys indicated that a large number of eggs had been removed from the spawning grounds, but only some of this reduction was due to the sampling technique. In 1978 the number of eggs per square meter was not significantly reduced over a period of eleven days ($p>0.05$, Mann Whitney, Table 1.7.1), although cod was seen to consume herring spawn. The mean egg density was reduced by 20–65% ($p<0.05$, Mann Whitney) over a similar time period in 1979 in three of the four sites examined (Table 1.7.2). Decline in the mean egg number per square meter was also observed during the first two weeks of the incubation period in 1980 in seven of the eleven sites examined

Table 1.7.1. Egg loss in 1978. Mean number of eggs per square meter by date and age of spawn at selected sites, with differences in egg density (Mann Whitney's U-test) indicated if statistically significant.
+: P<0.05, ++:P<0.01, ns: P≧0.05.

Days post-spawning		1–4	12–14		
	Date	5–8 April 1978	17–18 April 1978		
Site	Substrate	Egg no. per m^2 Mean $\sigma_{\bar{x}}$	Egg no. per m^2 Mean $\sigma_{\bar{x}}$	Loss %	P
Syslakvåg	Rocks	128.7± 46.5	33.4± 6.5	74.0	ns
	Rocks	81.3	147.9± 68.0	–81.9	ns
	Sand	0 ± 0	20.6± 10.6	–	ns
	Rocks	65.9± 10.9	36.4± 7.5	44.8	ns
Bjørnøy	Rocks/ boulders	224.1± 38.7	94.4± 28.2	57.9	ns
	Sand	9.6± 4.1	9.2	4.2	ns
Gølna	Rocks/ *Lithothamnion sp.*	205.9± 36.3	303.5± 81.5	–47.4	ns
	Rocks	345.9±131.1	333.6±123.3	3.6	ns

Table 1.7.2. Egg loss in 1979. See Table 1.7a for explanation.

Days post-spawning		3	13		
	Date	15 April 1979	25 April 1979		
Site	Substrate	Mean± $\sigma_{\bar{x}}$	Mean± $\sigma_{\bar{x}}$	Loss %	P
Bjørnøy	Rocks	321.8±11.4	112.2±10.5	65.1	++
	Rocks	218.3±17.2	170.0±13.3	22.1	+
	Rocks	131.0±10.2	45.7±17.2	65.1	+
	Rocks	150.0±14.5	159.1±43.9	–6.1	ns

Table 1.7.3. Egg loss in 1980. See Table 1.7.1 for explanation.

Days post-spawning		2–5	16		
	Date	15–18 April 1980	29–30 April 1980		
Site	Substrate	Egg no. per m^2 Mean $\sigma_{\bar{x}}$	Egg no. per m^2 Mean $\sigma_{\bar{x}}$	Loss %	P
Syslakvåg	Rocks	417.6± 43.0	741.1±108.9	–77.5	++
	Rocks/ *Lithothamnion sp.*	567.5±102.5	873.8±155.0	–54.0	ns
	Shells and Echinoderms	869.5± 145.8	979.3±294.7	–12.6	ns
	Seaweeds	3073.1±2355.1	1203.6±535.6	60.8	ns
	Hard bottom (pooled data)	772.0± 32.0	717.4± 29.7	7.1	ns
	Rocks (eternit)	1213.8± 38.7	482.5± 54.4	60.2	+
	Rocks (gill net stone)	514.2± 34.0	616.7±128.5	–19.9	ns
	Rocks	975.3± 114.3	914.9± 28.6	6.2	ns
	Rocks	1200.3± 43.4	917.6± 40.6	23.6	++
	Rocks	1023.0± 34.1	1226.2± 54.0	–19.9	ns
	Rocks	565.4± 61.3	489.6± 34.9	13.4	ns
	Rocks	917.3± 42.7	602.8± 40.3	34.3	++
	Rocks	1289.0± 42.4	1020.9± 29.9	20.8	++
	Rocks	713.8± 31.3	460.2± 63.5	35.5	++
	Rocks	564.0± 26.2	439.0± 31.9	22.2	+
	Rocks	1091.2± 47.3	676.1± 65.8	38.0	+

($p<0.05$, Mann Whitney, Table 1.7.3). This latter is attributed mainly to predation by fish and bottom invertebrates. However, the grand mean number of eggs per square meter on rocky surfaces was observed to increase during the same period ($p<0.01$, Table 1.7.3). Whether this increase was due to a second spawning on selected surfaces was not determined, but eggs in different stages of development were observed at several sites.

Fish feeding on herring eggs

Predatory fish seem to select specific feeding sites in areas with herring spawn, usually feeding along a narrow path a few centimeters broad, resulting in steep-sided depressions in the spawn cover. During April 1978 (one week after herring spawning), May 1979 (shortly before hatching) and May 1980 (one week after main spawning and also close to time of hatching), 34 cod and 20 haddock were examined for stomach contents.

The percentage of cod and haddock feeding on herring spawn was high in all three examined years (Table 1.8). Cod longer than about 50 cm had occasionally ingested adult herring in addition to herring spawn. In 1980, a cod

Table 1.8. Relative proportion (%) of cod and haddock with herring spawn in the stomach.

Species	Cod (*Gadus morhua*)				Haddock (*Melanogrammus aeglefinus*)			
Year	1978	1979	1980	Total	1978	1979	1980	Total
Days after Spawning	13–14	21–26	5–17		13–14	21–26	5–17	
Fish feeding on eggs (%)	89	93	100		100	100	100	100
Mean No. eggs per stomach	10587	5855	40565	15110	4595	1258	16420	3666
Range	0–15000	0–17924	30–207220	0–207220	468–11812	117–5030		468–16420
Mean standard length (cm)	38.4	43.8	44.8	42.3	50.2	46.4	39	48.0
Range	31–53	37–58	31–78	31–78	44–60	35–52		35–60
No. fish	9	15	10	34	10	9	1	20

of 55 cm was recorded with 5 adult herring and no spawn, and another, 49 cm cod, with one adult herring and 28 000 herring eggs. Small fractions of algae and other bottom substrates were also ingested.

The number of herring eggs per stomach showed great variability at any particular time. Feeding intensity appeared to be higher in 1980 than in previous years, which may be explained by the greater spawn density that year. The correlation between number of eggs per stomach and standard lenght of cod was significant at 5%-level ($r^2 = 0.50$).

HATCHING MORTALITY

Substrate samples with spawn were collected by scuba divers 16 days after spawning in 1980 and transferred to a field laboratory to study hatching mortality of eggs at different egg densities. The water temperature in the laboratory was maintained at 6–8°C.

Hatching mortality increased with increasing egg density (Table 1.9), although the small number of samples and the large variability did not make the results conclusive. At egg densities up to 500 000 eggs/m^2, about 50% (range 16–83%) of the eggs did not hatch, whereas this proportion increased to

Table 1.9. Proportion of unhatched herring eggs in 1980.

No. eggs per m^2	N	Mean %	Range %
<250 000	13	49.5	15.6–82.8
250 000– 500 000	6	52.8	22.0–73.3
500 000–1 000 000	3	72.3	63.9–79.6
Pooled data	22	57.2	15.6–82.8

more than 70% (range 64–80%) at egg densities between 500 000 and 1 000 000 eggs/m^2.

On 12 May 1980 in areas where spawn had been recorded in one or two layers, divers found hardly any unhatched eggs left on the substrate, indicating an overall low egg mortality and nearly 100% hatching succes. These findings indicate that in the experimental situation hatching success at low egg densities is probably underestimated due to the stress of transfer.

In areas where spawn depositions had initially been heavy, great egg mortality was recorded. At egg densities with thicknesses greater than four layers, usually not more than the upper one or two layers of eggs were able to hatch. Occasionally where spawn lay in regions exposed to direct sunlight, algae were found on the uppermost egg layers. This probably affects egg mortality, even in the deeper egg layers which had, by the end of main hatching, started a process of decomposition and emitted an unpleasant odour when disturbed by divers. Hatching success of eggs in thick patches of spawn is considered to be low.

SPAWNING STOCK SIZE

Annual egg production and the estimation of spawning stock size

Given the total annual egg production of a spawning stock, the absolute size of that stock can be estimated. This requires detailed knowledge about several other parameters, including fecundity of females, sex ratio of the spawning stock, and egg mortality between spawning and sampling time. In the subsequent calculations this mortality factor is presumed to be negligible due to the short time period between spawning and sampling. The relationship between egg production and spawning stock size is described as

$$P = \frac{E}{F \cdot S(1 - m)}$$

where P is parent stock size, E is total annual egg production of the stock, S is sex ratio, i.e., proportion of females in the spawning stock, m is egg mortality due to egg loss from the spawning ground between spawning and sampling, F is fecundity, i.e., mean number of eggs produced per year per female. Annual fluctuations in fecundity are not considered in this study. A weighted mean fecundity was derived for the whole spawning stock based on annual calculations of mean fecundity of length groups (Lie *et al.* 1978) and the length distribution of the spawning stock during each season (Dahl and Gjøsæter unpubl.).

The spawning stock was dominated by the 1969 and 1972 year classes from 1977 onwards with a progressive increase in the proportion of the 1972 year

class up to 1980. In 1980, however, the first-time spawning 1977 year class comprised an estimated one half of the spawning stock. These recruit spawners were observed to have substantially lower fecundity (mean 5 269 eggs per female) compared with the remainder of the spawning stock (range 30 000–50 000 eggs per female). The extremely low fecundity of spawning recruit females observed in 1980 has not been recorded previously or since (DAHL pers. comm.).

Table 1.10 shows that the spawning fraction of the herring stock in Lindaaspollene was similar in 1977 and 1980, amounting to approximately 40 tons. In 1978 and 1979 the spawning stock size was estimated at only 1 and 6 tons, respectively, from the observed spawn records. Secondary spawnings, whether they occur in unrecognized areas or later in time, are not included in the present estimates.

Table 1.10. Egg production and estimated spawning stock size of the herring stock in Lindaaspollene. Annual estimates for the period 1977–1980.

Year	Egg production ± 95% confidence interval 10^8	Mean individual weight kg	Mean fecundity Number of eggs per female	Sex ratio ♀ : ♂	Spawning stock size Number 10^3	Weight (tons)
1977	51.0±35.2	0.162	40501	47 : 53	272.6	44.2
1978	1.4± 0.3	0.150	39045	47 : 53	7.5	1.1
1979	6.9± 0.5	0.172	41891	50 : 50	32.9	5.7
1980	40.3± 8.0	0.127	24570	50 : 50	328.4	41.9

In 1978 it is likely that spawning occurred in Lindaaspollene in unobserved localities since the size of the spawning stock staying in the known pre-spawning areas was negligible compared to the main spawning stock (AKSLAND unpubl.).

Also in 1979, some spawning probably occurred in unrecognized areas, as is indicated by the bimodal hatching curve (p. 184). Some also took place later, as indicated by fish stomachs containing herring spawn and the appearance of newly hatched larvae in the net catches after some weeks.

DISCUSSION

The local herring stock in Lindaaspollene resembles some other herring stocks in preferring shallow water for spawning, e.g., Baltic herring (ANEER 1979, WEBER 1971), White Sea herring, Okhotsk herring (GALKINA 1971), and Pacific herring (OUTRAM and HUMPHREYS 1974). Some stocks prefer spawning grounds located at intermediate depths, e.g., Clyde herring, which spawns in the Ballantrae Bank area at 13–24 m depth (PARRISH *et al.* 1959). Atlantic herring in the Georges Bank area seem to prefer deeper waters (50 m depth) for spawning (CADDY and ILES 1973), as does Norwegian spring spawning herring.

The latter seem to prefer spawning grounds located at 20–80 m depth, although spawn has been recorded from 5 m to approximately 150 m (RUNNSTRØM 1941).

In Lindaaspollene herring spawn was distributed from the surface to approximately 10 m depth, if allowed. The egg density recorded in the upper 0.5 m was significantly lower than in deeper waters. No relation between egg density and depth was otherwise recorded. Abrupt changes in egg density with area indicate that spawning females are in close contact with the substrate when the spawn is deposited. This is also consistent with the direct observations of the spawning act in 1979 and with other observations on Baltic herring (ANEER *et al.* 1983) and Pacific herring (HOURSTON *et al.* 1977 and STACEY and HOURSTON 1982).

Spawn in Lindaaspollene was in general deposited on rocks and boulders, which were either bare or covered with carpets of red calcareous algae (*Lithothamnion* sp.), and occasionally on seaweeds. Spawn, even in small concentrations, was rarely recorded on sandy bottom, and mud seemed to be avoided. Substrate preferences for spawn deposition similar to those reported for Lindaas herring have also been found for other herring stocks, although specific preferences for bottom substrates may be highly variable between stocks (e.g., JENKINS 1927, RUNNSTRØM 1941, PARRISH *et al.* 1959, MCKENZIE 1964, HUMPHREYS and HOURSTON 1978, BOWERS 1980 and de GROOT 1980).

Egg mortality was studied to estimate the hatching potential of the Lindaas herring stock. Natural mortality of herring eggs up to the time of hatching is generally reported to be low (e.g., RUNNSTRØM 1941 and BAXTER 1971), and such was the case in Lindaaspollene at egg densities below 1 000 000 eggs/m^2. However, at an egg density of 1 200 000 eggs/m^2 FUREVIK (1976) reported 80% mortality one day prior to hatching. Mortality rates of 40–80% in egg masses of similar thicknesses were also reported by RUNNSTRØM (1941). The irregular rate of development of eggs in various layers of spawn as reported in *C. pallasi* by GALKINA (1971), may cause the death of embryos in deeper layers.

Egg mortality is assumed to be only slightly affected by unsuccessful fertilization. FUREVIK (1976) found that close to 100% of all eggs were fertilized in Lindaaspollene, although some authors believe that high egg mortality in thick layers of spawn are related to incomplete fertilization, e.g., HEMPEL 1979.

If spawning occurred outside the main spawning ground, mortality of eggs was seriously affected, as was observed in the high mortality of eggs deposited on sand or mud as opposed to those on rocks and boulders. Eggs in heterogeneous stages of development were, however, observed in Lindaaspollene in both 1977 and 1980, primarily on sandy bottom. This was proposed to be a consequence of non-optimal conditions for egg development, although the possibility of secondary spawning on the already occupied spawning grounds cannot be excluded.

At the time of hatching, egg mortality increased considerably, with the mean

hatching failure rate reaching values of more than 50% and increasing with increasing egg densities. By estimating the number of larvae produced, hatching success was calculated at 1–17% of the observed egg records in years with dense spawn and was probably greater in years with light spawn (p. 183). This is also consistent with observations from diver surveys in Lindaaspollene at the time of hatching in 1980. TAYLOR (1971) and GALKINA (1971) also found that densely packed eggs had a rather low hatching success, and many larvae succumbed in the egg shell or were deformed. Approximately 100% of the eggs in solitary layers produced viable larvae, while in eggs of 12–16 layers thickness, less than 10% of the larvae were viable (TAYLOR 1971). It is therefore not unreasonable to assume that mortality of eggs and non-viable larvae can reach 70–80% of the egg number present in years with heavy spawning. TAYLOR (1964) claimed that this explains the domeshaped reproduction curves suggested for several herring stocks.

Cod was frequently observed feeding on spawn from smooth rock surfaces, and stomach content analyses of cod and haddock near the spawning area also indicate that herring spawn is a preferred food item when available. These analyses also revealed a high rate of natural herring egg mortality (averaging approximately 25%) compared with that of spawning ground investigations (less than 10% on average). This difference was probably due to the fish sampling technique using gill nets. The added time lapse between capture and the cessation of digestive activity, while the stomach contents were being fixed, imposed a higher mortality rate on the eggs. Active methods of capture, such as trawling, would be more appropriate for this aim and are supported by HEMPEL & HEMPEL (1971) who report low mortality of herring eggs prior to hatching (0–11%) in stomachs of haddock sampled with bottom trawl. Species-specific feeding habits and large variability in observed egg mortality will, however, make estimates of egg mortality imprecise when using such indirect sample collection methods.

Egg loss ascribed to predation by fish and bottom invertebrates was estimated to be of the order of 20–60% (mean 34%) during the first two weeks after spawning in 1980. CADDY & ILES (1973) reported an increase in the abundance of fish, hermit crabs and snails when herring spawn was available. They estimated from photographs that approximately 8% of the herring spawn had been removed by predation within the first two days on the Georges Bank at 50 m depth. During the incubation period COOPER *et al.* (1975) reported predation by various fish species and invertebrates accounted for the loss of 30–70% of the total number of herring eggs deposited in the same area, which concurs with the loss reported in Lindaaspollene in 1980. FUREVIK (1976) estimated that egg loss in the Syslakvaag spawning ground in 1974 amounted to 59% of the total number of eggs spawned. For Norwegian spring spawning herring DRAGESUND and NAKKEN (1973) suggested that at least 95% mortality

occurred between spawning and hatching largely due to predation by haddock and saithe.

The daily energy requirements of a 45 cm cod are met by one stomachful of 15 000 herring eggs (DAAN 1973, JONES 1974, JOHANNESSEN 1980), an amount which can be easily ingested in the course of a day. Digestion requiring 1–6 days is considered to be appropriate for cod, depending on temperature, size and kinds of food items (DAAN 1973, KARPEVICH and BOKOVA 1937, TARVERDIEVA 1962, TORESEN 1982 and TYLER 1970).

As long as spawn is available and easily accessible on the spawning grounds, the predatory fishes are assumed to be eating it. During the egg incubation period (about 20 days at a temperature of 5–6°C), each cod is assumed to have a predator potential of 86 000–440 000 herring eggs. Based on the data of TORESEN (1982) on experimental feeding of haddock, and with assumption of 200 fish in the area, based on scuba diving observations and fishing experiments, egg loss due to fish predation is estimated to lie between 0.3 and 12%. The exact number depends on whether the spawning was heavy, as in 1977 and 1980, or light, as in 1978 and 1979. Similar estimates would be 1.7% and 63% when applying data on stomach depletion rates (TYLER 1970, JOHANNESSEN 1980). These estimates vary considerably according to the method used. It is supposed, however, that in years with heavy spawn, more predator fishes are attracted to the spawning grounds and more food is also likely to be ingested than is necessary to satisfy their basic energy requirements. Estimates of egg loss due to fish predation of up to 60% of total spawn therefore do not seem unreasonable.

Birds, mainly common eiders (*Somateria mollissima*), are also assumed to be important herring spawn predators, when spawn is deposited in shallow areas. In 1977 a flock of nearly 100 prenesting common eiders was encountered on the spawning ground in the northern part of Gølna. Estimates of daily food consumption of adult common eiders, approximately 680 kcal/bird/day (CANTIN *et al.* 1974), indicate that roughly 750 000 herring eggs would be ingested daily per bird if this was the sole food item. However, the same investigator found that herring eggs make up only 40% by volume of common eider diet in the St. Lawrence estuary. During the period of incubation (approximately 20 days), the number of eggs removed by a hundred common eiders would therefore be in the order of nearly 30% of the total egg production in Lindaas in 1977. OUTRAM (1958) indicated that egg loss of Pacific herring due to bird predation (seagulls and ducks) was of the order of 25% of the number of eggs spawned within the first three days after spawning, increasing to 30% after six days and to 39% (30–55%) by the end of incubation. HAEGELE *et al.* (1981) stated, however, that predation by birds and mortality due to wave action are confined only to that portion of total spawn of *Clupea harengus pallasi* exposed to air and wave action, amounting only to 10%. GJØSÆTER and SÆTRE

(1974a) reported, however, diving ducks feeding on capelin eggs (*Mallotus villosus*) at depths of 25–50 m, but they estimated that less than 2.5% of total egg production of capelin was vulnerable to predation from diving ducks.

The present study indicates annual variations in time of spawning as well as in the spread of the spawning grounds and the density of eggs on various kinds of substrate types. The years 1977 and 1980 were similar in many regards, specifically with respect to intensity of spawn deposition and area of the spawning ground. In 1978 and 1979 the spawning grounds recorded were of limited extension and the intensity of spawning was rather low. It is likely that only a fraction of total spawn was observed, whereas the main part was probably deposited in unobserved locations or at a later date.

Observations of two small spawning grounds about one kilometer apart and no findings of larvae hatched after the main hatching season indicate that additional spawning in 1978 might occur at the same time in unrecognized localities. Delayed spawners might also deposit their eggs outside Lindaaspollene. Aksland (1983) reported that the fraction of the parent stock staying in the observed spawning area immediately before spawning in 1978 was negligible compared to the size of the major spawning stock. For 1979, estimates of spawning stock size based on egg data conflict with both acoustic surveys (Aksland 1983) and fish stomach content analyses. Observations of delayed spawning groups in 1979 also indicated heterogeneous maturation of the stock. It is therefore supposed that egg data underestimates the spawning stock size in 1978 and 1979. The estimates of parent stock size derived from egg data in 1977 and 1980 agreed reasonably well with the estimates obtained from tagging experiments in 1977 (Lie and Dahl 1981) and with acoustic surveys in 1980 (Aksland 1983) of approximately 40 tons.

Despite small individuals, the 1977 year class made up the majority of recruit spawners in 1980, and up to 50% of the total spawning stock. The contribution of recruit-spawners to the spawning stock in the other years was very low, with the strong 1969 and 1972 year classes dominating the spawning stock in 1977, 1978 and 1979. The recruit-spawners of the 1977 year class, although contributing significantly to the spawning stock in 1980, had remarkably low fecundity compared with their larger-sized counterparts. This caused an additional variability in estimating spawning stock size. However, recruit spawners with low fecundity do not seem to be a common phenomenon in Lindaas, and in 1981 normal fecundity of the 1977 year class appeared (Dahl pers. comm.). The effect of age and body size on fecundity has not been extensively studied (Hempel 1979), although Schopka (1971) reported that older fish of a given size group produce more eggs. On the other hand, feeding conditions for pre-spawning herring may influence fecundity of a given size group (Anokhina 1960, 1971 and Hempel 1971), and egg quality may change with parental factors. Blaxter and Hempel (1963) showed that the dry weight

of eggs from recruit spawning Downs herring was less than that of older fish, which has implications for the survival of eggs and larvae.

Several sources of error are involved in estimating parent stock size of fish stocks on the basis of spawning products. The major sources of error are associated with the sampling procedures, with consequences for the calculation of fecundity, sex-ratio, egg number and mortality.

Close up photography with an 80 mm lens proved most adequate for the purpose of abundance estimation of spawn in Lindaaspollene. The precision of counting eggs by the photographic method decreased, however, with increasing egg layer thickness, but was compensated for by the increasing number of samples obtained from high eggdensity areas. Substrate samples used for calibration of the photographic method and closer examination of the eggs were used to supplement the calculations.

Variability in space and time is considered to be a main factor contributing to the variance of stock size estimates (ENGLISH 1964, SAVILLE 1964, ULLTANG 1977). In most sampling cases a compromise between a dense grid of stations and frequent coverage is required. For the estimation of spawn abundance of fish that spawn during a brief period and whose demersal eggs remain stuck to the substrate within a well-defined area, the sampling coverage over time is not overly critical, whereas fish with pelagic eggs who spawn for an extended period of time over a wide area may offer greater difficulties for adequate sampling coverage.

2. ABUNDANCE, DISTRIBUTION AND MORTALITY OF LARVAE

INTRODUCTION

From the viewpoints of both fisheries administrators and scientists it is desirable to forecast the strength of recruiting year classes before the fish enter the exploitable part of the stock. No simple diagnostic sign to characterize the strength of a year class is yet available, although most authors agree that various factors influencing survival exist during the early stages of development, probably within the first half year. Comprehension of the relationship between the spawning stock size and egg production, i.e., spawning potential of the parent stock, larval production, and subsequent recruitment has therefore been one of the main goals of fishery research during the last century (e.g., CUSHING and HARRIS 1973, WARE 1975, LETT and KOHLER 1976, SHEPHERD and CUSHING 1981).

Though indications for the existence of some relationship between the spawning potential and subsequent recruits are demonstrated in some small stocks of Pacific herring (TAYLOR 1963) and in the Downs stock of herring in the North Sea (BURD and HOLFORD 1968), no direct relationship between parent stock size and subsequent recruits has been documented for most of the major fish stocks.

HJORT (1914) proposed that high mortality takes place at the end of the yolk-sac period when the larvae change from endogeneous food reserves to exogeneous feeding. Though he had no measurements to support his idea of a critical period, many scientists find it attractive even today (MAY 1974).

The topics taken up in the present work concern the population dynamics of herring larvae during the first two months after hatching. Two different methods for the estimation of larval production are presented for comparative purposes, and daily rates of mortality from hatching up to an age of about 2.5 months are determined. Diurnal vertical distribution of larvae is studied in relation to post-hatching age (stage of development) and environmental factors, and the dispersal of larvae is followed from known hatching centres.

MATERIAL AND METHODS

FIELD SAMPLING – VESSEL, GEAR AND SAMPLING OPERATIONS

The material used in this paper was collected from April to June during the years 1977–1980. Fish larvae were sampled with paired 20 cm Bongo nets (POSGAY, MARAK and HENNEMUTH 1968) fitted with 0.275 mm mesh size Nitex nets. After the main hatching these were changed to paired 61 cm Bongo nets (0.505 mm mesh size Nitex) to increase the filtering volume and reduce the retainment of undersized planktonic organisms. Newly hatched herring larvae retained in these nets could indicate delayed hatching, although their use in quantitative assessment of larval production would be doubtful. The Bongo nets had no opening-closing device and a 24.5 kg V-fin depressor was attached to the wire one meter below the nets. Beyer's Low-Speed Midwater Trawl (BLSMT) was occasionally used for sampling larger larvae (age 45–60 days). The rectangular mouth had an area of one square meter and the overall length was approximately 5.5 meters. The 5.5 m net was fitted with Monodur 0.9 mm mesh size and in the rectangular mouth a net of 40 mm mesh size was mounted obliquely to minimize the number of hydromedusae per haul.

The Bongo nets were towed along a double-oblique path from surface to close to the bottom in shallow areas, or as deep as the towing distance or bottom topography allowed. The Bongo nets were released and retrieved at the same speed of 20 meters per minute. The BLSMT-net was towed along a similar path, but released at 50 meters per minute and retrieved at 15 meters per minute. Bias due to variations in amount of sampling with depth is inevitably included in the estimates of larvae density, but this kind of bias is not assumed to seriously affect the obtained estimates.

Horizontal hauls with 61 cm Bongo nets were made at 0, 5, 10, 15, 20, 25, 30 and 40 m depth to investigate vertical distribution of herring larvae in relation to time of the day.

Wire angle was monitored during each tow with an inclinometer, and sampling depth was determined from the relation between wire angle and lenght of wire paid out. Estimated sampling distances ranged from 50 to 800 meters. Volume of seawater strained per tow was determined in cubic meters from a calibrated TSK-flowmeter (Tsurumi Seiki Kosakusko Co. Ltd) inside the mouth of the Bongo net, while that of the BLSMT-net was determined by towing distance, depth and net mouth area. The speed of the towing vessel was maintained at 2.0–2.5 knots (1.0–1.25 m/s) using the Bongo nets and at approximately 3.0 knots with the BLSMT-net.

A 29-foot vessel, the R/V KNURR, with a hydraulic winch was used for Bongo net operations, while the BLSMT-net was operated from the 48-foot R/V AUGUST BRINKMANN.

All samples were fixed in 4% formaldehyde solution in seawater buffered

with 2% sodium borate. Temperature and salinity were monitored routinely during the sampling period with a T/S-recorder (Yellow Spring Instruments) and Nansen bottles. Data on surface illumination were collected 2 m above the sea surface with a digital photometer (Tektronic). The speed and direction of water currents were monitored by moored current meters (GYTRE 1979) and by surface drifting drogues (LANDLESS and EDWARDS 1976) positioned 1.0–1.5 m below surface.

SAMPLING DESIGN

The sampling area was divided into 11 smaller regions, based on the location of the spawning grounds and environmental conditions, such as bottom topography, hydrography and depth (Figs. 2.1 and 2.2). The regions ranged from 5×10^4 m^2 to 18×10^4 m^2. There were up to four stations in each region.

The annual cruise dates were selected to cover the main hatching period, but the sampling coverage in time and space had to be modified on several occasions due to vessel failure or weather conditions. In the case of the Fjellangervaag area (region 4 in Fig. 2.1), sampling was limited because the area had little importance for distribution of herring larvae during the first few week after hatching.

Oblique sampling was conducted preferentially at dusk and at night, although no corrections were made for samples collected during daylight hours.

SAMPLE PROCESSING

All fish eggs and larvae, as well as the most commonly occurring planktonic invertebrates, were sorted from each net-sample under a 10 x – magnifying lens for later identification and enumeration. Herring larvae could be easily distinguished from most other fish larvae with the exception of sprat (*Sprattus sprattus*), where identification was based on morphological characteristics such as myomere counts (RUSSEL 1976).

Herring larvae were enumerated, separated into developmental stages (DOYLE 1977), and measured with an ocular micrometer in a dissecting microscope using up to 50 x– magnification. About 6000 herring larvae were examined for developmental stages, gut contents and morphological characteristics. In 1977–1979 between 20 and 50 herring larvae were processed per station and in 1980 10 larvae per station. The following characteristics were measured: standard lenght or SL (measured from the snout to the end of the notochord), eye-diameter (measured as the greatest diameter of the eye), eye-height (measured along the vertical axis that passes through the center of the eye), headheight (from the upper jaw to the top of the head), body height (in yolk-sac larvae measured anteriorly and approximately midway along the

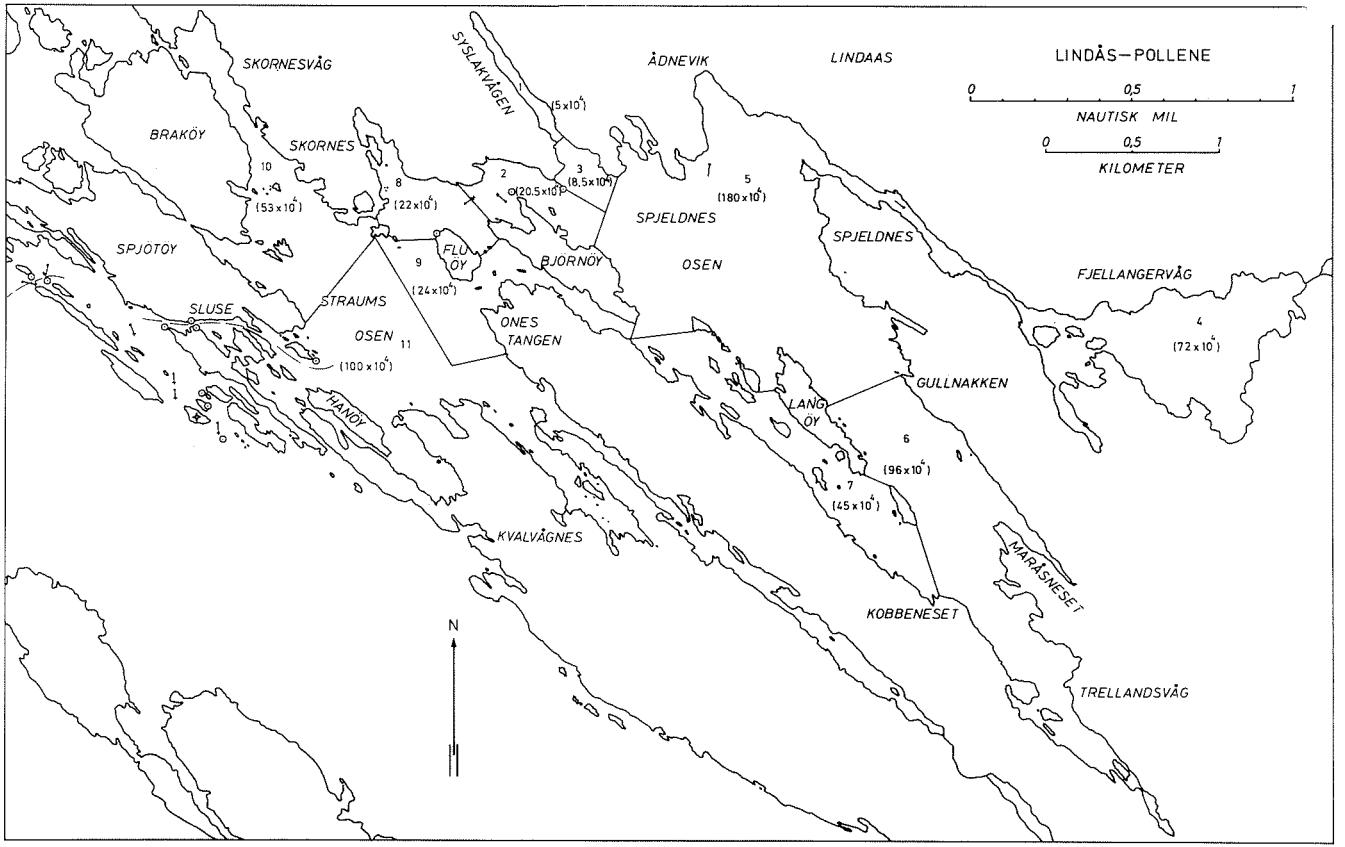

Fig. 2.1. Regions of Lindaaspollene, indicated by numbers, and areas in square meters indicated in parenthesis.

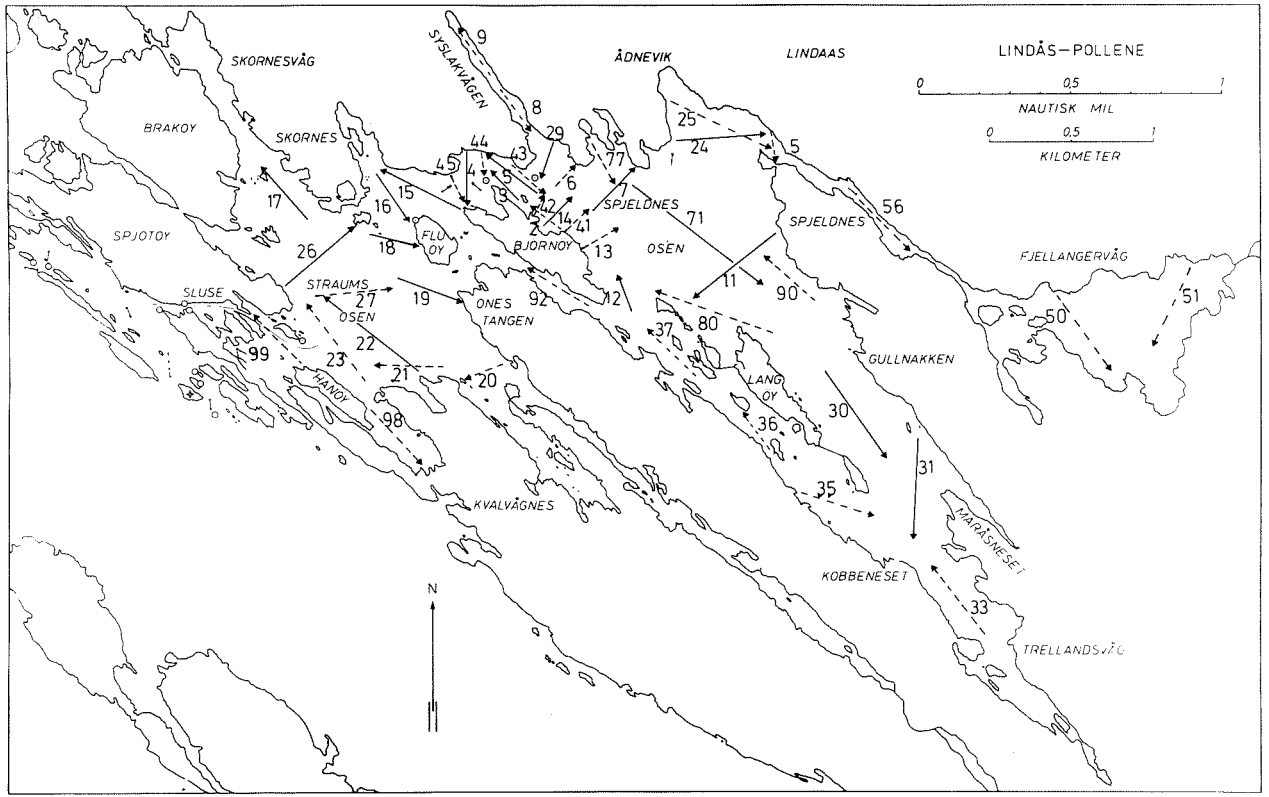

Fig. 2.2. Larval sampling stations in Lindaaspollene sampled regularly (unbroken lines) and irregularly (broken lines) with time. The direction of towing is indicated by arrows.

yolk sac length, in post yolk-sac larvae (≥ stage ld) measured at the transition point between the anterior and posterior parts of the gut).

DOYLE's (1977) morphological staging system is supplemented with stage ld for larvae where all remnants of the yolk sac have disappeared and no fin rays are as yet discernible.

All body measurements, with the exception of SL, were measured with 50 × magnification to the nearest 0.05 mm. Standard length, was measured under 10 × – magnification to the nearest 0.1 mm below. The dry weights of individual larvae were determined to the nearest 0.001 mg using a CAHN electrobalance after drying in open-ended aluminium envelopes at 60°C for at least 24 hours until constant weight was obtained.

DATA ANALYSIS

All data collected from cruise stations and laboratory processing were analysed on a UNIVAC 1100 digital computer. Standard statistical tests were carried out using SPSS programs (NIE *et al.* 1975) and procedures described by ZAR (1974).

Regression analysis was used to estimate the mortality from a catch curve. Since the variables of estimated age and larval abundance were subject to errors of measurement, a functional regression was used instead of a predictive one to describe the relationship between the two variables, as recommended by RICKER (1973), despite the mathematical implications (JOLICOEUR 1975, RICKER 1975).

The confidence limits of the regression coefficient Z were calculated as

$$Z\ (\sqrt{B+1} + \sqrt{B}) \text{ and } Z\ (\sqrt{B+1} - \sqrt{B})$$

where B is $F\ (1-r^2) / (N-2)$, r^2 is the coefficient of determination, N is the number of pairs of variables, and F is the variance ratio at the 95% confidence level with degrees of freedom $n_1 = 1$ and $n_2 = N - 2$ (RICKER 1975).

Catches of herring larvae were analysed at each station to give the number in each developmental stage under one square meter of sea surface:

$$n_j = \frac{c_j \cdot z_j}{v_j}$$

where n_j is the number of individuals at station j under one square meter of sea surface, c_j is the catch in numbers of herring larvae at station *j*. z_j is the depth of tow in meters at station *j*, and v_j is the volume filtered by the net at station *j*.

Stations with herring larvae in such a condition that identification of developmental stages was difficult, were assigned a relative mean proportion of each developmental stage based on the stage distribution in catches from

closely spaced stations or, alternatively in catches from the same station on the immediately preceding and following cruises.

Mean density of larvae per square meter (p_a) was then calculated for each region:

$$P_a = \frac{1}{s} \sum_{j=1}^{s} n_j$$

where s is number of stations per region, and multiplied by its surface area in order to estimate the total number of larvae within the region. The total number of larvae, as well as the number of larvae in the separate developmental stages, were estimated for the entire area of distribution by summing the values for individual regions:

$$P_i = \sum_{a=1}^{k} P_a$$

where P_i is the survey estimate, i.e., total number of larvae estimated in the area represented by survey *i*, and P_a is estimated total number of larvae in the region *a*.

Variance estimates of the abundance of larvae, within and between regions, were obtained for each survey. Regions with inadequate sampling coverage during a survey were assigned an estimated arithmetic mean larval abundance based on mean larval abundance in neighbouring regions. Estimates of variance for such regions were similarly derived from the ratio of the standard error of mean to the mean larvae density of neighbouring regions.

An estimate of the variance of number of larvae produced during the hatching season was obtained, with the assumption that sampling, as well as distribution of the larvae, was random.

$$S_P^2 = \sum_{i=1}^{r} S_{Pi}^2$$

where S_P^2 is the variance estimate of number of larvae hatched during the hatching season, *r* is number of surveys upon which the estimate of larval production is based, and S_{Pi}^2 is the variance estimate of the number of larvae produced during the period represented by the survey *i*.

The overall variance estimate of larval production and variance estimates of individual cruises are not entirely reliable, because the assumptions of random sampling and normally distributed catches were seldom fulfilled. Deviations from the normal curve may cause large estimating errors, especially for

variance and confidence limits (ENGLISH 1964). Therefore the variance estimates obtained here are not best estimates, although they are considered as reasonable approximations for the area of Lindaaspollene.

ESTIMATION PROCEDURE FOR LARVAL PRODUCTION

No standard procedure for estimating larval production is available. Several procedures, each with different assumptions, have been used (SETTE and AHLSTROM 1948, SAVILLE 1956, 1964, SIMPSON 1959), but none of these methods is considered well suited for estimating larval production during the brief hatching period (approximately 3 weeks) which characterizes this stock.

An estimate of the larval production during the main hatching season was obtained from cruise data on larval abundance of stage 1a-larvae under the following assumptions:

a. Each herring larva starts its life in developmental stage 1a.
b. Mortality during developmental stage 1a is presumed negligible due to the short duration of this stage. FOSSUM (1980) found that the time spent in stage 1a in general ranged from 1 to 4 days, with a mean of approximately one day, depending on temperature.

The proportion of larvae in stage 1a is supposed to decrease exponentially with time according to the formula:

$$\frac{N_{1a}(t)}{N_o} = e^{-kt} \qquad k > 0, \tag{1}$$

where N_o is the initial number of herring larvae produced at age 0 under experimental conditions, $N_{1a}(t)$ is the number of these larvae observed to stay in stage 1a at time t after hatching, k is the rate of decline in the proportion of 1a-larvae with time after hatching, which is proportional to the rate of daily larval production. The parameter k was estimated by the least squares method on the basis of data from 0–6 days old larvae of the Lindaas herring stock in 1978 and 1979 (FOSSUM 1980).

An arithmetic mean value of $k = 1.7$ was used in the calculations of larval production. In spite of the temperature dependence of the k-value, this effect was not considered relevant in this paper.

The population of 1a-larvae is described by the equation:

$$\frac{dN_{1a}(t)}{dt} = -kN_{1a}(t) + n(t) \tag{2}$$

where $-kN_{1a}(t)\,dt$ is the number of 1a-larvae leaving stage 1a (to stage 1b) in the time interval dt, $n(t)dt$ is the number of larvae hatched in the time interval dt.

Reordering of the equation gives:

$$n(t) = \frac{dN_{1a}(t)}{dt} + kN_{1a}(t) \tag{3}$$

The first expression on the right hand side can be redescribed according to definition:

$$\frac{dN_{1a}(t)}{dt} = \lim_{\Delta t \to 0} \frac{N_{1a}(t_i) - N_{1a}(t_i - \Delta t)}{\Delta t} \tag{4}$$

Here Δt is estimated to be one day, i.e., $\Delta t = (t_i - t_{(i-1)}) = 1$, which implies that

$$\frac{dN_{1a}(t)}{dt} = N_{1a}(t_i) - N_{1a}(t_{(i-1)}) \tag{5}$$

Equation (3) can then be written:

$$n_i = n(t_i)\ (t_i - t_{(i-1)}) = N_{1a}(t_i) - N_{1a}(t_{(i-1)}) + kN_{1a}(t_i)\ (t_i - t_{(i-1)}) \tag{6}$$

and the total number of larvae produced, P, can be written:

$$P = \sum_{i=1}^{m} n_i = \sum_{i=1}^{m} N_{1a}(i) - \sum_{i=1}^{m} N_{1a}\ (i-1) + \sum_{i=1}^{m} kN_{1a}(i) \tag{7}$$

where *m* is number of days between start and end of hatching. The two first expressions at the right will cancel each other if the start and end of hatching are equal to the zero level of larval production, which implies that

$$P = \sum_{i=1}^{m} kN_{1a}(i) \tag{8}$$

Estimates of total larval production can thus be obtained if the daily rate of larval production $P_i = kN_{1a}(i)$ is plotted against the midpoint of surveys dates. The area under the resulting curve will then equal total larval production, P.

LARVAL PRODUCTION AT LENGTH

For comparative purposes, the production of herring larvae was also estimated as the number of larvae of size less than a certain standard length l_c which were present in the area at each sampling time. The length limit l_c, was based on an assumed growth rate of 0.2 mm per day. Given the mean standard length at the preceding sampling time (l_1) and also the mean time interval to the succeeding sampling ($t_c - t_1$), the assumed mean length without recruitment at the last sampling would be

$$l_c = l_1 + 0.2\ (t_c - t_1)$$

The number of larvae less than this assumed size would thus be hatched after the preceding sampling. Adding the number of larvae smaller than l_c over successive time intervals during the hatching season would thus provide an index for total larval production.

RESULTS

HYDROGRAPHY AND LARVAL DISTRIBUTION

Circulation of surface waters and dispersion of herring larvae

The herring larvae were observed to stay in the surface waters for several days after hatching. An attempt was therefore made to map the circulation of surface water masses in the vicinity of the spawning grounds in 1979 and 1980. Free-floating current drogues (LANDLESS and EDWARDS 1976) were released on a calm surface at 1.5 meter depth from selected sites along the main drift of larvae. A schematic presentation of their drift is given in Fig. 2.3.

A major part of the tidal exchange of water between Straumsosen and Spjeldnesosen seems to occur through the area north of Fluøy and Bjørnøy,

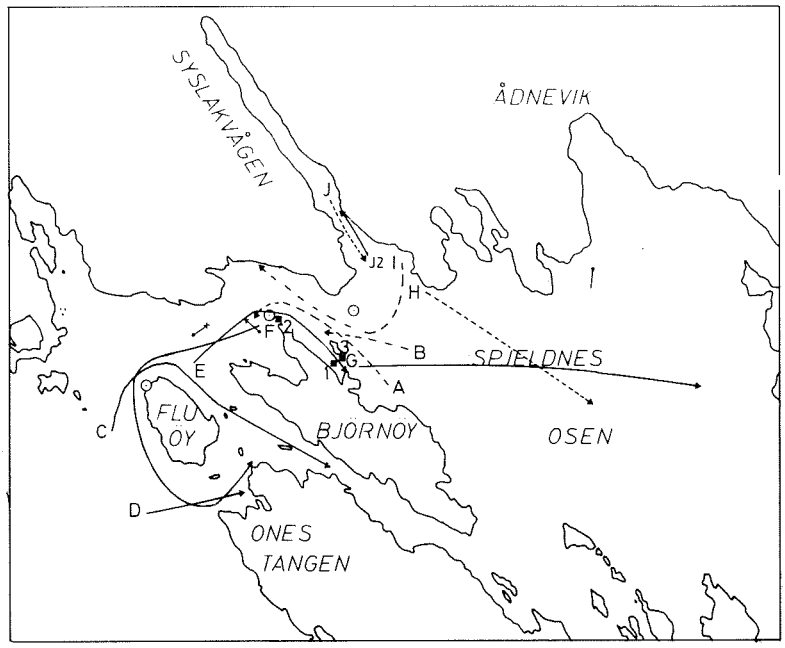

Fig. 2.3. Paths of current drogues and position of moored current meters in Lindaaspollene during 1979–80. Letters indicate points of release of current drogues and arrow heads indicate their piont of recovery. Full lines indicate that current drogues were released at flooding tide, while dashed lines indicate release at ebbing tide. This numbers 1, 2 and 3 indicate positions of current meters. See also Table 2.1. and 2.2.

though transport of superficial water masses also seem to occur between Fluøy and Bjørnøy (C and D in Fig. 2.3).

The current drogues were in general tracked along the main tidal flow direction at the time of release (Fig. 2.3). Observed exceptions from this general view might be explained by local hydrograpic conditions. Differences in time between setting of the drogues and release into the main flow were therefore taken into consideration when determining the prevalent flow direction at any actual time.

The combined effect of wind and tide on the distribution of larval density was apparent within the first few days of hatching.

Young herring larvae were in general first recorded along the main drift path from Spjeldnesosen to Straumsosen, and a few days later herring larvae were also found in the southern parts of Spjeldnesosen, depending on wind strength and direction. Observations of recently hatched larvae in the southern parts of Spjeldnesosen were frequently associated with strong northerly winds, while high larval densities in the northern parts were often correlated with southerly winds.

The current speed during a tidal period generally fluctuates between zero and 35 cm/s. A current meter moored about 1 m off the bottom northeast of Bjørnøy, as shown in Fig. 2.3 and Table 2.1, indicated current speeds of 19–27 cm/s (0.4–0.5 knots), with flow directions inconsistent with the main flow direction. This was probably caused by backwater gyres or turbulent mixing at the site of measurement (number 2 in Fig. 2.3). Another current meter moored at the Bjørnøy spawning ground (numbers 1 and 3 in Fig. 2.3 and Table 2.2) indicated current speeds of about 25–35 cm/s, with flow directions largely consistent with the main tide water flow, i.e., southwards on flood tide and northwards on ebb tide.

Table 2.1. Time of release and recovery of current drogues in Lindaaspollene 1979 and 1980. The point of release refers to Fig. 2.3.

		Release		Recovery		
Point	Year	Date	Hour	Date	Hour	Tide flow at release
A	1980	17 April	1930	18 April	1250	Ebbing
B	1980	17 April	1930	18 April	1250	Ebbing
C	1980	2 May	1345	3 May	1400	Flooding
D	1980	2 May	1345	2 May	2000	Flooding
E	1980	29 April	2100	30 April	0830	Flooding
F	1980	29 April	2100	2 May	1300	Flooding
G	1980	30 April	0900	30 April	1530	Flooding
H	1979	24 April	1930	24 April	2030	Ebbing
I	1979	23 April	1920	24 April	1900	Ebbing
J	1980	17 April	1950	18 April	1000	Ebbing
J2	1980	18 April	1000	18 April	1250	Flooding

Table 2.2. Current meter readings in periods of 50 seconds from fixed points in the spawning area of Bjørnøy 1980. (See Fig. 2.3).

Location	Date	Hour	Depth	Flow direction degrees	Current velocity cm/s	Remarks
1	8 April	1245	1 m	165	25	Reversal of tide flow
1	8 April	1310	Bottom	150,195,225	35	Start of flooding
1	8 April	2045	1 m	150,240,225	21	Middle between high and low tide
2	8 April	1435	Bottom	345	27	Close to high tide level
2	8 April	1445	1 m	30,45	19	Close to high tide level
2	8 April	2035	1 m	195,210	11	Towards ebb tide
3	9 April	1010	1 m	315	19	Towards ebb tide

Temperature and salinity

Temperature conditions at different depths in Spjeldnesosen during the period of study are indicated in Figs 2.4–2.8. Increasing stability of the water column in spring was indicated by the formation of a thermocline at 10–20 meters depth in April or May (Figs 2.5–2.8). Surface water masses were characterized by large variations in both temperature and salinity. Temperatures in the upper 10 m increased steadily from about 5°C in April up to about 15°C in June, and salinities in surface waters fluctuated between 27 and $31^{0}/_{00}$ (Figs 2.6–2.8). The hydrographic conditions below about 20 m depth seemed to be rather constant during the period of study, with a temperature of approximately 5°C and salinity of approximately $32^{0}/_{00}$ (Figs 2.6–2.8).

Temperature conditions on the spawning grounds (0–10 m depth) during the period of hatching in 1977 and 1979 was lower than in 1978 and 1980. By the time of 50% hatching, the temperatures at the spawning grounds were approximately 5, 8, 7 and 9°C for successive years.

Vertical distribution of herring larvae

To gain detailed information about the spatial distribution of herring larvae for the estimation of larval abundance, diurnal vertical distribution was studied in relation to developmental stage, standard body length (Fig. 2.8), and time of day for several 24–hour stations (Figs. 2.5–2.8).

It appears that 0–6 weeks old larvae are mainly distributed in the upper 30 m. Early yolk-sac larvae (stages 1a and 1b) were recorded both day and night without any marked depth preference. The highest number of larvae per cubic meter was recorded at night (2300–0100 hrs) in the upper 10 m with an

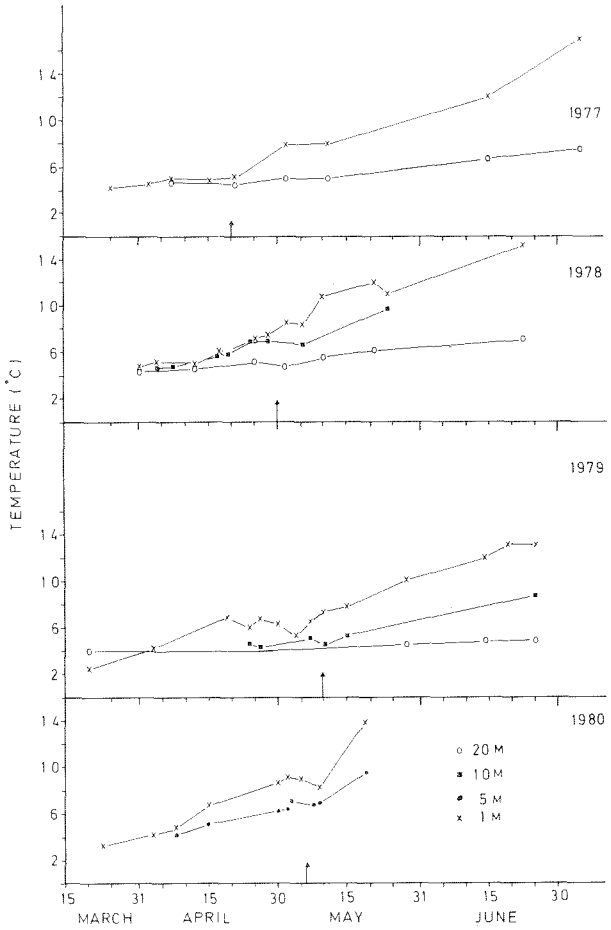

Fig. 2.4. Temperature conditions at different depths in Lindaaspollene during the annual survey periods. Date of 50% hatching is indicated by vertical arrows.

apparent maximum (3.1 larvae per m^3) made up mainly by late yolk-sac larvae (stage 1c) (Fig. 2.5). Inadequate sampling from near-bottom waters revealed little about larval distribution in this depth layer.

The amplitude of vertical migration seemed to increase with age and stage of development and varied in relation to light and time of day (Figs. 2.5–2.8). The most marked amplitude of migration in yolk-sac larvae was observed by 1c–larvae, while 1a- and 1b-larvae showed only slight variations with time of the day. The ascent seemed to start at 2200–2300 hrs (sunset) when surface illumination dropped below 1 lux (Fig. 2.5), while the descending migration from superficial water layers began at about 0300 hrs, coinciding with the start of feeding (p. 215). Intermediate depths of 10–30 m seemed to be increasingly preferred with improving light conditions (Figs. 2.5 and 2.6).

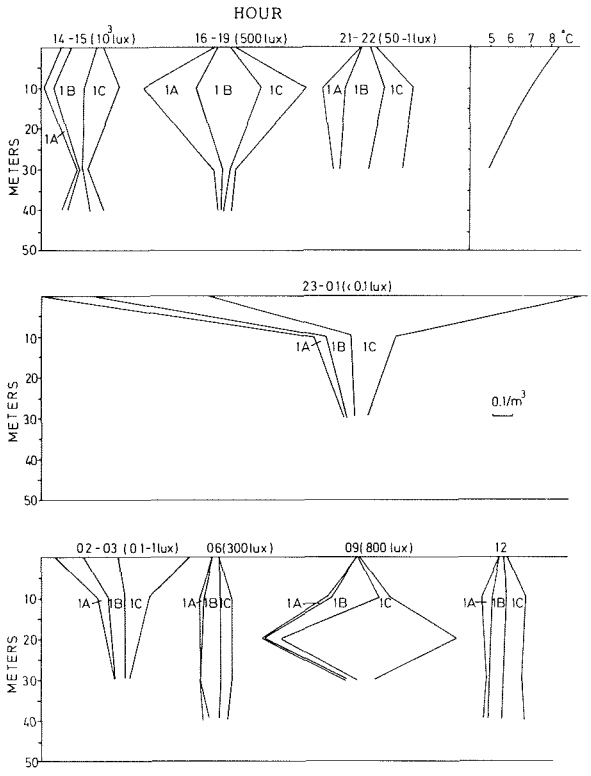

Fig. 2.5. Vertical distribution of yolk-sac herring larvae by different developmental stages (DOYLE 1977) (age: 0–14 days) in relation to time of the day (local time) at station 26 on 5–6 May 1978. Surface illumination (lux) is given in parantheses. Unit of larval density (m^{-3}) is indicated at the middle right. The temperature with depth is indicated at the upper right.

In four-to-seven weeks old larvae, however, no clear relationship between vertical distribution and time of day was observed (Fig. 2.8). The highest number of larvae was recorded in subsurface waters (5–25 m depth) at night, although a more narrow depth interval closer to the surface (5–15 m depth) seemed to be preferred before dawn. No strong relationship between body length and vertical distribution was found for these larvae.

The temperature conditions during the sampling periods, 5–12°C, did not seem to influence vertical migration of herring larvae, although high densities of larvae were frequently associated with the thermocline.

Net avoidance in older larvae (at least stage 3a) is assumed to be significant, as is indicated by the relatively small number of larvae caught per unit volume by day compared with the number caught in darkness (Fig. 2.8).

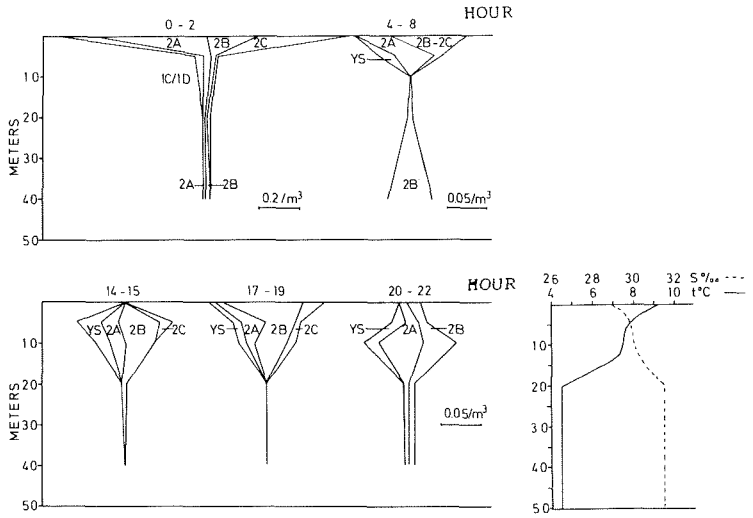

Fig. 2.6. Vertical distribution of herring larvae by different developmental stages (DOYLE 1977) (age:1–4 weeks) in relation to time of day (local time) at station 26 on 28–29 May 1979. Yolk sac larvae are pooled under the designation YS. Unit of larval density (m^{-3}) is indicated at each time interval. Temperature and salinity variations with depth are indicated at the right.

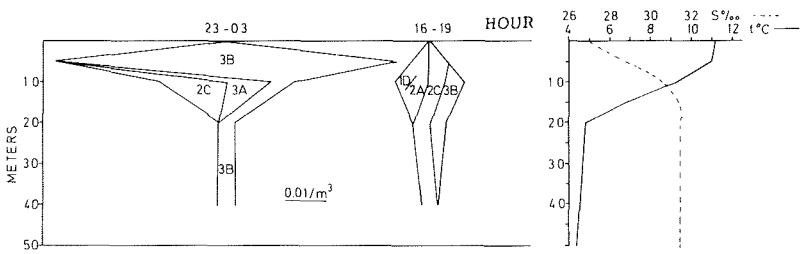

Fig. 2.7. Vertical distribution of post-yolk-sac herring larvae by different developmental stages (age: 3–6 weeks) at station 26 on 14–16 June 1979. Unit of larval density (m^{-3}) is indicated at the middle of the figures. Temperature and salinity variations with depth are indicated at the right.

ABUNDANCE AND MORTALITY OF HERRING LARVAE

Larval production

Knowledge of the spawning grounds and time of hatching coupled with frequent sampling during the hatching period formed the basis of larval production estimates in Lindaaspollene during 1977–1980. It was believed that multiple cruises within the period of peak hatching would be the best approach

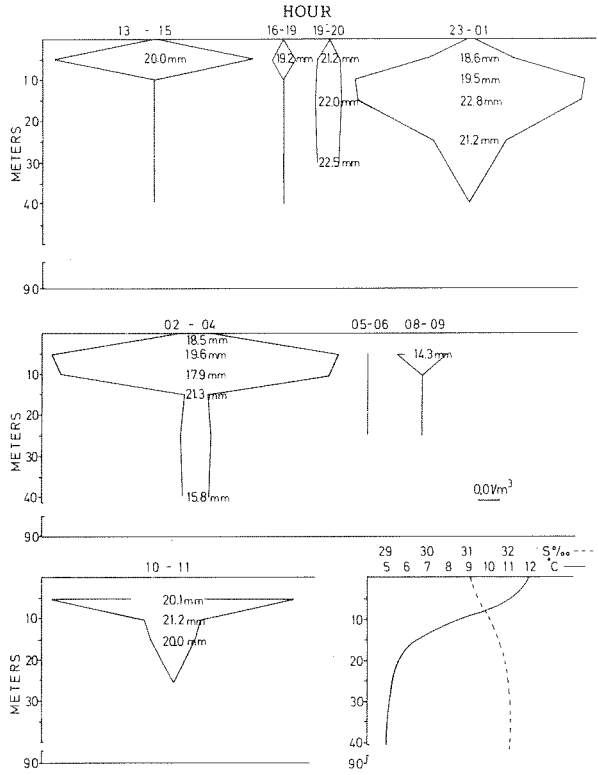

Fig. 2.8. Vertical distribution of herring larvae (age 4–7 weeks) in relation to time of the day (local time) at station 71 on 2–3 June 1977. Mean body lenght of larvae in millimeters are given at the different depths of the figures. Unit of larval density (m^{-3}) is indicated at the middle right. The hydrographic conditions are indicated at the lower right.

to increase precision in estimating larval production fram hatching surveys. Therefore, up to eight cruises were conducted during this period, at intervals of 1–8 days depending mainly on vessel availability.

Secondary larval cohorts originating from delayed spawning groups were not included in the estimates, though direct evidence for delayed secondary hatching was available in June 1979.

Daily rates of larval production, which form the basis for the estimates of larval production, are plotted in Figs 2.9–2.12. Seasonal estimates of larval production were obtained during 1977–1980 by integrating the area under the curves, and are given in Table 2.3–2.6.

After an egg incubation period of some 20–30 days, depending primarily on temperature (Blaxter 1956), hatching commenced and lasted for approxi-

mately three weeks. In general it seems as if hatching intensity increases rapidly to near peak level and then gradually decreases towards the end of the hatching period. The relatively brief hatching period and the shape of the hatching curve indicate that the newly hatched larvae make up a relatively homogeneous population with insignificant contribution from other spawning groups. The bimodal shape of the curves in 1978 and 1979 indicate that hatching occurs at more than one spawning ground, though variations in intensity of hatching may be due to both genetic and environmental conditions or sampling artifacts. The bimodal shape of the 1977-curve is probably caused by such secondary factors.

Abundance estimates of herring larvae at successive time intervals during the hatching season, and data on body length and on daily growth rates (0.2 mm/day), formed the basis for an alternative estimate of seasonal larval production (Table 2.3–2.6) (VAN DEN KAMP 1976 and CORTEN 1978).

The 95% confidence limits, ranging from 8 to 33% of the estimate of larval production, include only some portion of the variance stemming from between-station variability. Other sources of variance are discussed later, although SAVILLE (1964) suggested 95% confidence limits as half or double the estimate to be common in stock assessment studies.

1977

Larval sampling in 1977 was initiated on 14 April. The occurrence of some larvae in developmental stage 1c (age 3–5 days) on 15 April indicated that hatching had begun three days previously. Date of 50% hatching was estimated to be 20 April. The hatching period lasted for three weeks with a main peak in larval production recorded on 17 April. The reason for the apparent bimodal shape of the hatching curve (Fig. 2.9) is not clear. According to observations of one spawning ground in 1977, a unimodal distribution would be expected. Integration of the area under the observed distribution curve gives an estimated total production of 56×10^6 larvae (Fig. 2.9 and Table 2.3). Lack of available vessels during the period of presumed maximum larval production (17–25 April) may have underestimated total larval production.

On the basis of length-data, total larval production was estimated as 42×10^6 larvae, which is 75% of the estimate based on stage 1a-larvae.

It was assumed that the egg number recorded on the spawning ground in 1977 contained the majority of herring eggs spawned during this season. Given that the estimated larval production in 1977 originated from the recorded spawn, mean hatching success was estimated to be of the order of 1%.

Table 2.3. Estimation of larval production in 1977 based on 1a-larvae and abundance-at-length of herring larvae.

Survey time	Days between surveys	Abundance of 1a-larvae ($x10^4$) N_{1a} mean±95% conf.lim.	Rate of larval production ($x10^6$) kN_{1a} mean±95% conf.lim.	Limit of larval length l_c(mm)	Larval production at length ($x10^6$) N_{lc} mean±95% conf.lim.
Year 1977					
11 April		0	0		
14 April	3	131.9± 42.8	2.2±0.7		
15 April	1	315.8± 81.5	5.4±1.4		
16 April	1	225.5± 97.6	3.8±1.7		
17 April	1	392.2±232.7	6.7±4.0		18.7±11.8
25/26 April	8.5	85.9± 31.9	1.5±0.5	9.2	20.0± 5.2
2 May	6.5	0	0	8.9	3.3± 1.7
11/12 May		0		9.3	0.3±0.08
2/3 June		0			
14/16 June		0			
28/29 June		0			
Total larval production ± 95% confidence limits. ($x10^6$)			56.3±16.4		42.3±12.5
Time of 50% hatching: 20 April					

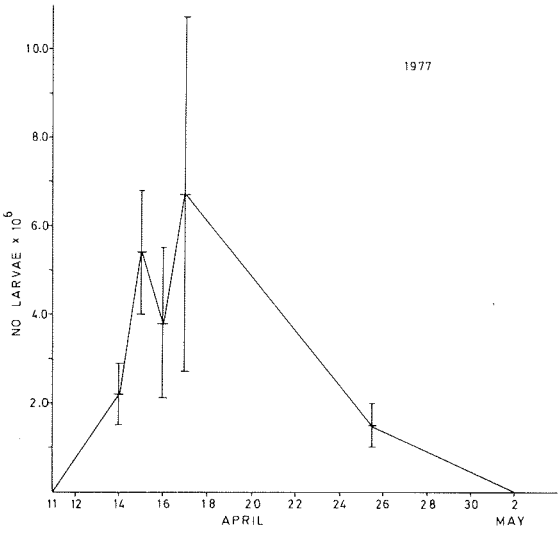

Fig. 2.9. Larval production curve for 1977 based on daily rate of release of 1a-larvae (kN_{1a}) ± 95% confidence limits during the hatching season. See text for further explanation.

1978

Larval sampling in 1978 began on April 25. The appearance of two peaks of hatching in 1978 (Fig. 2.10) is consistent with the recordings of two spawning grounds (p. 146, Fig. 1.3). The relatively short distance between the two grounds (1 km) and the overlap between the two distributions demonstrate that herring larvae from separate spawning grounds are rapidly mixed after hatching. This makes it difficult to distinguish between the two larval cohorts for any considerable length of time. Larval production from the two spawning grounds was therefore pooled, giving an integrated estimate of 118×10^6 larvae (Fig. 2.10 and Table 2.4). The hatching period lasted for approximately four weeks and the date of 50% hatching was estimated to be 30 April.

Total larval production based on length data was estimated to be 32×10^6 larvae, which is roughly one-fourth of the estimate based on 1a-larvae.

Assuming that only a fraction of the parent stock spawned at the observed spawning grounds, and that the remainder spawned in unrecognized localities outside Lindaaspollene, larval production in Lindaaspollene from the observed spawning grounds had a mean hatching success of the order of 23–86%.

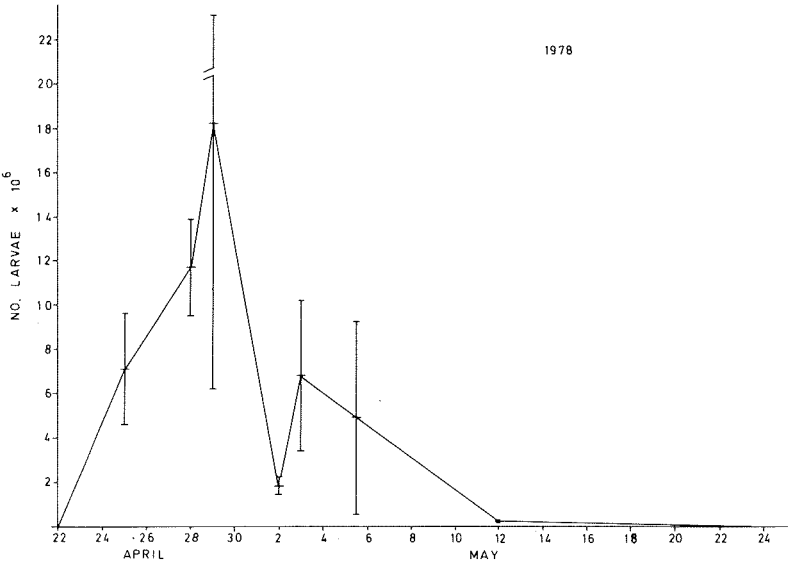

Fig. 2.10. Larval production curve for 1978 based on daily rate of release if 1a-larvae (kN_{1a}) ± 95% confidence limits during the hatching season. See text for further explanation.

Table 2.4. Estimation of larval production in 1978 based on 1a-larvae and abundance-at-length of herring larvae.

Survey time	Days between surveys	Abundance of 1a-larval ($x10^4$) N_{1a} mean±95% conf.lim.	Rate of larval production ($x10^6$) kN_{1a} mean±95% conf.lim.	Limit of larval length l_c(mm)	Larval production at length ($x10^6$) N_{lc} mean±95% conf.lim.
Year: 1978					
22 April		0			
25 April	3	418.2±146.4	7.1± 2.5		10.8±3.7
28 April	3	690.3±129.1	11.7± 2.2		
29 April	1	1068.7±708.2	18.2±12.0		
2 May	3	107.5± 26.0	1.8± 0.4	9.4	15.2± 5.8
3 May	1	400.5±199.2	6.8± 3.4		
5/6 May	2.5	285.3±257.9	4.9± 4.4		
11 May	5.5	14.4± 0.5	0.2± 0.01	9.8	5.8 ±2.6
24/25 May	13.5	0	0	10.7	0.14±0.08
27 June		0	0	14.0	
Larval production ($x10^6$) ± 95% confidence limits:			118.4±22.2		31.9±10.5
Time of 50% hatching: 30 April					

1979

Larval sampling in 1979 started on 30 April. The fluctuations in intensity of hatching make the interpretation of the shape of the hatching curve difficult. The appearance of two clearly distinguishable peaks in 1979, with maximum

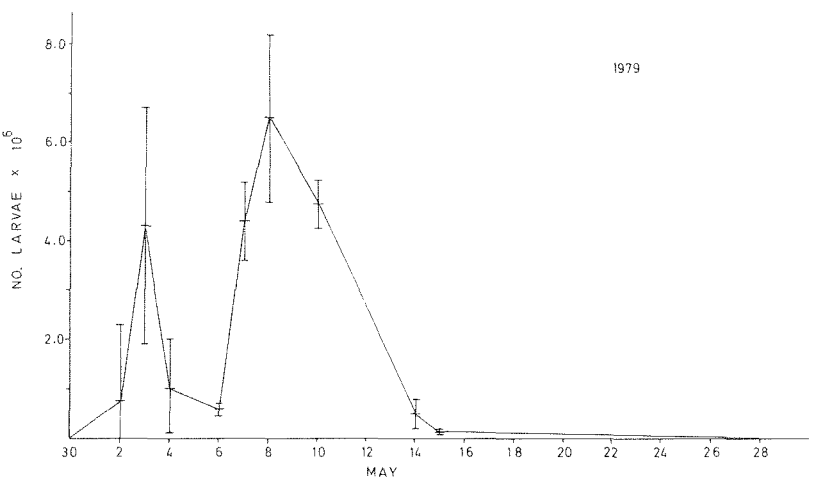

Fig. 2.11. Larval production curve for 1979 based on daily rate of release of 1a-larvae (kN_{1a}) ± 95% confidence limits during the hatching season. See text for further explanation.

rates of daily larval production five days apart, is apparantly not the result of there being multiple spawning grounds, as only one spawning ground was found (p. 146, Fig. 1.3).

Larvae were produced for a rather long period, approximately four weeks, as indicated by recordings of recently hatched larvae as late as 28 May. Newly hatched herring larvae were also observed on 14 June, but these most likely belonged to a delayed spawning cohort. The date of 50% hatching was estimated to be 9 May. Sampling coverage in time and space was not adequate to assess newly hatched larvae after the main hatching period, so that no reliable estimates of larval production from delayed hatching cohorts could be obtained. Integration of the area under the curve describing the rate of daily larval production over time (Fig. 2.11) gives an estimate of larval production equal to 38×10^6 larvae. Larval production based on length-data was 48×10^6 larvae (Table 2.5), which is 25% greater than the estimate based on stage 1a-larvae.

Assuming that larval production comes from the observed spawning grounds, mean hatching success would be in the order of 5–7% of the spawned egg number.

Table 2.5. Estimation of larval production in 1979 based on 1a-larvae and abundance-at-length of herring larvae.

Survey time	Days between surveys	Abundant of 1a-larvae ($x10^4$) N_{1a} mean±95% conf.lim.	Rate of larval production ($x10^6$) kN_{1a} mean±95% conf.lim.	Limit of larval length l_c (mm)	Larval production at length ($x10^6$) N_{lc} mean±95% conf.lim.
Year: 1979					
30 April		0	0		
2 May	2	44.3± 95.0	0.8±1.6		
3 May	1	252.1±142.6	4.3±2.4		7.5± 4.1
4 May	1	61.5± 57.6	1.0±1.0		
6 May	2	34.0± 7.8	0.6±0.1		
7 May	1	258.7± 47.9	4.4±0.8		
8 May	1	382.8±100.2	6.5±1.7		
10 May	2	279.8± 29.5	4.8±0.5	8.9	31.2± 5.7
14 May	4	27.5± 18.4	0.5±0.3		
15 May	1	7.7± 1.9	0.1±0.03	8.5	8.3±12.3
28/29 May	13.5	0	0	10.2	0.5±0.5
14/15 June		41.3± 48.3		10.5	0.3± 0.2
25/26 June		0			0
Larval production ($x\ 10^6$) ± 95% confidence limits: (June not included)			38.4±3.1		47.8±11.6
Time of 50% hatching: 9 May					

1980

The unimodal shape of the hatching curve in 1980 is consistent with the observation of one spawning ground (p. 146, Fig. 1.3). The hatching period lasted for about three weeks, and the date of 50% hatching was estimated to be 7 May. Sampling of recently hatched larvae started on 2 May, and the appearance of stage 1d-larvae in the samples confirmed that hatching had commenced a few days previously. Diver observations from different sites in the spawning ground and catches of recently hatched larvae implied that hatching in the more exposed parts of the spawning ground (Grunnavik) had started several days before that in the more protected areas. Insolation as well as wave action and tide water exchange were very different in the two areas, and the

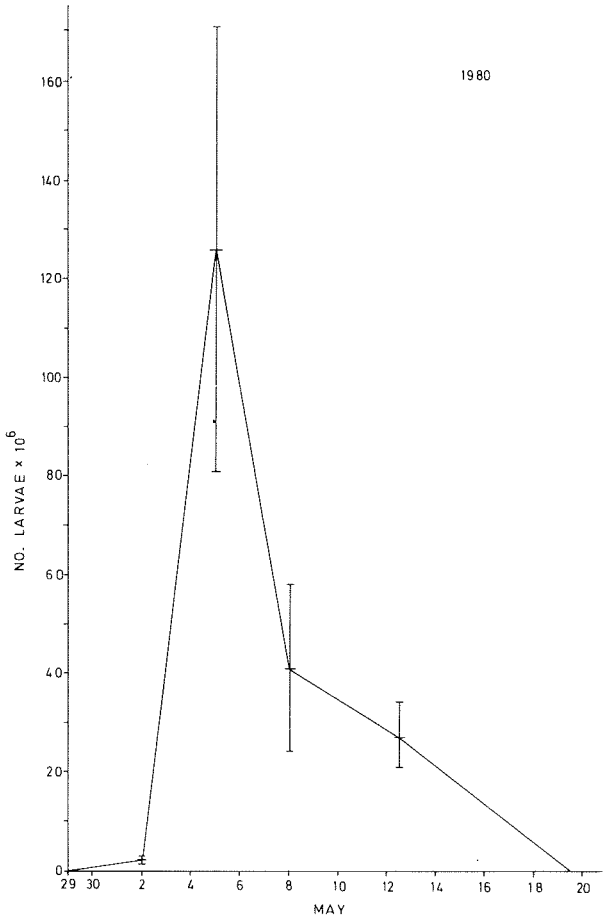

Fig. 2.12. Larval production curve for 1980 based on daily rate of release of 1a-larvae (kN_{1a}) ± 95% confidence limits during the hatching season. See text for further explanation.

Table 2.6. Estimation of larval production in 1980 based on 1a-larvae and abundance-at-length data of herring larvae.

Survey time	Days between surveys	Abundance of 1a-larvae ($x10^4$) N_{1a} Mean±95%conf.lim.	Rate of larval production ($x10^4$) kN_{1a} Mean±95%conf.lim.	Limit of larval length l_c(mm)	Larval production at length ($x10^6$) N_{lc} Mean±95%conf.lim.
Year: 1980					
29 April	0	0	0		
2 May	3	131.3± 48.7	223.2± 82.8		25.4± 7.1
5 May	3	7407.0±2679.3	12591.9±4554.8		
8 May	3	2409.9±1020.3	4096.8±1734.5	9.2	150.4±64.1
12/13 May	4.5	1606.6± 386.5	2731.2± 657.0	8.8	79.1±18.8
19/20 May	7	0 ± 0	0	9.1	10.2± 5.2
27 May	7.5	0 ± 0	0	9.1	5.4± 1.5
Total larval production ± 95% confidence limits ($x10^6$)			695.1±101.7		270.5±65.0
Time of 50% hatching: 7 May					

increasing daytime temperatures on the spawning ground were assumed to accelerate the embryonal development.

Total production of herring larvae under the hatching curve was estimated to be 695 × 10^6 larvae (Fig. 2.12 and Table 2.6). Total larval production in 1980, on the basis of abundance-at-length data is 270 × 10^6 larvae (Table 2.6). This is approximately 40% of the estimate based on stage 1a-larvae.

The larval production in 1980 most likely comes from the observed spawning grounds with estimated mean hatching success in the order of 7–17%.

Abundance

Table 2.7 gives cruise time, age of larvae determined in relation to date of 50% hatching, and estimated larval abundance on separate cruises. Total larvae abundances ranged between 6 × 10^4 and 206 × 10^6 on the basis of separate cruise estimates. Larvae in developmental stages 1a to 4c were collected and ranged in lenght (SL) between 6.1 mm and 28.2 mm. In the following calculations, estimates of larval production are based on developmental stage 1a herring larvae unless otherwise stated.

Fig 2.13 shows the relationship between abundance of separate year classes and age in days after hatching during the observation periods in 1977–1980. The curves indicate great variations in the amount of larvae production followed by a period of density-dependent mortality. The abundance of larvae seems to stabilize after approximately 2½ months after hatching, and the relative size of the year classes is probably established by this age, with the 1977 and 1979 year classes relatively stronger than those of 1978 and 1980.

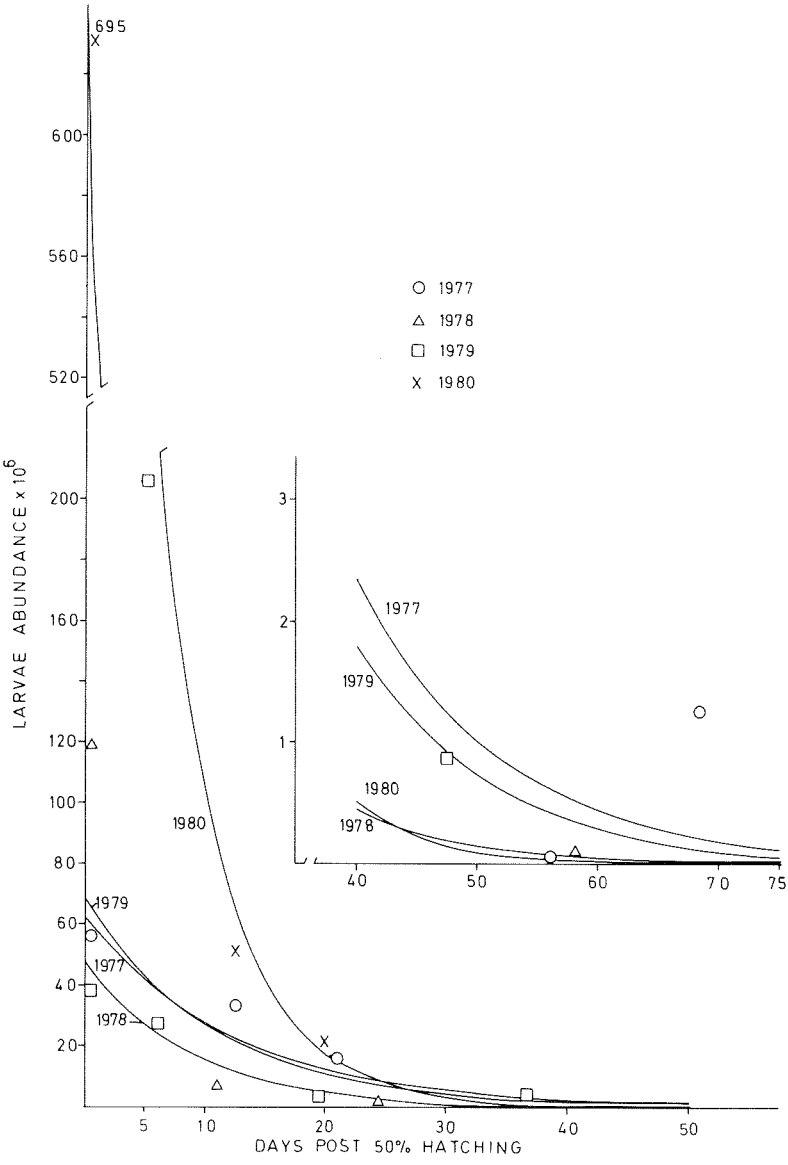

Fig. 2.13. Abundance of herring larvae by age in days after 50% hatching during 1977–1980. Expanded ordinate scale inserted.

Table 2.7. Estimates of larval abundance by date and age post-50%-hatching. Larval abundance at age 0 equals larval production based on stage 1a-larvae.

Year	Survey date	Mean age (days)	Larval abundance × 10^4 N	95% conf.lim.
1977	20 April	0	5630.9	1636.7
	2–3 May	12.5	3285.2	1678.2
	11 May	21	1556.7	397.4
	14–16 June	56	6.3	5.7
	28–29 June	68.5	125.2	166.6
1978	30 April	0	11842.9	2220.7
	11 May	11	720.2	336.5
	24–25 May	24.5	144.0	85.5
	27 June	58	8.1	8.4
1979	9 May	0	3840.2	310.7
	14 May	5	20597.7	10637.0
	15 May	6	2781.1	4348.2
	28–29 May	19.5	415.5	354.3
	14–15 June	36.5	383.0	340.2
	25–26 June	47.5	87.6	44.2
1980	7 May	0	69512.7	10174.0
	19–20 May	12.5	5113.2	2941.1
	27 May	20	2149.7	589.8

Due to gear avoidance after age 50 days post-hatching, corresponding to standard lengths exceeding 20 mm (pp. 203, App. Figs III.1 and III.2), the observed values of larvae abundance beyond this age most likely were underestimated in both 1977 and 1978.

The very rapid decrease in number of larvae during the first two weeks after hatching in 1978 most likely reduced this year class to a level below the average of 1977–1980.

During 1979 a five-fold increase in number of larvae was recorded five days after 50%-hatching (Table 2.7), which differs considerably from the expected curve (Fig. 2.13). A high proportion of young larvae (stage 1b) and hardly any newly hatched ones (stage 1a) may indicate that the majority of these larvae stemmed from unrecognized spawning grounds some distance away. Only a fraction of these larvae were recorded on the next day (15 May in Table 2.5), indicating that several sources of bias are included during data collection thus reducing the precision of abundance estimates. Fossum (1985) found that a majority of herring larvae in 1979 hatched in the 1b-stage, probably due to the low temperature, which may explain the large proportion of larvae in this stage.

Interpretation of the 1980-curve (Fig. 2.13) must be considered with care beyond the first twenty days after hatching due to lack of observations. However, there seemed to be a dramatic decline in larvae numbers during this period despite the few observation points.

Mortality

Mortality estimates were obtained from a model that was fitted to abundance at age data, using age 0 as age at 50%-hatching. The decrease in numbers with age appears to be exponential. Therefore the model

$$N_t = N_o e^{-Zt}$$

was proposed, where N_t is the number of larvae alive at age t after hatching, N_o is the larval production and Z is the instantaneous mortality rate.

In the abundance estimates used for estimating early larval mortality, delayed hatching groups and differences in day and night catches are disregarded. Larval emigration from the study area and sampling inadequacy cannot be excluded as sources of error in the present estimates of mortality, though the value of these errors is assumed to be small.

Annual abundance estimates as well as estimates of the instantaneous mortality rate (Z) and percentage of daily mortality rate ($(1-e^{-Z})$ 100%), are given in Table 2.8. Mean rates of decline in abundance, derived from catch curves, ranged between 7.9 and 16.3% per day for the different years (Table 2.8). During the first 50 days after hatching, mortality of the order of 98.3–99.9% occurred.

Table 2.8. Mortality of herring larvae. Parameters of the predictive regression line $\ln N_t = \ln N_o - Z\ t$, coefficients of determination, r^2, and percentage of daily mortality rate, $(1-e^{-Z})$ 100%.

Year	No. samples N	ln N_o	Z	r^2	$(1-e^{-Z})$ 100%
1977	5	17.960	0.082	0.73	7.9
1978	4	17.705	0.117	0.94	11.1
1979	6	18.040	0.091	0.79	8.7
1980	3	20.252	0.177	0.98	16.3

The slopes and elevations of the semi-logarithmic relationship between abundance and age in different years (Table 2.8 and Fig. 2.14) were not significantly different (covariance analysis, $F_{slope} = 0.7$ $p>0.05$; $F_{elevation} = 1.6$ $p>0.05$). All the material was therefore pooled and a functional regression line

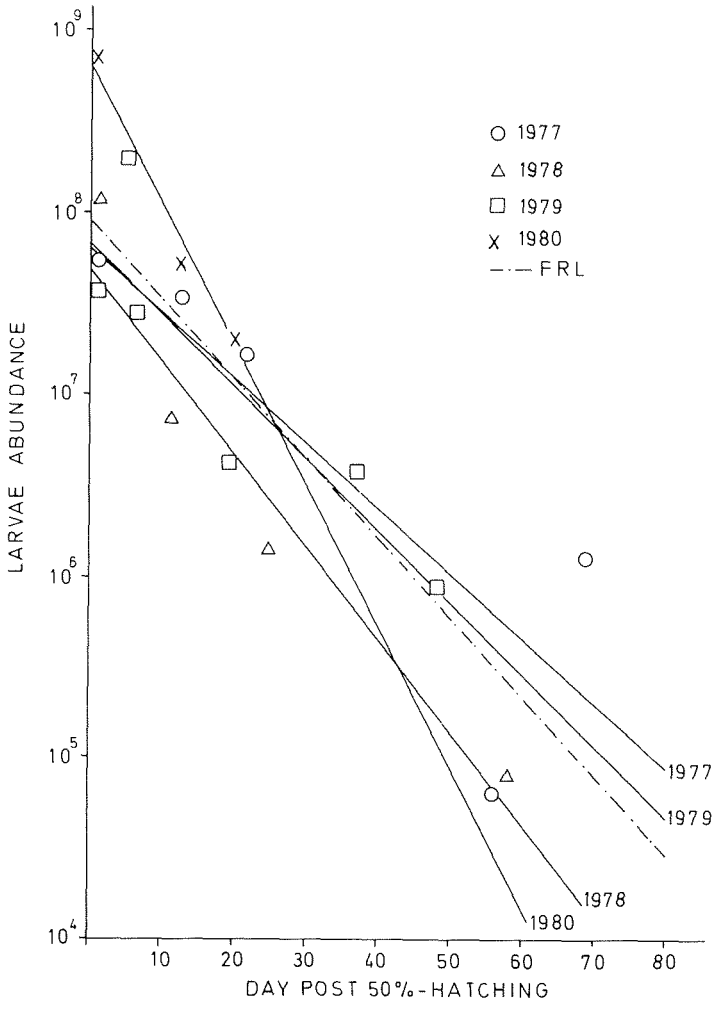

Fig. 2.14. Mortality of herring larvae in separate years. A pooled functional regression line (FRL), ln N = 18.6 − 0.1146 t, is also inserted.

was fitted to the data, as recommended by RICKER (1973) in cases where both variables are subjected to error of measurement:

$$\ln N_t = 18.62 - 0.1146\ t \qquad \text{or}$$
$$N_t = 1.2 \cdot 10^8 e^{-0.1146\ t}$$

where t is age in days after 50%-hatching and N_t is number of larvae alive t days after hatching. The coefficient of determination was $r^2 = 0.77$, and the 95% confidence limits of the regression coefficient were 0.09 and 0.15.

Predation

Scuba divers on the spawning grounds before and during the hatching period in 1980 observed that several species of pelagic invertebrates, including the ctenophores *Bolinopsis infundibulum* and *Pleurobrachia pileus* and the hydromedusae *Sarsia tubulosa* and *Rathkea octopunctata,* occurred with increasing abundance at the time of hatching of herring larvae. On several occasions *Bolinopsis sp.* was observed *in situ* with up to three newly hatched herring larvae (stage 1a) in the stomach. *Sarsia sp.* and *Rathkea sp.* were also occasionally observed with single 1a-larvae under digestion.

Occasional observations on the feeding behaviour of *Bolinopsis sp.* and *Sarsia sp.* in the laboratory also confirmed that newly hatched herring larvae were consumed by both species. *Sarsia sp.* was observed paralyzing single larvae first, and then ingesting afterwards, with the posterior end entering the mouth tube first. The process of consumption of a single herring larva was completed in one hour of daylight. *Bolinopsis sp.* was observed to catch herring larvae with their «lobes» extended only in darkness during the experiment, while *in situ* observations indicate that *Bolinopsis sp.* also preys on newly hatched herring larvae in daylight. *Bolinopsis sp.* was observed to be capable of completely digesting at least 3 newly hatched herring larvae in 8 hours of darkness, hence at a rate of about 0.4 herring larvae per hour.

DISCUSSION

In the preceding paper, the principal spawning grounds of the local Lindaas herring stock were documented, and data on spawning time, abundance, density distribution and mortality of eggs were presented for the years 1977–1980 (pp. 141–164).

The present paper has dealt with the population dynamics of larvae during the same period, with special emphasis on hatching, distribution, abundance and mortality.

Newly hatched herring larvae were in general recorded during April and May with the hatching season lasting for some 3–4 weeks. At the presumed date of hatching, a sampling plan for herring larvae was put into effect with the objective of estimating larval production and mortality rates for the first two months after hatching. Newly hatched larvae from predetermined spawning grounds were closely followed in space and time during the main hatching period.

DISTRIBUTION

In order to provide some measure of the larval production of fish stocks it is necessary to know the spatial distribution of larvae of different ages. Larvae were found in most of the study area a few days after hatching. Tide excerted a

relatively strong influence on the hydrographic conditions of the spawning grounds and in the surface waters of Lindaaspollene, and the larvae were thus rapidly carried away from their spawning beds. However, some of them remained in the area for a considerable length of time, perhaps due to the reversal of tidal flow direction and wind stress. Tide as a means of transport of herring larvae was demonstrated earlier by GRAHAM and DAVIS (1971) and GRAHAM (1972).

The behaviour of recently hatched 1a-larvae was especially important, since this stage formed the basis of estimates of larval production. SCUBA-diving observations on the spawning beds at the time of hatching revealed that recently hatched larvae started migrating towards the surface shortly after hatching. Generally no herring larvae in Lindaaspollene were observed to stay close to the bottom for 1–3 days, as suggested by SAVILLE (1971), CADDY and ILES (1973) and SELIVERSTOV (1974), but this kind of behaviour may be linked to the depth of the spawning grounds. However, DRAGESUND and NAKKEN (1971) found newly hatched herring larvae in the upper 50 m of the sea over the spawning grounds of Atlanto-Scandian herring. Newly hatched larvae of the Pacific herring, which spawns in shallow waters, also behave in a way similar to those of Lindaaspollene, the larvae being highly consentrated in the upper 2 m–zone (STEVENSON 1962).

The amplitude of vertical migration increased with larval age. In general, the distribution of yolk-sac larvae was less variable with time of the day and depth than that of larger larvae. These observations agree with those of other authors, e.g., LISIVNENKO 1961, SCHNACK 1972, SELIVERSTOV 1974, GRAINGER 1978, SJØBLOM and PARMANNE 1978. Temperature and salinity conditions did not seem to be significant factors in the distribution of herring larvae as shown by the rather extensive vertical migration of post-yolk-sac larvae through temperature gradients of approximately 6–7°C per 30 m. The high tolerance to temperature changes in herring larvae has also been documented by others (e.g., BLAXTER 1960, SELIVERSTOV 1974, SJØBLOM and PARAMANNE 1978).

LARVAL PRODUCTION

Several methods have been used to estimate the seasonal production of eggs or larvae of fish stocks (SETTE and AHLSTRÖM 1948, SAVILLE 1956, 1964,SIMPSON 1959, GJØSÆTER and SÆTRE 1974b, VAN DEN KAMP 1976 and CORTEN 1978), all based on reliable determination of age. Length is most commonly used, though GJØSÆTER and SÆTRE (1974b) found yolk-sac size to be a better measure of age for recently hatched capelin larvae. When hatching occurs in a brief time period, quantitative estimates of larval production should be based on parameters which are rather sensitive to short-term variations in the rate of production.

In the present study, a morphometrical staging system developed by DOYLE (1977) for herring larvae was selected for age determination. Stage 1a-larvae were selected to estimate daily variations in rate of larval release, as mortality between hatching and sampling here was regarded to be negligible. This method of estimation of larval production is particularly suited to stocks with demersal eggs which have a brief hatching period, where the spawning loci are precisely known and where the larvae are accessible for sampling immediately after hatching. If these requirements are fulfilled, the area of distribution of larvae should be limited and primarily determined by hydrographic conditions. The parameter «k» describing the instantaneous rate of decline in the proportion of 1a-larvae is a sensitive parameter affecting the estimates of larval production. Variations in egg size and therefore yolk-sac size (BLAXTER and HEMPEL 1963) due to racial or environmental reasons will certainly affect the precision of estimates of larval production. Therefore the k-value should be routinely adjusted, particularly if the age composition of the parent stock or environmental conditions, especially temperature, vary considerably.

Compared with estimates of larval production based on abundance of larvae by length composition and growth data, the present estimation procedure gives higher values. The only exception was recorded in 1979 when the estimate of larval production based on 1a-larvae was 20% less than that based on the other method, probably caused by sampling artifacts or unreliable values of the k-parameter. FOSSUM (1986) observed that only about 75% of the Lindaas herring hatched as 1a-larvae in laboratory experiments performed in the field in 1979, when the sea temperature was lower than average. Consequently, the criterion used by DOYLE (1977) for identifying newly hatched 1a-larvae should be modified according to racial and environmental conditions such as yolk-sac size and temperature at hatching.

The shape of the hatching intensity curves, describing variations in the daily rate of larval production over time, is characterized by skews to the right. These tails are suggested to be related to non-optimal conditions during the embryonal development, such as a retarded rate of development in deeperlying egg layers and inadequate bottom substrates for spawn attachment.
The bimodal shape of the hatching intensity curve in 1978 is related to the occurrence of two recognized spawning grounds. The bimodal curves in 1977 and 1979 are more difficult to explain. The age composition of the parent stock in these years (DAHL, pers. comm.) gives no reason to assume that young spawners deposit their eggs prior to older ones, as BRIDGER (1961) suggested for the Downs herring. The existence of additional unidentified spawning grounds seems more likely in 1979. Sampling artifacts and heterogeneous environmental conditions could, however, also produce variations in hatching rate. Some parts of the spawning grounds were subjected to greater insolation than other parts, hence the littoral sea bed was differently heated during the

period of embryonal development. Accelerated embryonal development in these areas may thus produce the polymodal shapes of the hatching intensity curves. Mortality due to unsuccessful hatch may also induce irregularities in the observed hatching rates. GAMBLE *et al.* (1981) found approximately 95% hatching success of herring eggs in plastic enclosures, but 80–90% of the newly hatched larvae died during the first day.

Inadequate sampling coverage in time and space is generally considered to be among the most severe sources of error in estimates of abundance, e.g., SAVILLE 1964, ENGLISH 1964, ULLTANG 1977, SAVILLE and SCHNACK 1981, but bias due to distribution of the larvae, larval mortality and sampling methods is also important. Generally a compromise has to be made between a dense grid of stations per survey and frequent coverage. In Lindaaspollene the surveys were generally separated by only a few days, at least during the main hatching period, so that the variance in time would be small. Large variations in larval abundance per unit area indicate, however, that either the number of stations or the number of samples per station should be increased.

NET SELECTIVITY

Bongo nets were generally used for collecting larvae for assessment studies, in accordance with SMITH and RICHARDSON (1977), who recommended the slow, bridleless Bongo net for ichthyoplankton surveys. Samples from nets with high filtering rates are, however, associated with increased larval damage and extrusion of larvae(MCGRODDY and WYMAN 1977, COLTON *et al.* 1980). Errors due to net damage of larvae resulting in loss of the yolk-sac and misidentification of developmental stages will therefore have serious consequences for the estimation of larval production by the present procedure.

Bias due to gear handling and towing procedures may greatly influence the accuracy of sampling, depending on variations in current velocity with depth and density of larvae. Control procedures were attempted to eliminate bias caused by unequal sampling with depth in oblique hauls.

Corrections for time of day and sample size were not made because of the inconsistent magnitude of diurnal catch differences. In general, cruises were conducted whenever practicable between dusk and dawn in order to minimize gear avoidance. Up to a length of about 20 mm (approximately 50 days after hatching) the gear avoidance capacities of herring larvae are assumed to be small (pp. 203, App. Fig. III.1). BLAXTER (1962) suggested that the improved swimming performance was related to the development of a functional caudal fin at a length of 15–18 mm.

The relationship between towing speed, mesh width and larval size is important in the evaluation of net selectivity. Little bias is assumed to result from mesh width in the present investigation, because the mesh width was

increased with increasing time from hatching. LENARZ (1972) found that close to 100% of all anchovy larvae *(Engraulis mordax)*, which are smaller than herring larvae at similar ages, were retained by a 0.505 mm mesh nylon net, which also implies that extrusion of herring larvae in the present account can be neglected. Delayed hatching cohorts of larvae could not be adequately assessed by BLSMT-hauls, but with only one cruise per year, the incurred bias was probably negligible.

MORTALITY

The relationship between egg production and larval production may have important implications for stock management. In this study no clear relationship was found between egg abundance and subsequent larval abundance in 1977 and 1980. This is supported by observations of similar amounts of eggs deposited in 1971 and 1972, but the strength of the 1971 year class was insignificant compared to that of the 1972 year class (LIE *et al.* 1978a).

The great range in mortality rates of herring larvae during the first few weeks after hatching, when food levels are critical, was apparently also affected by initial larval numbers. In 1977 and 1979 food conditions were good after the winter deep water replenishment of 1976–77 and 1978–79, which provided adequate growth and survival conditions for the herring larvae (MCLEAN 1979 and AKSNES 1981). In 1978, however, the environmental conditions during the spring bloom were extraordinary (MCLEAN 1979), providing herring larvae at the feeding stage with inadequate food conditions and consequently slow growth (p. 205, Table 3.4) and high mortality. In 1980 the number of larvae hatched was very high but the food availability was low (AKSNES 1981), which may have caused the high mortality rate observed.

After a post-hatching age of approximately 2.5 months, the abundance of herring larvae reached a level at which increasing stability in mortality might be expected. With increasing age, greater bias due to sampling and distribution of larvae is incorporated into the abundance estimates, thereby influencing the rate of mortality. Mortality estimates may be affected by the efficiency of the sampling gear as discussed above, but larval emigration from the sampling area may also be a contributing factor. Emigration of larvae from the study area is assumed to exceed immigration from surrounding waters, resulting in overestimation of mortality. Delayed hatching cohorts of herring larvae were negligible in the catches, except in 1979 (Table 2.5), and therefore did not influence the calculated rates of mortality.

Mean rates of decline in abundance from the time of hatching to 2.5 months of age were between 8 and 16% per day (average 10.2% per day) and were not significantly different over the period 1977–1980 in Lindaaspollene. This means that less than 20% survive the first 20 days after hatching, which is

comparable with the time up to the «point of no return» of non-feeding larvae (BLAXTER and HEMPEL 1963, ØIESTAD 1983). High mortality rates of newly hatched larvae are characteristic for many clupeids, including herring, but because of difficulties in determining the age, few estimates of age-specific mortality rates have been reported. DRAGESUND and NAKKEN (1973) suggested that Atlantic herring larvae of length between 9 and 13 mm were susceptible to mortality rates of the order of 70–95%, or 5–13% per day. SAVILLE (1965) found a similar reduction of spring Clyde herring larvae shortly after the main hatching peak, with mortality rates of the order of 35 and 18% per day in two different years. Also, GRAHAM and CHENOWETH (1973) estimated high mortality rates, 28% per day on average, for recently hatched herring larvae on Georges Bank. Average winter mortalities in post-yolk-sac larvae of autumn spawned herring of the order of less than 5% per day are, however, reported to occur in the northwestern Atlantic (GRAHAM and DAVIS 1971, LOUGH *et al.* 1979) and in the North Sea (WOOD and BURD 1976). The mortality rates observed for herring in Lindaaspollene agree reasonably well with those referred to above for similar periods of development. A somewhat lower mortality rate with age was observed by GAMBLE *et al.* (1981) in plastic bag experiments with 11% mortality per day for the first ten days after hatching, diminishing to 5% per day for the next 40 days. Herring larvae seem to have mortality rates similar to several other clupeids of temperate and subtropical marine waters, 8–16% per day (AHLSTRÖM 1954, NAKAI and HATTORI 1962 and HOUDE 1977). They are also similar to those reported for haddock, 4–16% per day (SAVILLE 1956), but much higher than those of North Sea plaice larvae, 2–7% per day (HARDING and TALBOT 1973, BANNISTER *et al.* 1974), and considerably lower than those of scombroid larvae, 20–28% per day (FARRIS 1961 and WATANABE 1970).

There may be several causes of the high larval mortality, though herring larvae are assumed to have wide tolerance limits for environmental parameters (BLAXTER 1960, BISHAI 1961, BLAXTER and HOLLIDAY 1963 and DE SILVA and TYTLER 1973). Short-term variations in oceanographic conditions have indicated that some relationship exists between stability of the water column and success of anchovy year classes (LASKER 1978), and large variations in densities of nauplii between years have also been found in the hatching areas of cod-larvae in Lofoten (ELLERTSEN *et al.* 1977, TILSETH and ELLERTSEN 1981)

The major causes of larval mortality are believed to be starvation and predation. Starvation is assumed to be an important factor of mortality at the time of first-feeding, when very high food densities are required (HUNTER 1980). In yolk-sac larvae, however, predation and environmental stress is thought to be most critical for survival.

Several species of planktonic invertebrates occurred with increasing abundance in the hatching area at the time of larval release, of which *Bolinopsis*

infundibulum, *Sarsia tubulosa* and *Rathkea octopunctata* were observed *in situ* to prey upon recently hatched herring larvae (stage 1a) on the spawning grounds. Experimental feeding of *Bolinopsis* sp. and *Sarsia* sp. with recently hatched 1a-larvae also pointed to the importance of the two invertebrate species as predators on herring larvae, at least within the first few days of hatching. LEBOUR (1925) also observed *Rathkea octopunctata* eating larval herring, but suggested that *Bolinopsis* sp. and *Sarsia* sp. did not prey upon fish larvae. Several species of fish and plankton are known to prey upon fish larvae (LEBOUR 1923, FRASER 1969, LILLELUND and LASKER 1971, THEILACKER and LASKER 1974, SHEADER and EVANS 1975, VON WESTERNHAGEN and ROSENTHAL 1976 and MØLLER 1980). Their predation on larval fish populations is difficult to assess, however, because little quantitative information is available.

Predation is also thought to be linked with food availability and growth pattern, since increasing growth rates enable the larvae to grow rapidly through successive fields of predation (CUSHING 1976, CUSHING and SHEPHERD 1981, JONES 1981). In predator-free basin experiments with limited food supply, ØIESTAD (1983) found close to 100% survival of Lindaas herring larvae during the first 2–3 weeks after hatching, diminishing to 50% at the end of 40 days. When exposed to predators, however, the survival rate of the herring larvae dropped rapidly (ØIESTAD op. cit.). Even at high food levels, predation is assumed to be important for density regulation of large year classes (DEKHNIK *et al.* 1970, JONES and HALL 1974 and JONES 1981).

In the future, quantitative larval studies should encompass the interrelated processes. Growth, distribution and mortality of larvae should therefore be studied in relation to aspects of density and to environmental factors such as food availability, competition, predation and hydrography.

3. GROWTH AND FEEDING OF LARVAE

INTRODUCTION

It is widely believed that rates of larval growth and survival are of great importance in determining fish year class strength (GULLAND 1965), although the existence of critical periods in larval life is not clearly established (MAY 1974). A great deal has been written on feeding and growth of larval herring from wild populations (MARSHALL *et al.* 1937, BHATTACHARYA 1957, RUDAKOVA 1971, SCHNACK 1972, BJØRKE 1978), whereas the majority of quantitative information is obtained from controlled feeding experiments both in laboratories (BLAXTER 1965, ROSENTHAL and HEMPEL 1970, BLAXTER and STAINES 1971, WERNER and BLAXTER 1981) and in enclosures (GAMBLE *et al.* 1981, ØIESTAD 1983).

Larval growth is influenced by feeding characteristics and environmental conditions. To evaluate the interaction between growth and feeding, it is necessary to estimate the amount of time available for feeding each day, the incidence and intensity of feeding for each size group of larvae, as well as to determine the size of prey.

This investigation seeks to describe the growth and physical condition of the larvae from the time of hatching up to an age of approximately two months after hatching in 1977–1980 and relate these measurements to the abundance and survival of the studied larvae (pp. 165–198).

MATERIAL AND METHODS

FIELD COLLECTION

Samples used to investigate growth and feeding in herring larvae were collected in Lindaaspollene between April and June in the years 1977–1980 using paired Bongo nets without opening-closing device (POSGAY, MARAK and HENNEMUTH 1968). Net opening diameters of 20 cm and mesh widths of 0.275 mm were used in the hatching period, and 61 cm and 0.505 mm were used after hatching. The nets were towed by a 29-foot boat, with hydraulic winch, at a speed of 2–2.5 knots. Volume of water filtered was derived from TSK (Tsurumi Seiki

Kosakusko Ltd) flowmeter readings, and sampling depth was calculated from the towing angle and wire length.

To examine the relationship between feeding characteristics, vertical distribution, and time of day, the larvae were sampled at several 24-hour stations with Bongo 61 cm nets (0.505 mm mesh size) hauled horizontally at depths of 0, 5, 10, 15, 20, 25, 30 and 40 meters.

SAMPLE PROCESSING AND DATA ANALYSIS

The majority of the samples were fixed in 4% formaldehyde in sea water buffered with 2% sodium borate. Age was determined by the rings in otoliths of larvae preserved in 96% ethyl alcohol. The otoliths were prepared for analysis according to a process described by ROSENBERG et al. (1981).

Up to 50 herring larvae per station were identified as to developmental stage (DOYLE 1977) and measured for standard length (SL) (measured from the anterior part of the maxillae to the end of the notochord) to the lowest 0.1 mm. Subsamples of up to 20 larvae per station were measured to the nearest 0.05 mm for the following morphological parameters: eye diameter (measured across the largest part of the eye), body height (in yolk-sac larvae measured as the myotome height at the middle of the yolk-sac length, in post-yolk-sac larvae measured at the transition between the fore- and hind gut), yolk-sac length (measured as the length of the yolk-sac content excluding the yolk-sac membrane), and yolk-sac height (measured as the largest height of the yolk sac, excluding membranes).

Yolk-sac herring larvae were classified into developmental stages 1a, 1b and 1c on the basis of the ratio of yolk-sac height to body height being more than 2.5, 1.0–2.5, and less than 1.0 respectively (DOYLE 1977). DOYLE's morphological staging system was supplemented with stage 1d, where no remnants of the yolk sac are left and no dorsal fin rays are yet discernible. For identification of post-yolk-sac herring larvae, see DOYLE (1977).

Growth rates were determined as daily length increment (DLI) in millimeter based on standard length, and specific growth rate (SGR), in percentage,

$$SGR = \frac{(\ln W_{t2} - \ln W_{t1})\ 100}{t_2 - t_1},$$ where W_{t1} and W_{t2} are

dry weights in µg at age t_1 and t_2 days past 50%-hatching.

Gut content analysis was performed on up to twenty larvae per station to examine food and feeding. The contents were identified as to species or systematic group and developmental stage (DOYLE 1977). The degree of digestion of the gut contents was determined according to a qualitative scale using the degree of dissolution of nauplii (ELLERTSEN *et al.* 1977): 1) no visible digestion, 2) a transparent zone between carapace and the interior of the

nauplii, and 3) the interior of the nauplii completely dissolved. The food organisms were measured for one or several of the parameters of total length (excluding setae), cephalothorax length and maximum body width.

Undamaged herring larvae were rinsed in distilled fresh water and dried in individual aluminium foil boxes at 60°C until constant weight was obtained (at least 24 hours). The dry weights were determined on a CAHN electrobalance to the nearest 0.1 µg.

The collected data were analysed on a UNIVAC 1100 digital computer using SPSS programs (NIE *et al.* 1975).

Regression analysis was used to describe the length – weight relationship of post-yolk-sac herring larvae in Lindaaspollene. Where the variables were subject to errors of measurement, a functional regression, as recommended by RICKER (1973, 1975) was used instead of a predictive one. The confidence limits of the regression coefficient Z were given as

$$Z\,(\sqrt{B+1} + \sqrt{B}) \text{ and } Z\,(\sqrt{B+1} - \sqrt{B})$$

where $B = F(1-r^2)/(N-2)$, r^2 is the coefficient of determination, N is the number of pairs of variables, and F is the variance ratio at the 95% confidence level with degrees of freedom equal to $n_1 = 1$ and $n_2 = N - 2$ (RICKER 1975).

RESULTS

GROWTH

Length and weight data of the different stages of development are shown in Appendix Table III.1.

Age

To identify herring larvae cohorts, some randomly selected specimens from 1978–1980 were aged on the basis of their otolith rings. Table 1 shows the measurements of standard body length and analysis of otolith ring deposition in herring larvae. The relationship between these two parameters revealed that length appeared to increase linearly with age of the larvae according to the predictive regression line

$$L = 0.63 \cdot R + 4.42 \qquad (r^2 = 0.97)$$

where L is standard body length and R is number of rings in the otoliths. Assuming that after 13 days following hatching one ring per day is deposited in

Table 3.1. Number of otolith rings in herring larvae from Lindaaspollene during 1977–1980. Date of hatching estimated from otolith readings is compared with observed hatching season.

Year	Date of collection	Larval length (mm)	No.rings	Estimated date of hatching	Observed hatching season
1978	6 Sept	84.0	120	27 April	22 April–20 May
		84.0	130	17 April	
1979	25 June	20.5	29	14 May	30 April–26 May
		23.7	37	6 May	
		25.2	36	7 May	
		22.7	25	18 May	
		28.2	42	1 May	
		15.0	25	18 May	
		21.7	26	17 May	
		21.7	32	11 May	
		24.2	23	20 May	
		24.5	22	21 May	
		13.7	23	20 May	
		20.5	24	19 May	
		23.4	25	18 May	
1980	19 May	8.7	9	27 April	29 April–20 May
		9.6	7	29 April	
	20 May	13.3.	10	27 April	
		7.5	5	2 May	

the larval otoliths (Fossum 1980), the calculated date of hatching agreed with the observed hatching season derived from net collections of herring larvae (Table 3.1).

Standard body length

During the first 50 days after hatching the standard length of herring larvae increased curvilinearly (Fig. 3.1). Mean length increased from 7.6 mm in recently hatched stage 1a-larvae up to about 22 mm at age 50 days. After Day

Table 3.2. The relationship between standard length and age in herring larvae during the first 50 days after 50%-hatching. Parameters of the semilogarithmic predictive regression, $\ln L = a + bT$, and coefficients of determination, r^2, are given.

Year	N	b	a	r^2
1977	1019	0.022	2.043	0.824
1978	1258	0.020	2.029	0.479
1979	833	0.021	2.056	0.799
1980	417	0.018	2.025	0.322

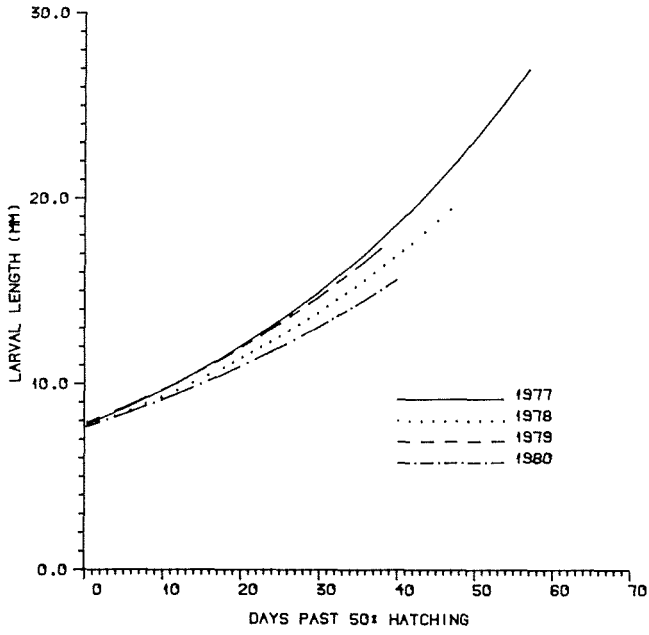

Fig. 3.1. Standard lenght of herring larvae in relation to age after 50% hatching in Lindaaspollene during 1977–1980.

50, a marked decline in length was observed in 1977 and 1978, perhaps due to inadequate daylight sampling of the larger larvae (Appendix Fig. III.1). In subsequent years sampling was confined to twilight or dark conditions, if possible, to reduce bias caused by net avoidance.

A predictive regression line of the type $\ln L = a + bT$, where L is standard body length, T is age in days after 50% hatching, and a and b are constants, was fitted to samples of herring larvae captured in the first 50 days after hatching each year (Table 3.2 and Fig. 3.1). The slopes were compared using covariance analysis (ZAR 1974) and proved to be significantly different ($F = 6.4$, $p<0.01$). Fig. 3.1 shows that the length increased at approximately similar rates in 1977 and 1979, faster than in 1978 and 1980. The small values of the coefficients of determination in 1978 and 1980 are probably due to the short time interval over which samples were collected.

Dry weight

Dry weight of herring larvae was examined in samples collected during the years 1977–1980. The dry weight increased curvilinearly with age from approximately 96 µg at hatching up to a mean of 3 mg at age 50 days (App. Figs III.3 and III.4). Because dry weight of herring larvae decreases with the

Table 3.3. The relationship between dry weight and age in post-yolk-sac herring larvae. Parameters of the semilogarithmic predictive regression line, ln W = a + bT, and coefficients of determination, r^2, are given.

Year	N	b	a	r^2
1977	439	0.090	–3.28	0.85
1978	74	0.052	–2.63	0.62
1979	444	0.089	–3.40	0.73
1980	135	0.059	–2.84	0.22

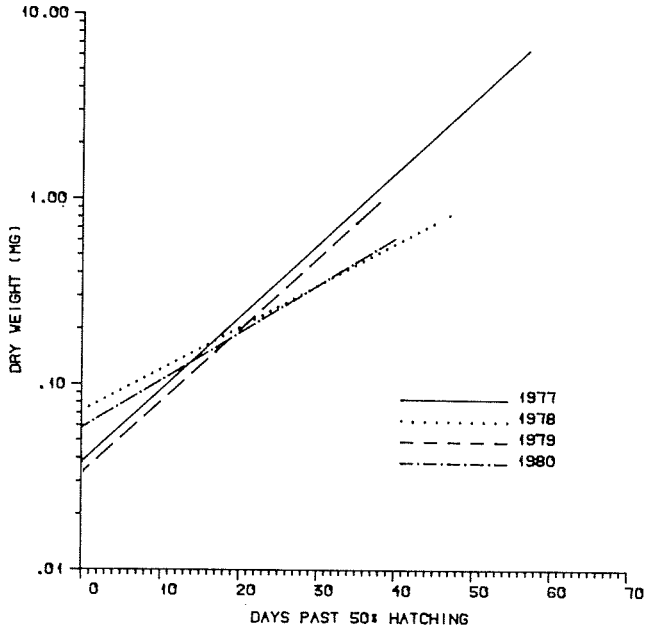

Fig. 3.2. Dry weight of herring larvae in relation to age after 50% hatching in Lindaaspollene during 1977–1980.

absorption of the yolk sac, only post-yolk-sac herring larvae were included in the regression analysis.

A semilogarithmic predictive regression line, ln W = a + bT (where W is mean dry weight of herring larvae, T is age in days after 50% hatching, and a and b are constants) was fitted to samples of post-yolk-sac herring larvae collected within 50 days of 50%-hatching each year (Table 3.3 and Fig. 3.2). The slopes were compared using covariance analysis (Zar 1974) and proved to be significantly different ($F = 15.0$, $p < 0.01$).

Fig. 3.2 indicates that post-yolk-sac herring larvae of the 1977- and 1979-year classes grew at similar rates, although their initial dry weights were small. These year classes differed considerably from those in 1978 and 1980, which grew at slower rates in spite of their higher dry weights at yolk-sac absorption.

Growth rates

Within age intervals of a few weeks duration, length was assumed to increase fairly linearly with age. Dry weight was assumed to increase with age in a semilogarithmic linear manner during the same time, enabling specific growth rates to be calculated. In the first age interval (5–12 days after 50%-hatching), length increments of 0.20–0.27 mm per day, with a mean of 0.23 mm/day, were observed in 1977, 1979 and 1980 (Table 3.4). In 1978, however, a growth rate of only 0.13 mm per day was found.

The next age interval of 12–20 days after 50%-hatching gave a slightly faster growth rate in all years but 1980, with an average rate of 0.25 mm/day.

From 20 to approximately 50 days after 50%- hatching, growth rates of 0.32 to 0.69 mm per day were observed, the highest rate being in 1978.

Specific growth rates (SGR) during the same age intervals ranged from 1.1 to 7.6% per day (mean 5.1%), 6.2–9.3% (mean 7.4%) and 10.7 to 20.7% per day (mean 14.3%), respectively (Table 3.4).

Table 3.4. Growth rates, as expressed by daily length increments (DLI) and specific growth rates (SGR), of herring larvae in Lindaaspollene in different years and at different ages.

Age interval	DLI mm/day				SGR %/day			
Days	1977	1978	1979	1980	1977	1978	1979	1980
5–12	.21	.13	.20	.27	7.6	1.1	5.1	6.6
12–20	.28	.25	.26	.20	6.2	6.9	7.3	9.3
20–50	.32	.69	.33	–	11.3	20.7	10.7	–

Length – weight relationship

It is commonly accepted that dry weight and length are related by some simple power law. The length-weight relationship was studied in samples of post-yolk-sac herring larvae (older than stage 1d) from the years 1977–1980. The data were logarithmically transformed and a predictive regression line of the type $\ln W = a + b \ln L$, where W is dry weight (mg), L is standard body length (mm) and a and b are constants, was fitted to each set of samples (Table 3.5 and Fig. 3.3). The slopes were compared using covariance analysis (Zar 1974) and proved to be significantly different ($F_{slope} = 51.3$, $p < 0.01$).

Table 3.5. Parameters of the predictive regression line ln W = a + b ln L, and coefficients of determination r^2) in samples of post yolk sac herring larvae.

Year	N	b	a	r^2
1977	452	4.071	–11.643	0.894
1978	77	3.364	– 9.88	0.912
1979	444	4.108	–11.857	0.932
1980	148	2.877	– 8.815	0.932

For the purpose of estimating the regression coefficient, one equation was calculated for the total material. In spite of the different slopes observed, a geometric mean functional regression line (RICKER 1973) was fitted to this material

$$\ln W = 4.029 \quad \ln L - 11.575 \text{ or}$$

$$W = 9.4\ 10^{-6}\ L^{4.029}$$

where N = 1121, r^2 = 0.91, and the 95% confidence limits of the regression coefficient equal 3.96 and 4.10. The value of the regression coefficient of 4.029 expresses the functional relationship between dry weight and standard length and describes allometric growth in the herring larvae.

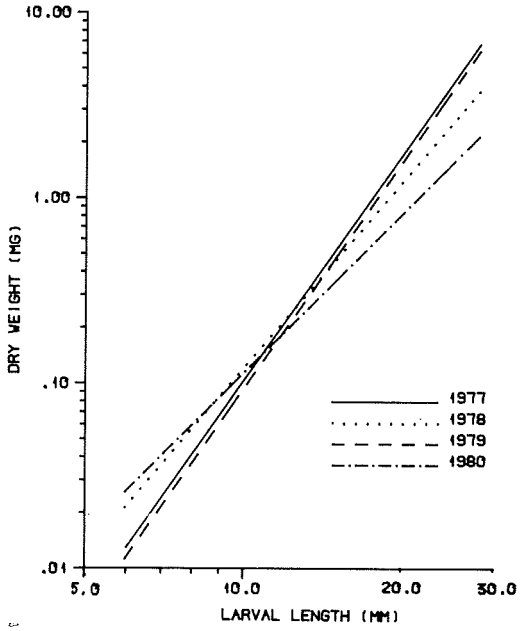

Fig. 3.3. Length-weight relationship of herring larvae in Lindaaspollene during 1977–1980.

Condition factor

Condition factors are generally used to indicate suitability of an environment or to compare the same species of fish from one area or year with those from another under different environmental conditions. They can also be used as a measure of the well-being of a fish. Since during the yolk-sac phase larvae lose weight continuously until the yolk sac is absorbed (HEMPEL and BLAXTER 1963), the condition factor (CF) was determined in post yolk sac herring larvae only. CF was expressed as dry weight in milligrams multiplied by 1000 and divided by standard length in millimeters to the third power,

$$CF = \frac{\text{dry weight (mg)} \cdot 10^3}{\text{standard length (mm)}^3}$$

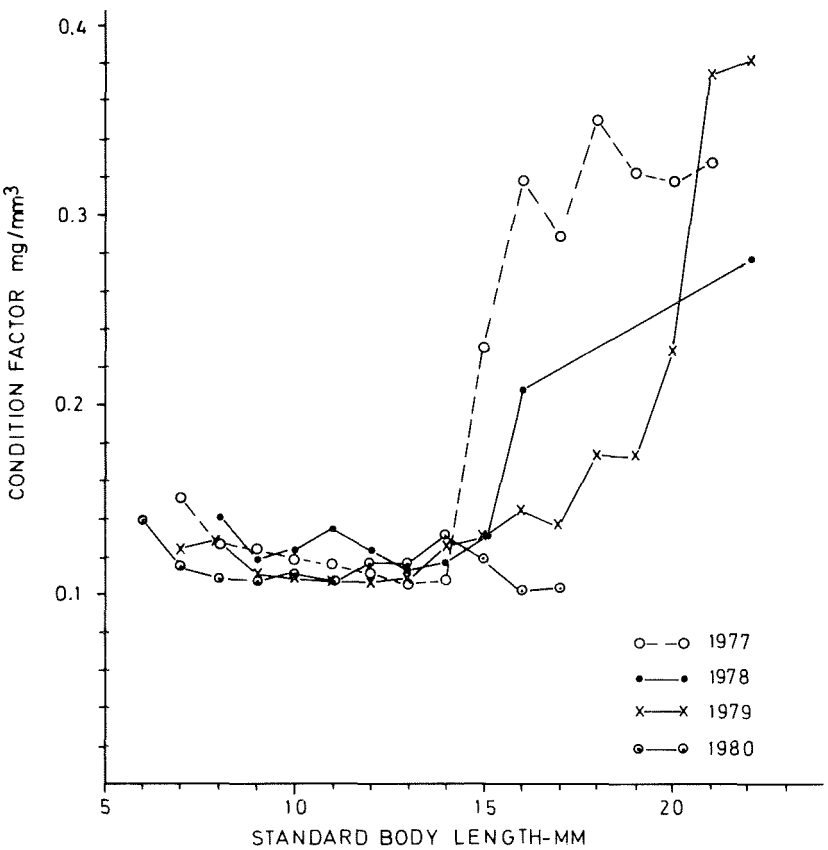

Fig 3.4. Mean condition factor in relation to standard body length of herring larvae from Lindaaspollene, during 1977–1980.

in order to compare the state of nutritional condition of larvae belonging to different year classes. High condition factors of equal-sized specimens indicate that the specimens are well fed.

Fig 3.4 shows that most post-yolk-sac herring larvae start with almost the same condition factor, a mean CF of between 0.10 and 0.14 mg/mm^3, remaining fairly constant up to a length of approximately 14 mm. Above this length, condition factor appears to increase with increasing body length, and the differences between year classes become more obvious.

In 1977 the condition factor rose abruptly to approximately 0.3 mg/mm^3 at a length of 16 mm and appeared to stabilize at that level up to a length of 21 mm. The increase seemed to be somewhat delayed in 1978 and 1979, and in 1980 the condition factor remained at a low level (approximately 0.1 mg/mm^3) up to a length of 17 mm.

Relative condition factor

The length-weight regression coefficient is frequently used as a measure of condition in fish (e.g., LE CREN 1951). In fish with allometric growth, a regression coefficient other than 3 is used under standard environmental conditions. As standard conditions are difficult to describe, this investigation used a value of the functional regression coefficient of the length-weight relationship equal to 4.029, as determined from the post-yolk-sac herring larvae material collected during 1977–1980.

The relative condition factor

$$\mathrm{RCF} = \frac{\text{dry weight (mg)}\ 10^5}{(\text{standard length (mm)})^b}$$

where b is the length-weight regression coefficient, was initially used by EHRLICH *et al.* (1976).

No obvious difference between years was found in RCF up to a length of 14 mm. Fig. 3.5 shows that the RCF dropped when the herring larvae were between 6 and 14 mm in length, although at lengths greater than 14 mm the RCF appeared to increase at varying rates.

In 1977 the relative condition factor rose abruptly from approximately 0.7 at a length of 14 mm to a level exceeding 1.5 at a length of 16 mm. The increase in relative condition factor in 1978 and 1979 seemed to be a little delayed, whereas in 1980 the relative condition factor had dropped to 0.5 at a length of 17 mm without a corresponding increase.

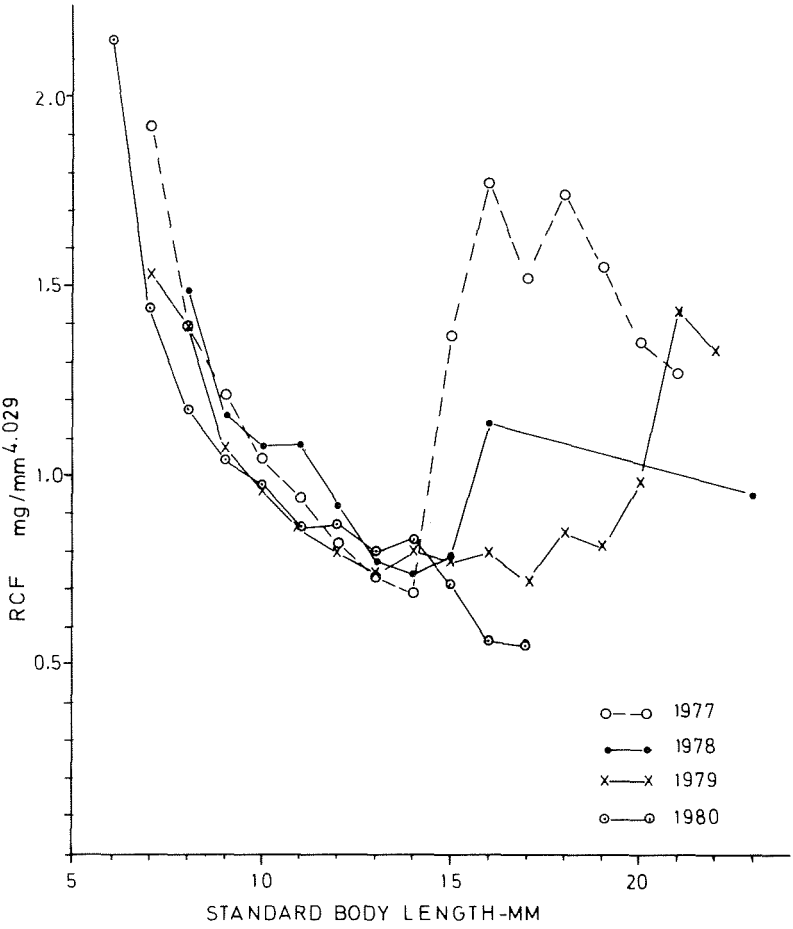

Fig. 3.5. Mean relative condition factor, RCF, in relation to standard body length of herring larvae from Lindaaspollene during each of the years 1977–1980.

Eye diameter

The eye diameter increased with increasing larval length within the examined size range (6–28 mm), although a change in slope at a body length of approximately 15 mm could be distinguished (Fig. 3.6). A predictive regression line (EYD = a + b L) was fitted to the observed data for each year (Table 3.6 and Fig. 3.7). In spite of the heterogeneous variances observed, the slopes were compared using covariance analysis (Zar 1974) and proved to be significantly different ($F = 94.3$, $p<0.01$).

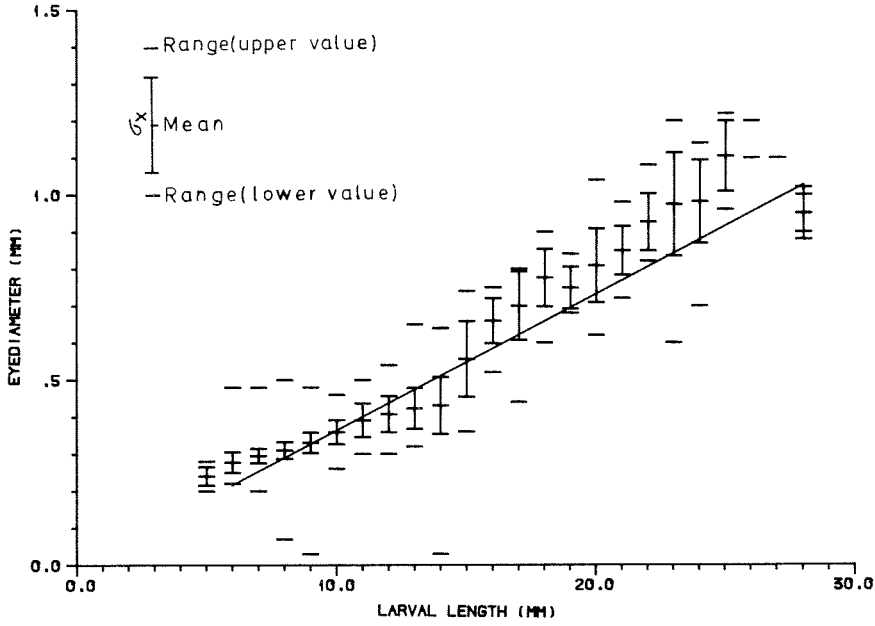

Fig. 3.6. Eye diameter in relation to standard body length of herring larvae from Lindaaspollene during 1977–1980. Mean, standard deviation (σ_x) and range are indicated.

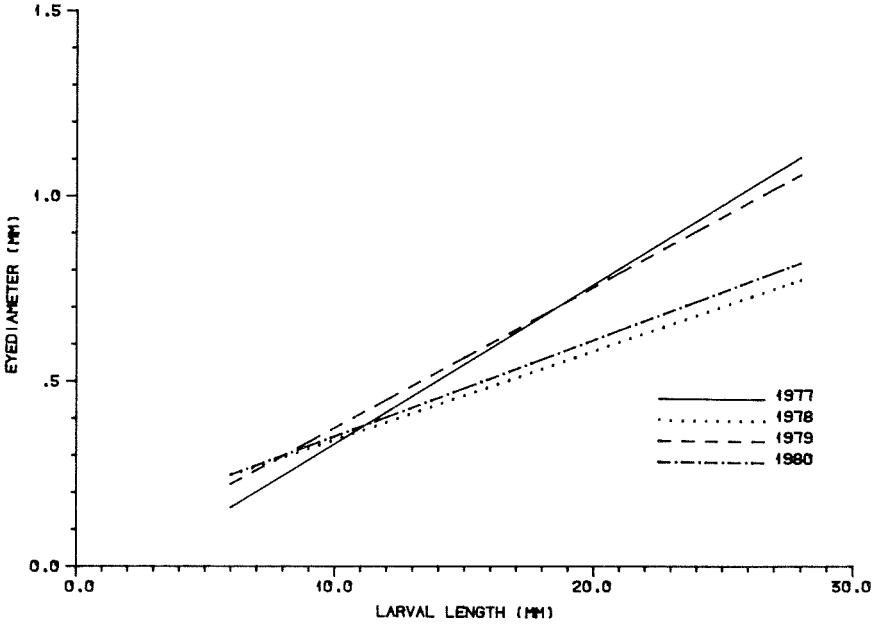

Fig. 3.7. Mean eye diameter in relation to standard body length of herring larvae from Lindaaspollene during 1977–1980.

Table 3.6. Eye-diameter-and-length relationship of herring larvae in Lindaaspollene. Parameters of the predictive regression line, EYD = b L + a, and coefficients of determination, r^2.

Year	N	b	a	r^2
1977	424	0.043	–0.099	0.86
1978	985	0.024	0.103	0.61
1979	1347	0.038	–0.006	0.88
1980	103	0.026	0.091	0.60

Body height

The relationship between body height and standard length was examined in 699 post-yolk-sac herring larvae during 1977–1980. Body height increased rapidly with larval size (Fig. 3.8). Individual variability also increased, as indicated by the larger standard deviations in larvae at increasing body lengths (Fig. 3.8). A predictive regression line (MYH = a + b L) was fitted to the observed data of each year (Table 3.7 and Fig. 3.9). In spite of the requirements of equal variances for use of covariance analysis (ZAR 1974), the

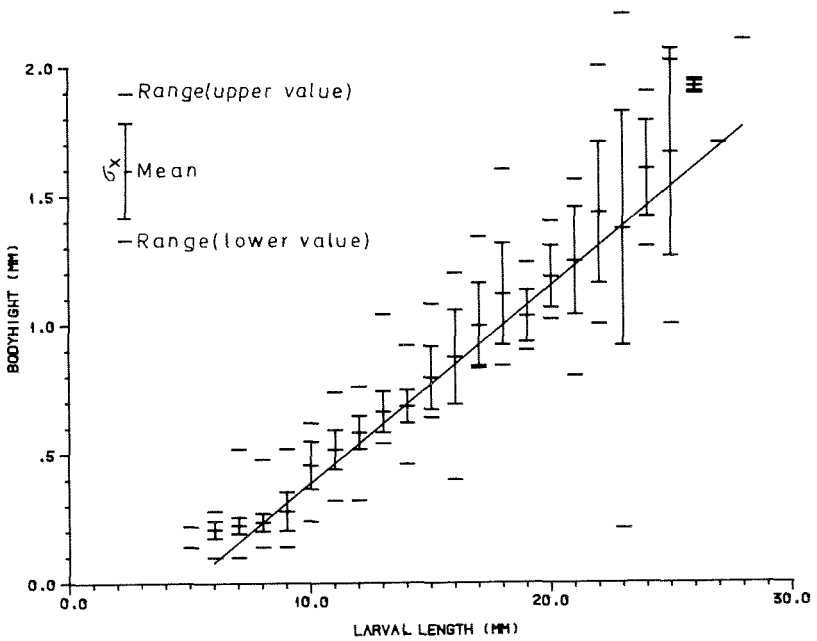

Fig. 3.8. Body height in relation to standard body length of herring larvae in Lindaaspollene during 1977–1980 Mean, standard deviation (σ_χ) and range are indicated.

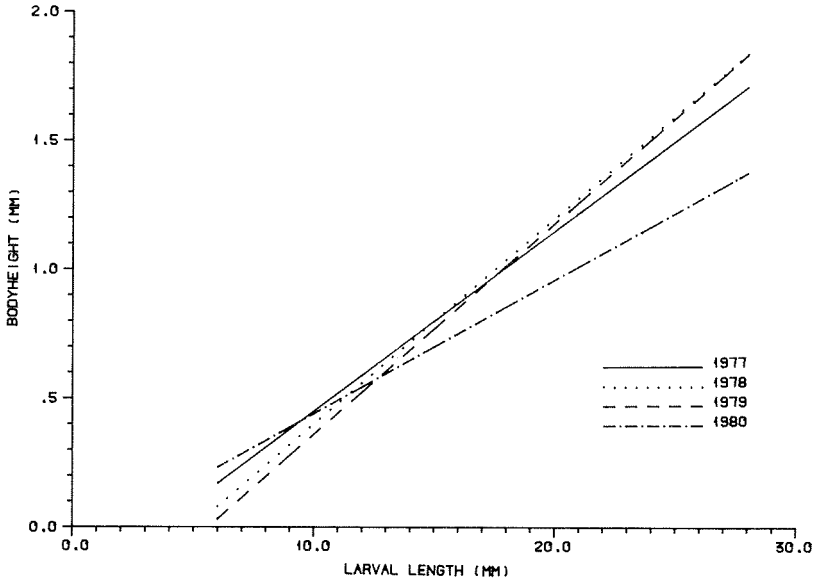

Fig 3.9. Mean body height in relation to standard body length of post-yolk-sac herring larvae in Lindaaspollene during 1977–1980.

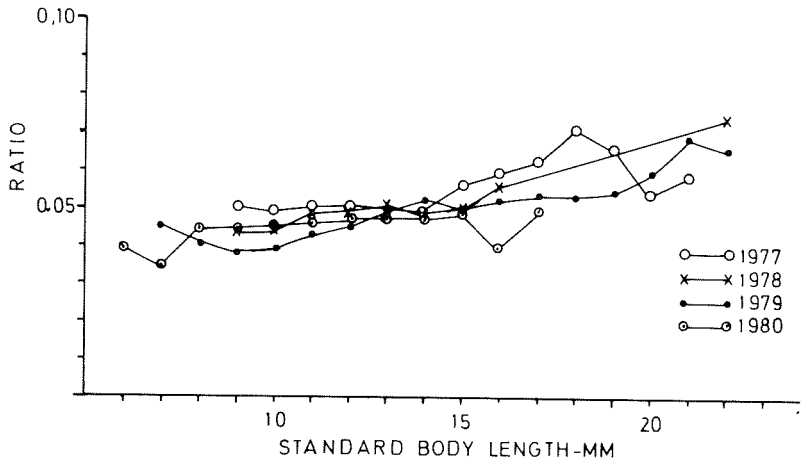

Fig. 3.10. Ratio of body height to standard length of herring larvae in Lindaaspollene during each of the years 1977–1980.

Table 3.7. Body-height-and-length relationship in post-yolk-sac herring larvae in Lindaaspollene during 1977–1980. Parameters of the predictive regression line, MYH = b L+a and coefficients of determination, r^2.

Year	N	b	a	r^2
1977	187	0.070	–0.25	0.81
1978	64	0.080	–0.40	0.88
1979	284	0.082	–0.46	0.87
1980	164	0.052	–0.08	0.85

method was used to compare the slopes, and they proved to be significantly different ($F = 23.7$, $p < 0.01$).

The ratio of body height to standard body length (RMYL) appeared to increase with increasing size of the larvae, although this trend was not very pronounced in 1980. Differences in RMYL were, however, difficult to interpret between the years (Fig. 3.10).

FEEDING

Feeding in herring larvae was studied from samples of larvae collected at different depths during 24-hour stations in Lindaaspollene during May and June 1977–1979.

Duration, incidence and intensity of feeding

The smallest herring larva with food in its gut was 8.2 mm in length with slight remnants of yolk (developmental stage 1c). Herring larvae containing recently ingested food were obtained from between 0500 hrs to 2200 hrs. Judging from

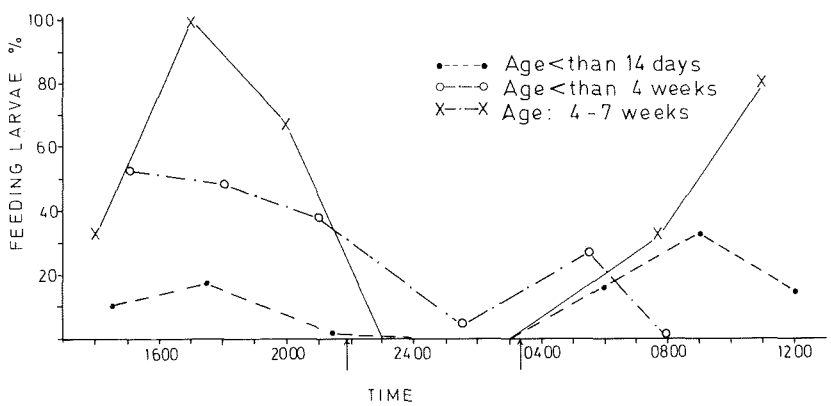

Fig. 3.11. Mean feeding incidence of herring larvae of different ages in relation to time of day in Lindaaspollene during 1977–1980. Surface illumination of 1 lux is indicated by arrows.

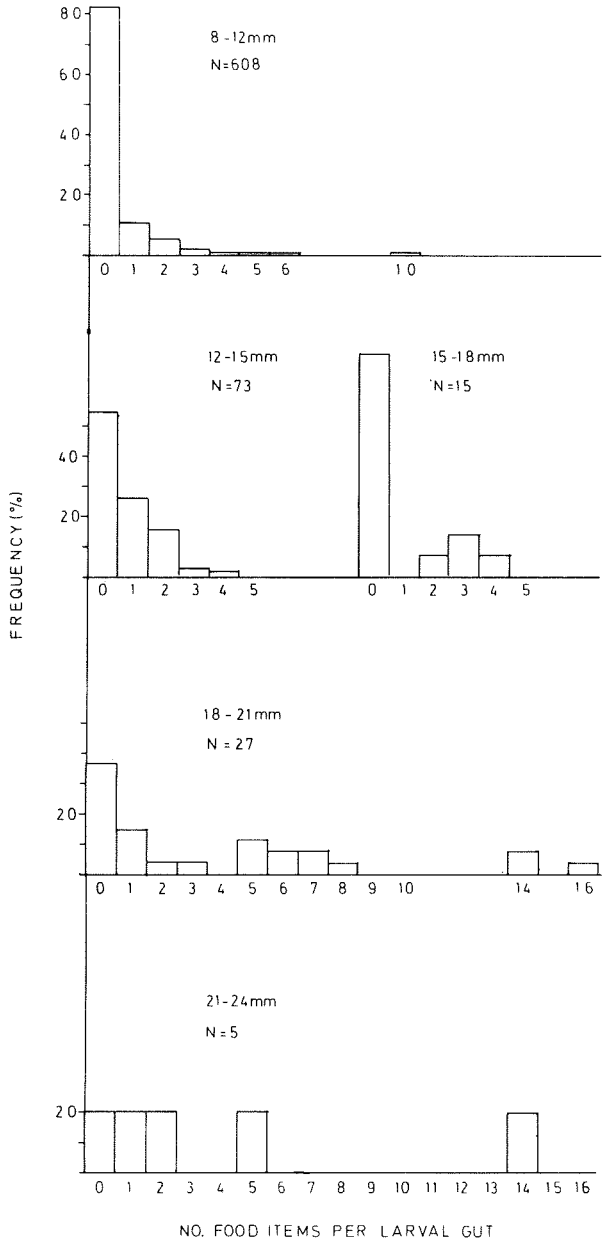

Fig. 3.12. Frequency of herring larvae (% numbers) and number of food items observed per gut in different length groups of larvae.

the observed relationship between feeding incidence of herring larvae beyond developmental stage 1c and time of day in May and June (Fig. 3.11), it appears that feeding begins after 0400 hrs and continues during most of the daylight hours, i.e., when surface illumination exceeds 1 lux, until approximately 2200 hrs. This implies that the daily foraging period of herring larvae between an age of 1–7 weeks lasts for approximately 18 hrs in May and June. Peak feeding apparently occurred between 0500 and 1200 hrs and between 1500 and 2100 hrs.

Feeding incidence of herring larvae was examined in the upper 30 m of the water column during several 24-hour stations, but only those larvae collected between 0400 and 2200 hrs were used in the evaluations. An average of 19% (range 10–40%) of the larvae examined at an age of less than 2 weeks after hatching possessed food in their guts. At an age of 4–7 weeks after hatching, an average of 65% of the larvae examined contained food in their guts (Fig. 3.11).

Intensity of feeding, as indicated by the number of prey items per larval gut, was examined in herring larvae 8–24 mm long between 0400 and 2200 hrs (the period of active feeding) in May and June 1977–1979 (Fig. 3.12).

In larvae smaller than 18 mm a relatively high proportion had empty guts, and feeding larvae were generally observed to have consumed less than 6 prey items. However, larvae exceeding 18 mm in length were recorded to have up to 16 prey items in their guts.

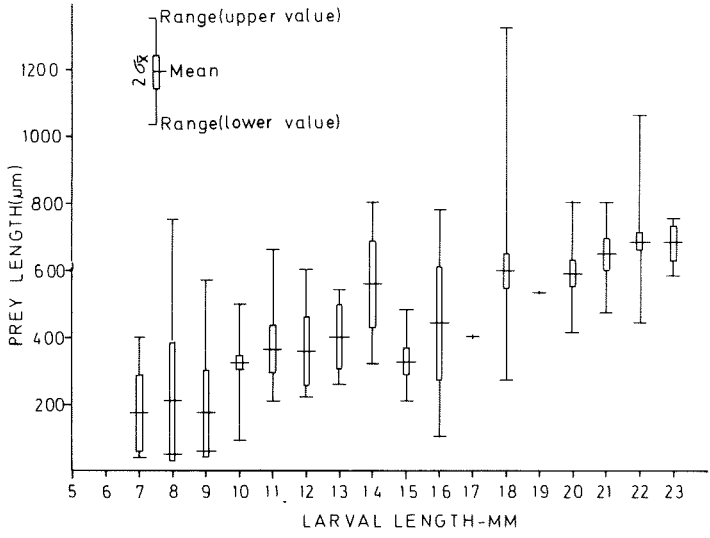

Fig. 3.13. Total length of prey organisms recorded in herring larvae from Lindaaspollene and standard length of the larvae. Mean, twice the standard error of mean (2 $\sigma_{\bar{x}}$) and range are indicated.

Food

Gut-content analysis of herring larvae 7–24 mm long indicated that larger prey items were consumed with increasing larval size (Figs 3.13 and 3.14).

The relative preference of prey groups is indicated in Figure 15. It appears that nauplii made up the majority of the gut contents in larvae less than 15 mm

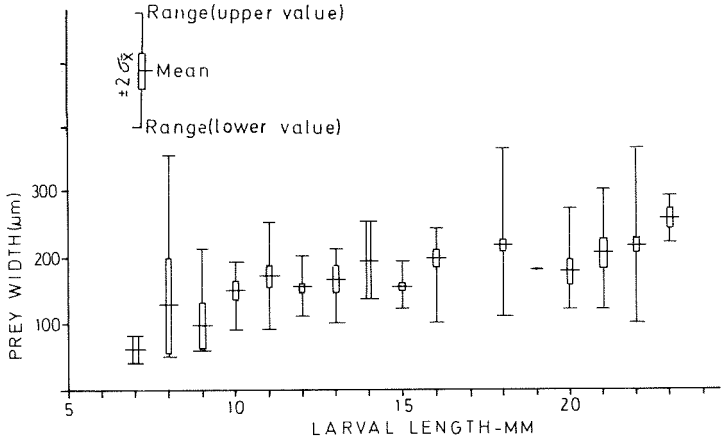

Fig. 3.14. Total width of prey organisms recorded in the guts of herring larvae in Lindaaspollene and standard length of the larvae. Mean, twice the standard error of mean (2 $\sigma_{\bar{x}}$) and range are indicated (see Fig. 3.13).

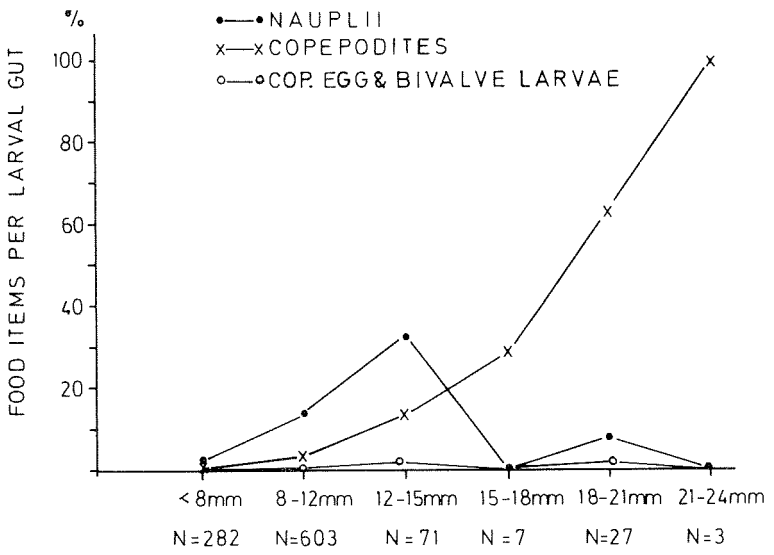

Fig. 3.15. Frequency of prey items in the guts of herring larvae of different length groups.

long, while larger larvae preferably consumed advanced copepodite stages. Other food items such as copepod eggs and veliger larvae also occurred in the gut, but to a smaller degree.

The most abundant species of copepod nauplii and copepodites recorded in the guts were *Pseudocalanus* sp., *Oithona* sp., *Acartia* sp., *Temora* sp. and *Centropages* sp.

DISCUSSION

When identifying larval cohorts in 1978–1980, analysis of daily increments in otoliths indicated that spawning outside the main spawning time was negligible. The age estimated from otolith data agreed reasonably well with the hatching period derived from net collections of yolk-sac larvae (pp. 179–187). Larvae originating from secondary spawning groups can therefore be considered insignificant in the interpretation of growth and mortality data.

Length has probably been the most frequently used parameter for age determination in studies of mortality and assessment in fish populations. Because body length is affected by body shrinkage due to preservation etc., other morphometric parameters were also measured, of which eye diameter was assumed to change little with netting and preservation (PACKARD and WAINWRIGHT 1974, EHRLICH *et al.* 1976, THEILACKER 1980). Eye diameter was therefore assumed to be a useful parameter for estimating average live size of both intact and damaged larvae. Eye diameter increased with increasing body length within the size range (6–28 mm in length) examined in herring larvae in Lindaaspollene, but annual differences appeared in the slope of the regression line

Length and dry weight were assumed to increase with age in a nonlinear manner, and for the first two months after hatching an exponential curve could be fitted to describe this relationship. The curves seemed to give a reasonably good fit to the observed data within the investigated time period.

The increase in observed length and dry weight of the herring larvae in Lindaaspollene appeared to change distinctly after an age of approximately 50 days following hatching, at a mean length of 22 mm and a dry weight of about 3 mg (Appendix Figs III.1–III.4). In 1977 and 1978 the sudden drop in mean length and dry weight at an age of 50 days after hatching coincided with an extraordinarily low larval number obtained from sampling during daylight hours (p. 189, Table 2.7). The decrease in length and dry weight was assumed to result from net avoidance of larger larvae, and these data were not therefore included in the growth analysis. STEVENSON (1962) also found that Pacific herring larvae exceeding 22 mm in length displayed a good capacity for avoidance of the sampling nets.

The 1977 and 1979 year classes of herring grew at similar rates regarding standard body length and dry weight. These year classes grew faster than those of 1978 and 1980, probably reflecting environmental conditions. Interpretation of the growth rates during specific age intervals in these years indicates that the 1977 and 1979 year classes had daily length increments exceeding 0.20 mm and specific growth rates of 5–11% per day up to an age of 50 days after hatching.

The plankton production in Lindaaspollene during the two years of good herring larvae growth and survival was considerably better than in the other two (McLean 1979 and Aksnes 1981). A large plankton biomass was also correlated with a good herring year class in 1972 (Haug 1972, Lie *et al.* 1978).

In 1980 the herring larvae grew at rates similar to those of 1977 and 1979 during the first 20 days following hatching, although the rate of daily length increments decreased from 0.27 mm/day during the first 5–12 days to 0.20 mm/day during the following 12–20 days. Although the plankton biomass in 1979 was maintained at a level greater than average, Aksnes (1981) observed that the adult population of *Calanus* sp. surviving the winter and spring of 1980 had declined. Assuming that herring larval production in 1980 was greater than average (pp. 186–187, and Fig. 2.13), it is therefore reasonable to believe that the observed high mortality rates (Table 2.8) together with the decreasing growth rates shortly after first feeding are closely linked.

The slow growth rate of first-feeding herring larvae observed during the 1978 season, with a mean daily length increment of 0.13 mm/day, specific growth rate of 1.1%/day, and a high mortality rate (p. 189 and Table 2.8) was probably linked with environmental conditions. A short-lived diatom peak appeared in March 1978 before the hatching of herring larvae, which McLean (1979) assumed was linked with the hydrographical situation in Lindaaspollene.

During April–May at the start of feeding by herring larvae, the biomass of species of other groups than Copepoda, such as Bivalvia and Echinodermata reached high levels, but these animals have inferior nutritive value for feeding herring larvae (e.g., Fossum 1983, Checkley 1982). The poor feeding conditions of first-feeding herring larvae in 1978 may therefore contribute to explaining the slow growth and high mortality of these larvae. A new peak production in late May–June 1978, with an abundance of *Temora* sp., probably provided good feeding conditions for the surviving larvae, which is also reflected in the improving growth conditions of herring larvae beyond an age of about 3 weeks.

Growth rates of 0.2–0.3 mm per day during the first 2–3 weeks after hatching have also been reported in other populations of herring larvae (Schnack 1972, Lough *et al.* 1980), and growth rates of up to 0.55 mm per day were found during the first month for several coastal populations (Marshall *et al.* 1937, Schnack 1972). Experiments of laboratory-reared herring larvae offered

adequate feeding conditions have yielded growth rates of up to 0.24 mm/day (BLAXTER 1968, EHRLICH *et al.* 1976, HAEGELE and OUTRAM 1978, FOSSUM and JOHANNESSEN 1979 and WERNER and BLAXTER 1981). This implies that with the exception of the period of first feeding in 1978, the feeding conditions in Lindaaspollene were adequate during most of the period investigated.

Specific growth rates (5–11%/day) of the Lindaas herring larvae during the first 2–3 weeks after hatching in 1977, 1979 and 1980 agree with those reported from plastic bag experiments in Lindaaspollene of 10%/day (FOSSUM 1980) and from enclosure experiments with Lindaas herring larvae (ØIESTAD 1983) and Clyde herring larvae of 6–8%/day (GAMBLE *et al.* 1981). Comparisons between larval growth rates of different stocks should consider that larval growth depends to a large extent on time of spawning and ambient environmental conditions. Annual differences in growth may also be caused by parental factors such as annual changes in the age composition and the structure of the spawning stock, thus affecting egg quality (cf. HEMPEL 1979).

The exponent relating standard length (mm) to dry weight (mg) is reported as 3.4 in Maine herring larvae (CHENOWETH 1973) and as 4.5 in wild Clyde herring larvae (MARSHALL *et al.* 1937). The values obtained in Lindaaspollene in 1977 and 1979 (4.07–4.11) fell within the reported range, while those of 1978 and 1980 (3.36 and 2.88, respectively) were under this. Lindaas herring larvae reared in the laboratory under adequate food conditions in 1978 had an exponent of 3.46 (FOSSUM 1980), slightly higher than that obtained on wild larvae in the same season (3.36).

The values obtained for standard condition factors (CF) of between 0.1 and 0.2 compare favourably with those reported from wild populations of post-yolk-sac herring larvae (less than 20 mm in length), (SCHNACK 1972, EHRLICH *et al.* 1976, GAMBLE *et al.* 1981 and ØIESTAD 1983). The CF and RCF (relative condition factor) rose rapidly in the 1977 year class. The delayed gain in CF of larger larvae in 1978 and 1979 is suggested to be linked with variable conditions of feeding and growth. The relatively low CF observed in all length groups of 1980 may be due to density dependent processes, larvae being more abundant during the first 2–3 weeks after hatching in 1980 than in the other years. Interpretation of changes in the CF's with concurrent events in the environment are difficult. Large differences in CF's of herring larvae have been observed with various feeding regimes (e.g., ØIESTAD 1983), between different stocks of herring larvae (BLAXTER 1971, VILELA and ZIJLSTRA 1971, SCHNACK 1972, VON WESTERNHAGEN and ROSENTHAL 1981 and ØIESTAD op.cit.), and between wild and captive herring larvae (BLAXTER 1975).

A common exponent of 4.029 was used to compare the RCF's of the pooled larval populations of 1977–1980. The decrease in RCF in post-yolk-sac herring larvae (stage 1d and older) up to a body length of 14 mm indicates that a major fraction of the consumed energy was allocated to growth in length without a

proportionate increase in weight. This probably improves the survival of the larvae through better swimming performance and increased ability to consume a wide size range of prey, processes which have been found to be closely related with length (e.g., BLAXTER 1962). Growth in length without a corresponding change in weight during a transitional phase was also observed in herring larvae in the Clyde area and in the central North Sea (BLAXTER 1971 and VILELA and ZIJLSTRA 1971).

The results of the analysis of the CF and RCF were also reflected in the curves describing the ratio of body height to standard body length, although annual differences were more easily detected using the CF and RCF. Morphometric weight parameters therefore seem to be more reliable measures of the condition of herring larvae than parameters based on length.

When the yolk sac reserves are completely utilized, the larva's survival is dependent upon its ability to find and capture prey. Sufficient quantities and kinds of prey organisms must be present, and the nutritive value, digestibility and size of food particles, as well as the time available for feeding, are also among the most important factors when predicting whether a particular feeding regimen will be favourable to a given species.

A gut content analysis was performed first to correlate the incidence and intensity of feeding with time of day and larval age, and to determine the prey preference of Lindaas herring larvae. Only those larvae collected during the period of active feeding were examined for feeding incidence and intensity. A feeding period of approximately 18 hours under light conditions exceeding 0.1 lux was consistent over a wide range of larval sizes, with peak feeding times at 0500–1200 hrs and 1500–2100 hrs. This agreed fairly well with the feeding period at corresponding times of the year and degrees of latitude derived from the work of BLAXTER (1966). It was also similar to those obtained by ØIESTAD (1983) on herring larvae from Lindaaspollene reared in enclosures in southern Norway and by BJØRKE (1978) from spring spawning herring larvae along the Møre coast.

Herring larvae start feeding in developmental stage 1c, at an age of 4–5 days after hatching, before the yolk sac is fully absorbed. This is consistent with the findings of BJØRKE (1978) and GAMBLE *et al.* (1981). A low proportion of herring larvae was found with gut contents during the first two weeks after hatching in Lindaaspollene (mean 19%) but increased with size to a mean of 65% in 4–7 weeks old larvae. The rather low-feeding incidence observed in larvae up to two weeks old is well known in clupeid larvae (e.g., BLAXTER 1965, BLAXTER and STAINES 1971, ROSENTHAL and HEMPEL 1970, HUNTER 1980 and CHECKLEY 1982). In cod larvae, however, mean feeding incidence at the time of first feeding was reported to be of the order of 50–60%, rising rapidly towards 100% (ELLERTSEN *et al.* 1981).

Several conflicting reasons could account for the high proportion of empty guts frequently observed in herring larvae. HAY (1981) found that netting and handling procedures prior to preservation, as well as the preservation technique itself, were responsible for much of the emptying of the guts in herring larvae. Contrarily, BLAXTER (pers. comm.) suggested that the larvae were quickly killed in towing nets, which would imply that the probability of defecation was comparatively small. In the present account, the observed values of feeding incidence are considered to reflect the *in situ* conditions of feeding herring larvae.

The diet of herring larvae at first feeding consisted primarily of copepod nauplii, copepod eggs and veliger larvae, 40–400 µm long. These observations agree with those reported on herring larvae by BLAXTER (1965) and FOSSUM (1980). Both large and small herring larvae consume small prey items, although increasing mean prey size was correlated with increasing larval size. The number and kind of prey remained steady, probably because growth of the prey animals coincided with that of the herring larvae. Provided that larger prey organisms are not significantly more difficult to capture than smaller ones, less effort would thus be required to fulfill the daily energy demands (e.g., BEYER and LAURENCE 1979).

Fore more precise evaluation of the growth and survival conditions of herring larvae, measures of the local abundance of food particles and their relative composition, together with estimates of competitors and predators, should be obtained, particularly during the period of first feeding.

ACKNOWLEDGEMENTS

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I wish to thank colleagues and students at the Departments of Fisheries Biology and Marine Biology, University of Bergen, and the Institute of Marine Research, Directorate of Fisheries, who took part in the field work, laboratory processing and discussions.

APPENDIX

Appendix table I.1. Mean egg density, standard error of mean ($\sigma_{\bar{x}}$) and total number of eggs in relation to stratum area, depth, substratum type and intensity of spawn deposition in 1977. Number of samples per stratum and sampling method (F= photo, S= substrate sampling) are also indicated for different sampling dates. *-estimated values.

YEAR	SPAWNING GROUND	STRATUM AREA (m^2)	DEPTH	SUBSTRATUM	METHOD	NO. SAMPLES	SPAWN INTENSITY	EGGS/M^2 $\times 10^3$ Mean $\pm$ $\sigma_{\bar{x}}$	$\sigma_{\bar{x}}$ Mean %	NUMBER OF EGGS $\times 10^6$
1977[1]	BJØRNØY/ GØLNA	4950	0-10	ROCKS, BOULDERS, SEAWEEDS	S	7	3	616.2 ± 184.8	30	3050.2
	"	2000	0- 6	ROCKS, BOULDERS, SEAWEEDS	S	3	3	965.1 ± 752.0	78	1930.2
	"	420	0- 6	ROCKS, BOULDERS, SEAWEEDS	S	0	2	228.2 ± 43.8		95.8 *
	"	450	0- 6	ROCKS, BOULDERS, CORALS, SEAWEEDS SAND	S	3	2	240.8 ± 43.9	18	108.4
	"	630	5- 5	SAND	S	0	1	6.9 ± 5.3		4.3 *
	BJØRNØY GØLNA	8450			S	13		614.1 ± 208.3	34	5188.9
1977[2]	"	4950	0 - 10	ROCKS, BOULDERS, SEAWEEDS	S	16	2	227.9 ± 73.5	32	1128.1
	"	2000	0- 6	ROCKS, BOULDERS, SEAWEEDS	S	17	2	151.3 ± 90.1	60	302.6
	"	420	0- 6	ROCKS, BOULDERS, SEAWEEDS	S	15	2	228.2 ± 43.8	19	95.8
	"	450	0- 6	ROCKS, BOULDERS, CORALS, SAND	S	11	2	177.4 ± 41.4	23	79.8
	"	630	5- 5	SAND	S	6	1	6.9 ± 5.3	77	4.3
	BJØRNØY GØLNA	8450			S	65		190.6 ± 48.1	25	1610.6

Appendix Table I.2. Egg data from spawning grounds in 1978. See Appendix Table I.1 for explanation.

YEAR	SPAWNING GROUND	STRATUM AREA (m^2)	DEPTH	SUBSTRATUM	METHOD	NO. SAMPLES	SPAWN INTENSITY	EGGS/M^2 $\times 10^3$ Mean $\pm$ $\sigma_{\bar{x}}$	$\frac{\sigma_{\bar{x}}}{\text{Mean}}$ %	NUMBER OF EGGS $\times 10^6$
1978	SYSLAKVÅG	30	0- 2	STEEP ROCKS	F + S	4	2	128.7 ± 46.5	36	3.9
	"	30	0- 2	ROCKS	F + S	11	2	120.1 ± 50.6	42	3.6
	"	10	0- 2	SAND, BOULDERS	S	4	1	21.7 ± 9.4	43	.2
	"	30	0- 2	ROCKS, BOULDERS	S	36	1	80.2 ± 13.4	17	2.0
	"	50	2- 2	SAND	S	4	1	19.7 ± 11.4	58	.9
	"	50	2- 2	MUD (GYTTJE)	S	3	1	1.2 ± 1.2	100	.06
	SYSLAKVÅG	200				62		53.9 ± 23.9	44	10.8
	BJØRNØY	335	0- 8	ROCKS, BOULDERS	F + S	37	2	224.1 ± 12.3	05	75.0
	"	200	0- 6	SAND, BOULDERS	S	7	1	9.6 ± 4.1	43	1.9
	BJØRNØY	535						143.7 ± 6.7	05	76.9
	GØLNA	200	0- 5	ROCKS, BOULDERS, CORALS, SEAWEEDS	S	30	2	249.1 ± 35.2	14	49.8
	TOTAL	935				136		147.1 ± 14.5	10	137.6

Appendix Table I.3. Egg data from spawning grounds in 1979. See Appendix Table I.1. for explanation.

YEAR	SPAWNING GROUND	STRATUM AREA (m^2)	DEPTH	SUBSTRATUM	METHOD	NO. SAMPLES	SPAWN INTENSITY	EGGS/M^2 $\times 10^3$ Mean $\pm$ $\sigma_{\bar{x}}$	$\frac{\sigma_{\bar{x}}}{\text{Mean}}$ %	NUMBER OF EGGS $\times 10^6$
1979	BJØRNØY/ GØLNA	950	0- 4	ROCKS, BOULDERS, SEAWEEDS, CORALS	F	25	2	321.8 $\pm$ 11.4	4	305.7
	"	150	0- 3	ROCKS, SAND (INTERFACE)	S	2	2	133.0 $\pm$ 63.7	48	200
	"	100	0- 2	ROCKS, STONES, SAND	S	1	1	61.5		6.2
	"	600	0- 3	ROCKS, STONES, CORALS	F	20	2	218.3 $\pm$ 17.2	8	131.0
	"	190	0- 3	ROCKS, SAND, SEAWEEDS	S	1	1	32.9		6.3
	"	260	0- 3	ROCKS, STONES, SEAWEEDS	S	1	1	61.5		16.0
	"	200	5	SAND	S	1	1	21.7		4.3
	"	1170	0- 3	ROCKS, STONES, CORALS, SEAWEEDS	F+S	64	2	163.7 $\pm$ 16.9	10	191.5
	"	125	0- 3	BOULDERS, SEAWEEDS	S	1	1	61.5		7.7
	BJØRNØY GØLNA	3745				116		183.9 $\pm$ 7.1	4	688.7

Appendix Table I.4. Egg data from spawning grounds in 1980. See Appendix Table I.1 for explanation.

YEAR	SPAWNING GROUND	STRATUM AREA (m^2)	DEPTH	SUBSTRATUM	METHOD	NO. SAMPLES	SPAWN INTENSITY	EGGS/M^2 $\times 10^3$ Mean $\pm$ $\sigma_{\bar{x}}$	$\frac{\sigma_{\bar{x}}}{\text{Mean}}$ %	NUMBER OF EGGS $\times 10^6$
1980	SYSLAKVÅG GRUNNAVIK	200	0- 3	ROCKS (SKERRIES) SHELLS	F	3	4	1091.2 ± 47.3	4	218.2
	"	200	0- 3	ROCKS, BOULDERS, CORALS, SHELLS	F+S	92	4	1156.1 ± 37.0	3	231.2
	"	300	2- 4	ROCKS, BOULDERS, CORALS, SHELLS	F+S	46	4	1116.2 ± 361.3	32	334.8
	"	3000	0- 7	STEEP ROCKS, SEAWEEDS	F+S	10	2	467.4 ± 35.0	7	1402.2
	"	1250	0- 8	STEEP ROCKS, SEAWEEDS	F	59	2	211.9 ± 12.5	6	264.8
	"	1430	0- 6	ROCKS, BOULDERS, SEAWEEDS	F	29	3	749.8 ± 43.9	6	1072.2
	"	900	0- 6	ROCKS, BOULDERS	F+S	2	3	567.5 ± 102.5	18	510.8
	SYSLAKVÅG GRUNNAVIK	7280				241		554.2 ± 55.1	10	4034.2

Appendix Table III.1. Standard length and dry weight in herring larvae of different developmental stages (DOYLE 1977) in Lindaaspollene during 1977–1980. Mean, standard deviation (σ_x) and range are given.

	Standard length (mm)				Dry weight (mg)			
Stage	Mean	σ_x	Range	n	Mean	σ_x	Range	n
1a	7.6	.7	5.3– 9.25	680	.096	.016	.048– .195	517
1b	8.0	.6	5.6–10.8	1851	.083	.015	.013– .189	1473
1c	9.1	1.0	5.75–12.4	1171	.097	.036	.019–	907
1d	9.3	1.5	5.0–13.0	225	.099	.041	.020– .260	197
2a	11.3	1.3	7.8 –16.2	503	.166	.062	.055– .551	459
2b	13.3	1.2	9.2 –16.7	235	.248	.072	.090– .499	227
2c	14.1	2.1	10.5 –21.6	81	.356	.189	.121– .994	68
3a	16.1	2.7	12.3 –19.5	26	.753	.343	.260–1.206	23
3b	19.3	3.0	13.4 –28.2	98	2.158	1.326	.456–6.736	90
3c	21.1	2.6	15.0 –25.0	32	2.919	1.248	.775–5.799	31

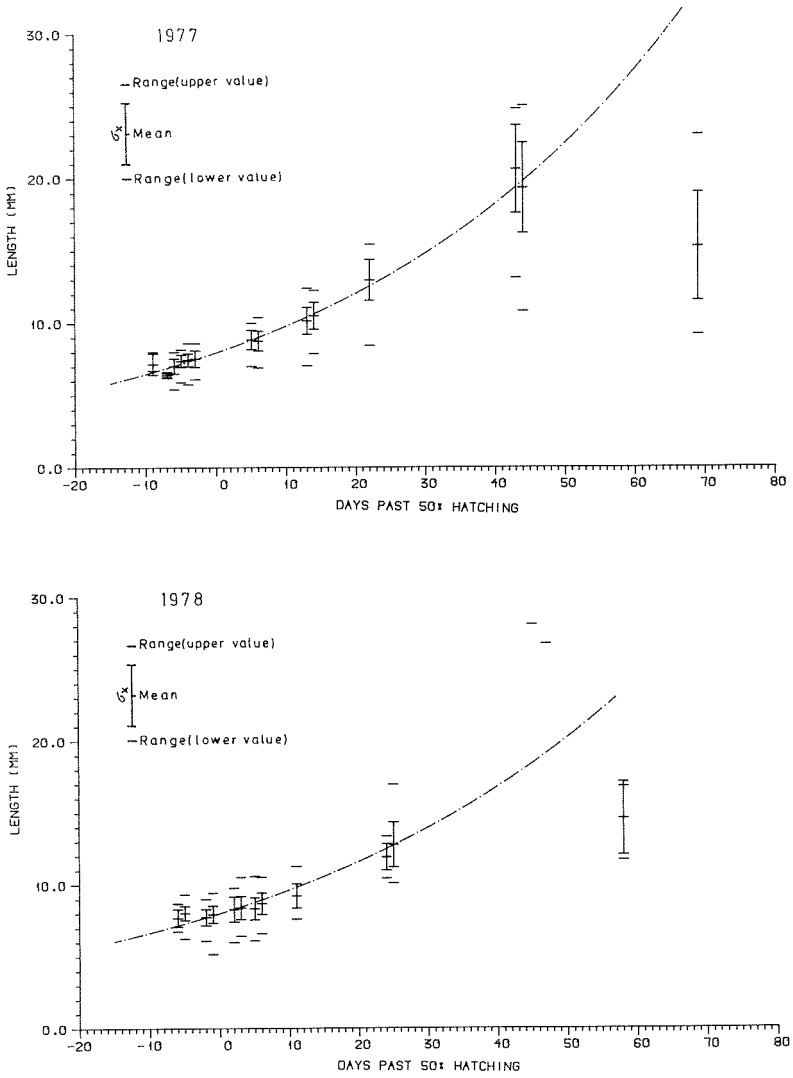

Fig. III.1. Standard body length of herring larvae in relation to age post – 50% – hatching in Lindaaspollene during 1977 and 1978. Mean, standard deviation (σ_x) and range are indicated.

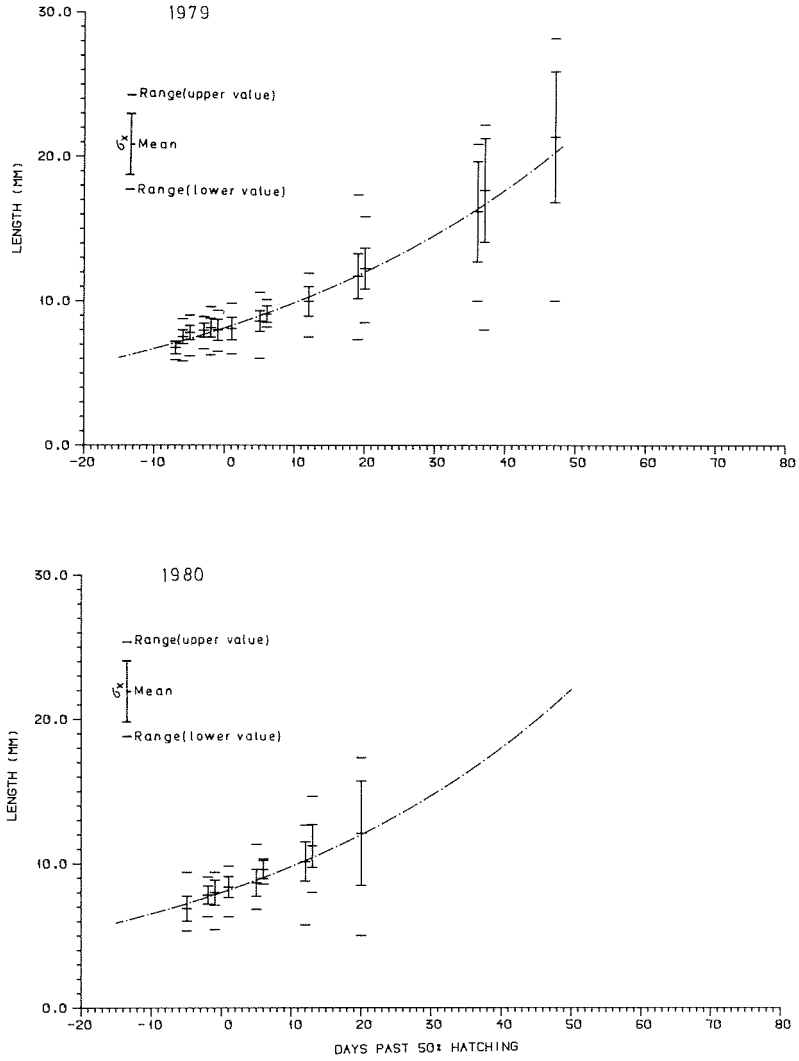

Fig. III.2. Standard body length of herring larvae in relation to age post – 50% – hatching in Lindaaspollene during 1979 and 1980. Mean, standard deviation (σ_x) and range are indicated.

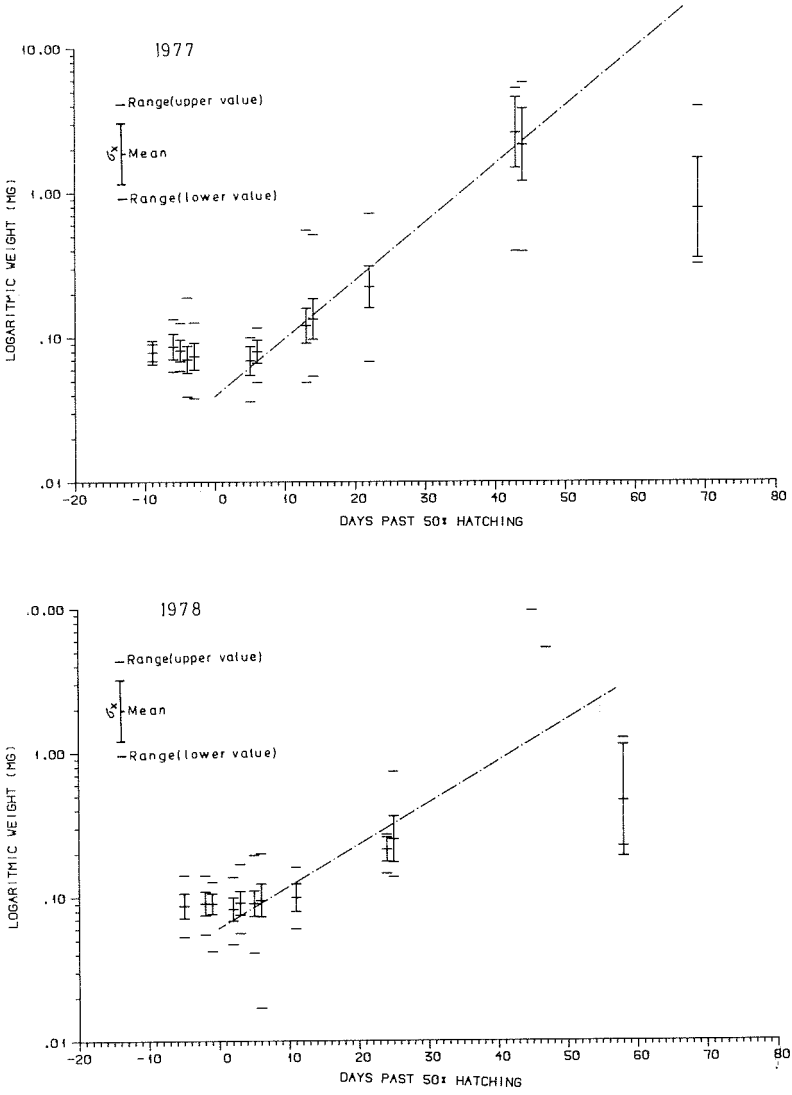

Fig. III.3. Dry weight of herring larvae in relation to age post – 50% – hatching in Lindaaspollene during 1977 and 1980. Mean, standard deviation (σ_x) and range are indicated.

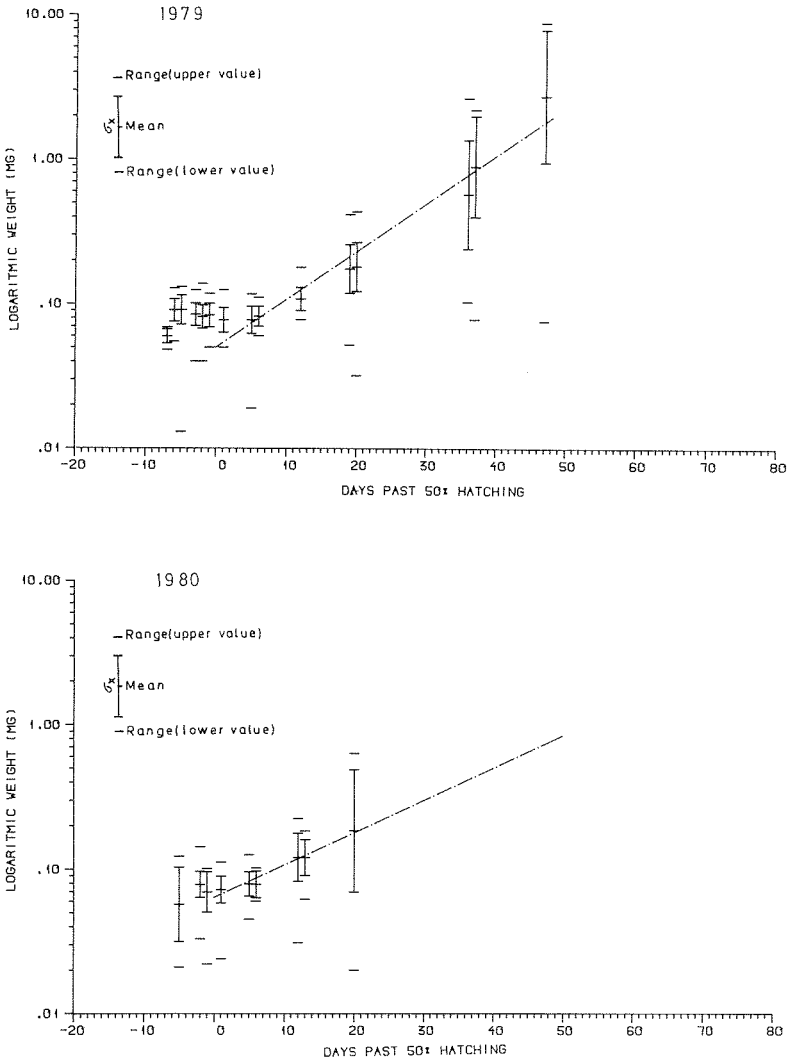

Fig. III.4. Dry weight of herring larvae in relation to age post – 50% – hatching in Lindaaspollene during 1979 and 1980. Mean, standard deviation (σ_x) and range are indicated.

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