

Studies of a larval herring (*Clupea harengus* L.) patch in the Buchan area.

II. Growth, mortality and drift of larvae

Peter Munk

The Danish Institute for Fisheries and Marine Research,
Charlottenlund Palace, Dk-2920 Charlottenlund, Denmark

Villy Christensen & Helge Paulsen

The Danish Institute for Fisheries and Marine Research,
The North Sea Centre, P.O. Box 101, Dk-9850 Hirtshals, Denmark

Abstract

A patch of herring larvae in the Buchan area was surveyed three times in 1983 and 1984. Larval abundance in both years was in the order of 10^{12} larvae. The patch obviously consisted of distinct cohorts of larvae. Cohorts were separated by use of a length frequency analysis and mean lengths and distributions were calculated. The growth rate of small larvae (~ 9 mm long) was about $0.14 \text{ mm} \cdot \text{d}^{-1}$ whereas larger larvae grew between 0.17 and $0.26 \text{ mm} \cdot \text{d}^{-1}$. The horizontal distribution of larval cohorts was interpreted as the result of a simple diffusion process and a two dimensional Gauss distribution was fitted to data. Larval dispersion and drift are described based on calculations on the cohort of intermediate sized larvae found in 1984. The mortality of these larvae was on the order of $8\% \cdot \text{d}^{-1}$. The limitations and possibilities in the used methods are discussed.

Introduction

The spawning grounds of the autumn/winter spawning North Sea herring are well described and yearly records of the distribution of herring larvae are maintained through the annual International Herring Larval Surveys (e.g. Saville & Rankine 1985). A major part of the spawning takes place in the north-westerly part of the North Sea whereas the major nursery grounds of the juveniles are found to the south. Thus, during the winter period herring larvae must cover a significant distance in order to reach the nursery areas. Larval drift has, traditionally, been interpreted as a simple passive process but attention has increased on the complexity of transport processes and of the potentially active influence larvae may have on their drift patterns by migrating vertically in the water column (e.g. Iles & Sochasky 1985). The drift process determines which environment the larvae have to cope with at each given stage of development and has, thereby, a significant influence on larval survival.

An investigation of the growth and survival of herring larvae, therefore, must take a number of important environmental factors (hydrography, prey production, etc.) into account.

The work described here is part of a multidisciplinary research project focusing on herring larvae from the 'Buchan stock'. The hydrography (Richardson *et al.* 1986a), primary productivity (Richardson *et al.* 1986b) and secondary productivi-

ty (Kjørboe & Johansen 1986) of the Buchan area during the 1984 study period are described elsewhere. In this paper, material based on sampling of herring larvae in the area is presented. The aim is to describe the distribution, abundance and drift of herring larvae in the area, with the ultimate purpose of relating these findings to hydrographic and biological events. A further aim is to present estimates of growth and mortality rates of herring larvae during their first weeks of life.

Materials and methods

Cruises were conducted with the R/V *Dana* from 20-29 September, 1983 and from 16-29 September, 1984.

Sampling of herring larvae was performed by the standard procedure of the ICES coordinated International Larval Surveys. The GULF III high speed plankton sampler (250 μm mesh size) was equipped with a CTD, an echo-sounder and an electronic flowmeter. All instruments transmitted through a cable to give on-deck readings during the haul. The sampler was towed double obliquely at 5 knots to within 5 meters of the bottom and was continuously lowered/raised approximately 10 meters per 1½ minutes.

Samples were preserved in buffered 4% formaldehyde. Herring larvae were counted and total lengths were measured to the nearest millimeter.

The numbers in each sample were converted to numbers per sq. meter using the method adopted in the IHLS-programme.

The area was surveyed twice in 1983 (20-21 and 26-28 September) and three times in 1984 (16-19, 20-21 and 27-29 September). In addition to the data collected by the R/V *Dana*, stations in the area were sampled by the Scottish R/V *Clupea* taking part in the International Herring Larval Survey Programme. Based on these data a third survey of the area (13-14 September) was included in the 1983 study.

In order to optimize the sampling strategy, subsamples were immediately worked up after each haul and estimates of larval abundance made. From these estimates, the direction and intensity of sampling could be established (between station distances of 3.5, 5 or 10 nautical miles were used).

Calculation of growth rates

Separation of Gauss distributions from the summed length frequency data from each period was made using a least-square fit to the equation:

$$\begin{aligned}
 F &= N_1 \cdot \exp(-(x - \mu_1)^2/2/\sigma_1^2)/\sqrt{2\pi\sigma_1^2} \\
 &+ N_2 \cdot \exp(-(x - \mu_2)^2/2/\sigma_2^2)/\sqrt{2\pi\sigma_2^2} \\
 &+ N_3 \cdot \exp(-(x - \mu_3)^2/2/\sigma_3^2)/\sqrt{2\pi\sigma_3^2}
 \end{aligned}
 \tag{1}$$

F = number of larvae in length group

N_1 , N_2 and N_3 = abundance in groups

x = length group

μ_1 , μ_2 and μ_3 = mean length of groups

σ_1^2 , σ_2^2 and σ_3^2 = variance of groups.

Calculation of mortality rates

A two-dimensional Gauss distribution was fitted to data of the distribution of each of the larval groups separated by the length frequency analysis. Least square fit was made to the equation:

$$\text{No} = A \cdot \exp(-((x - \mu_1)^2/\sigma_1^2 - 2\rho((x - \mu_1)(y - \mu_2))/\sigma_1/\sigma_2 + (y - \mu_2)^2/\sigma_2^2)/(1 - \rho^2)/2)/(2\pi\sqrt{\sigma_1^2\sigma_2^2(1 - \rho^2)}) \quad (2)$$

No = number of larvae, per area, in observation

A = total abundance of larvae

x and y = coordinates of observation

μ_1 and μ_2 = coordinates to ellipse centre

σ_1^2 and σ_2^2 = variances of ellipse

ρ = correlation coefficient.

Calculation of dispersion

Transformed data of variance from equation 2 were used in the calculation of lateral diffusion coefficients from:

$$K = \sigma^2/2t \quad (3)$$

t = time since start of diffusion

σ^2 = variance at time t

and of shear from:

$$\text{Shear} = ((3\sigma_a^2/\sigma_b^2)^{0.5})/t \quad (4)$$

t = time since start of diffusion

σ_a^2 = variance along longest axis of ellipse

σ_b^2 = variance along shortest axis of ellipse.

Linear regressions

The program GLM from 'Statistical Analysis System' (SAS Institute Inc., North Carolina) was used. In linear regressions data were weighted by reciprocal variances.

Results*Sampling of herring larvae in the area*

The survey covered approximately 1000 km² in 1983 and 1600 km² in 1984. Due to limited sampling time, the complete extension of larval distribution was not determined. However, peak concentrations were identified and surveyed. In Fig 1a-f the sampling grid and the estimated numbers per square meter are shown for the three periods in each year. Eye fitted isolines are drawn to illustrate the changes in distribution patterns during the periods of investigation. The two geographically

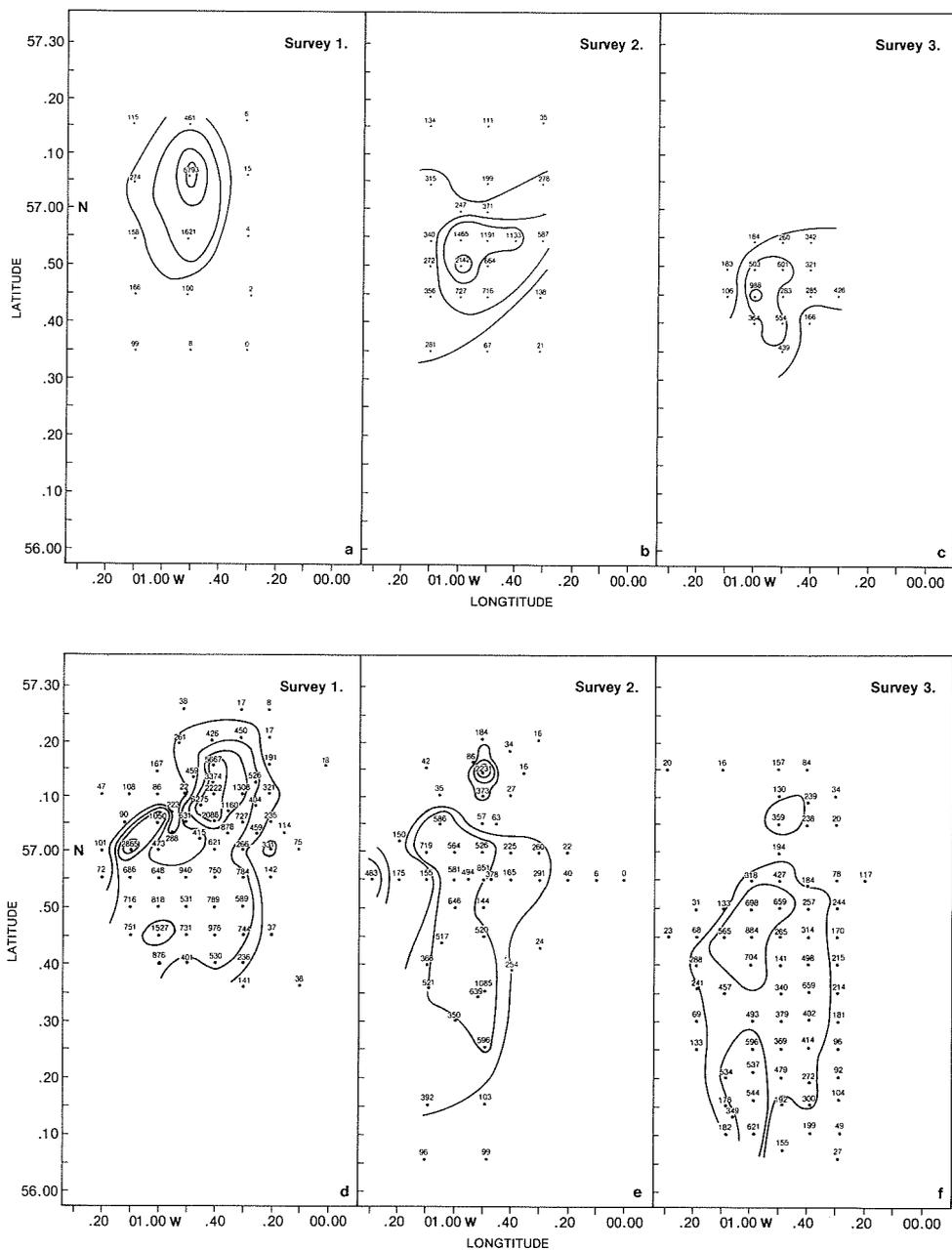


Fig. 1. a-c, 1983. d-f, 1984. Distribution of larval herring (*Clupea harengus* L.) in the Buchan area, surveyed in three periods. Numbers refer to number of larvae \cdot m $^{-2}$ at the given sampling position, and eyefitted isolines representing 250, 500, 1000 and 2000 larvae \cdot m $^{-2}$ are drawn on the figure.

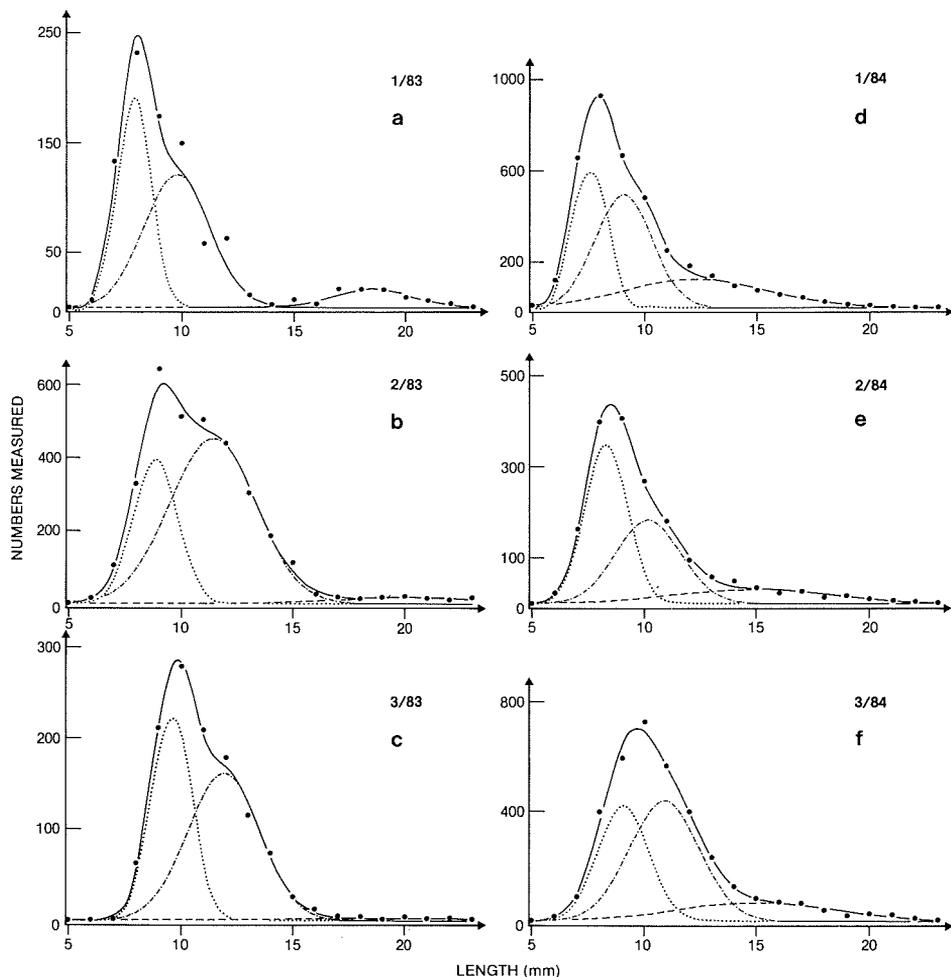


Fig. 2. a-f. Length frequency of larval herring (*Clupea harengus* L.) representing all length measurements for each year and period. The fitted curve calculated by length frequency analysis is drawn together with the estimated curves for larval cohorts.

distinct areas with relatively high larval abundances in 1984 indicate the existence of separate cohorts of larvae.

If successive cohorts have emerged at distinct time intervals, the samples would consist of groups of different ages and with different mean lengths. Thus, the length frequency distribution of the sampled larvae would be expected to show some degree of polymodality. In order to analyse the present data for the existence of separate cohorts, all length data from each survey period were pooled and length distributions representing the total catch have been produced. The numbers of larvae in each mm-length group are shown in Fig. 2a-f. Clear polymodality is seen in only a few cases. However, in most of the distributions, the presence of several superimposed distributions is apparent.

Table 1. Larval herring (*Clupea harengus* L.). Estimated mean length, growth rate and abundance of cohorts of larvae.

Year class, year	Co- hort no.	Period, day/ month	Mean length, mm	95 % conf. int. of mean l., mm		Var.* of cohort, mm ²	Growth rate, mean SE mm/d mm/d		Abun- dance, n·10 ¹¹	95 % conf. int. of abundance, n·10 ¹¹	
				mm	mm		mm/d	mm/d		n·10 ¹¹	n·10 ¹¹
1983	1	13-14/9	7.9	7.2	8.5	0.5			—	—	—
1983	1	20-22/9	8.9	8.6	9.1	0.9	0.13	0.005	—	—	—
1983	1	26-28/9	9.6	9.4	9.8	0.8			5.2	0.9	10.2
1983	2	13-14/9	9.8	8.7	10.9	2.1			4.6	2.4	6.8
1983	2	20-22/9	11.4	10.9	11.9	3.7	0.14	0.049	—	—	—
1983	2	26-28/9	11.9	11.4	12.4	2.6			—	—	—
1983	3	13-14/9	18.5	17.5	19.5	2.9			—	—	—
1983	3	20-22/9	20.3	17.4	23.3	11.4	0.25	—	—	—	—
1983	3	26-28/9	—	—	—	—			—	—	—
1984	1	16-19/9	7.5	7.4	7.7	0.6			4.3	0.4	8.2
1984	1	20-21/9	8.3	8.0	8.6	0.9	0.14	0.003	4.6	0.2	8.9
1984	1	27-29/9	9.1	8.2	9.9	1.3			6.9	5.0	8.8
1984	2	16-19/9	9.1	8.5	9.6	1.6			16.0	0.1	31.5
1984	2	20-21/9	10.2	9.4	10.9	2.1	0.17	0.018	9.3	6.8	11.8
1984	2	27-29/9	10.9	9.6	12.2	2.4			6.1	4.8	7.5
1984	3	16-19/9	12.2	11.2	13.2	10.0			3.9	2.2	5.6
1984	3	20-21/9	14.7	13.0	16.3	11.9	0.26	0.015	—	—	—
1984	3	27-29/9	14.9	13.1	16.8	11.9			—	—	—

—: could not be estimated. *: parameters in eq. 1.

As an approximation, we assume the length distribution of a larval group hatched in a relatively short period of time to be Gaussian distributed. Based on visual interpretation of the total length distributions, we assume the existence of three cohorts (1, 2 and 3) in the area and have analysed the length data as described above (eq. 1). The parameters of the least square fit are given in Table 1. These parameters were used to draw the fitted curve and curves for each cohort in Fig. 2a-f.

The indication of the existence of larval cohorts has implications in the interpretation of horizontal distribution of larvae as well as in the estimation of larval growth and survival.

Horizontal distribution of larval cohorts

As the cohorts of larvae are generated in different time periods, it may be expected that their horizontal distributions will differ (cf. Fig. 1). Using information from the length-frequency analyses, the individual samples were separated into their component proportions of each of the three cohorts. We assume that the mean length and variance of cohorts in each sample is the same as for the complete material in that period and calculate numbers of larvae per square meter for each cohort at each station.

In 1984, the high larvae concentrations in the northern region of the study area consist exclusively of larvae from cohort 1 (smallest larvae) whereas the major

component in the samples from the southern region is from cohort 2. The position of this cohort is illustrated in Fig. 3 a-c. Cohort 3 is dispersed over the area without any apparently significant center. The two significant cohorts found in 1983 were more mixed and not as clearly identifiable in the horizontal plane as the cohorts in 1984. The 1983 cohort consisting of the largest larvae was widely dispersed over the study area with highest abundances occurring in the northern part of the survey area.

By considering cohorts of larvae, that are assumed to have hatched in a limited area and over a relatively short time period, larval dispersion and, thereby, larval distribution can be analysed in relation to dispersion models.

Here, we consider only the most simple dispersion model. Thus, we assume that larvae behave as passive particles and that each cohort is generated at a single point at a fixed time. Horizontal homogeneity and vertical isotropy are also assumed. Given these assumptions, eddy diffusivity and shear due to tidal currents will result in dispersion that typically follows a Gaussian distribution along any axis through the centre (Nihoul 1975b). The shear effect results in enhanced dispersion in the direction of maximal tidal velocity. Thus, the Gaussian distribution will be elliptical. In an arbitrary coordinate system, the distribution of larvae can then be described by the total population, the ellipse centre, the variances of the two axes and the correlation coefficient (see eq. 2).

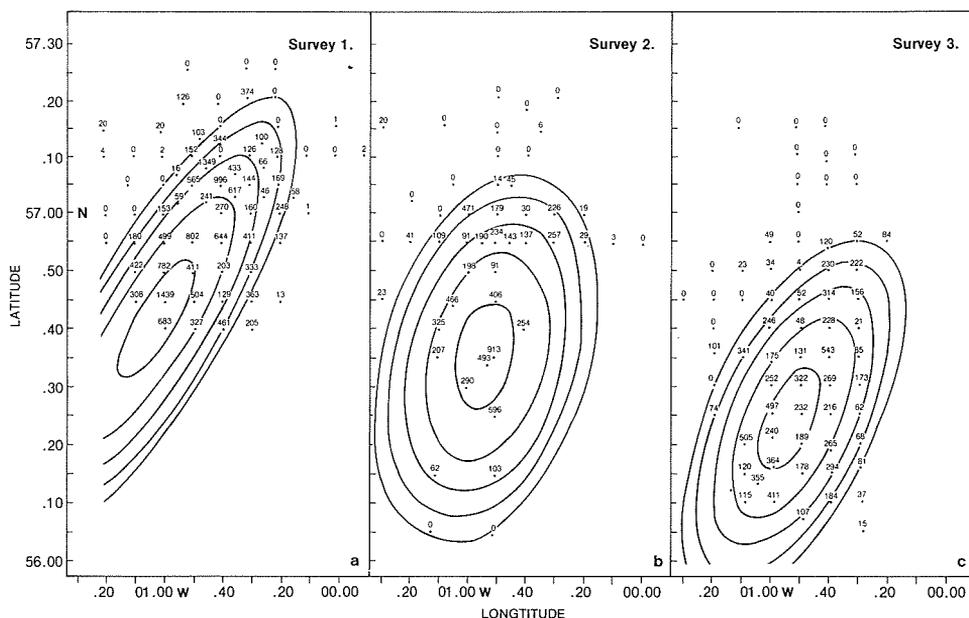


Fig. 3. a-c, 1984. Calculated distribution of the cohort of intermediate sized herring (*Clupea harengus* L.) larvae, surveyed in three periods. Numbers refer to the calculated number of larvae $\cdot m^{-2}$ at each sampling position. The estimated Gauss distribution is shown for each period by a series of ellipses. Isolines represent different larval densities.

The parameters of a Gaussian distribution are calculated according to eq. 2 using the distribution data for each cohort. In several cases it was not possible to make a reasonable regression. Abundance estimations are shown in Table 1 and the calculated Gauss distributions are drawn for cohort 2 for all three investigation periods (Fig. 3).

The procedures outlined above can then be used to calculate growth and mortality as well as dispersion and drift of larvae from separate cohorts.

Larval growth

Assuming linear growth in length, a linear regression relating mean length to the midpoint of the investigation period for each survey is made. In the regression, each length estimate is weighted with the reciprocal of its estimated variance. Growth estimates are given in Table 1. Growth rates are about $0.14 \text{ mm} \cdot \text{d}^{-1}$ for small larvae and increase to about $0.25 \text{ mm} \cdot \text{d}^{-1}$ for the larger larvae. Due to the short investigation period and the few observations made, confidence limits on the estimates are broad.

Larval mortality

The finding of concentrations of small larvae with yolk sac remains during survey 2 in 1984 suggests that new larvae had recently been introduced to the patch. Thus, cohort 1 was probably supplied with larvae during the study period and the abundance estimates for this cohort cannot be used in mortality estimates.

This leaves only data from cohort 2 (1984) for the calculation of mortality. Larval abundance is assumed to decline exponentially with time and a linear regression was made between the logarithm of abundance and midpoints of survey periods. The abundance values are weighted according to the reciprocal of the variance of the mean.

A specific mortality rate of $0.08 \cdot \text{d}^{-1}$ (standard error 0.003) is then estimated for this group of 9-11 mm long larvae.

Larval dispersion

The parameters of the Gauss distribution can be used to express some characteristics of larval dispersion. In the theory of diffusion, flux is proportional to the gradient of concentration and this proportionality is expressed by the diffusion coefficient. In the case of a Gauss distribution, the diffusion coefficient is given by eq. 3. Data from cohort 2 in 1984 are used and variances along the orthogonal axes of the ellipse are found from eq. 2. Mean values of variances from the three surveys have been determined ($8.1 \times 10^8 \text{ m}^2$ along the longest axis and $1.3 \times 10^8 \text{ m}^2$ along the shorter). Time since the hatching of larvae (i.e. release of substance) is calculated to 22 days by using a mean growth rate of $0.15 \text{ mm} \cdot \text{d}^{-1}$ and a growth in length from 6.7 mm (length at hatching) to 10.0 mm (length at intermediate survey). From eq. 3, we then calculate the diffusion coefficient along the longest axis to $213 \text{ m}^2 \cdot \text{s}^{-1}$ and the one along the shorter axis to $34 \text{ m}^2 \cdot \text{s}^{-1}$.

The diffusion coefficient can be used to assess the decline in abundance at center due to larval dispersion. Variances at a given period after hatching are found from

eq. 3 and from the equation of an ellipse with center in (0,0) the change in abundance due to changes in variances can be found. For a day in the middle of the investigation period we estimate dispersion of larvae to account for about 8% of the decline in the center of cohort 1 and for about 4% in the center of cohort 2.

The elongation of the patch caused by the tidal currents takes place along an axis south-southwest (cohort 2, 1984). Shear is calculated to $2.3 \times 10^6 \cdot s^{-1}$.

Larval drift

Larval drift measured as speed and direction of their net movement is found from the center-movement of cohort 2 (1984). From this, a speed of 3.4 km per day in the direction south-southeast is estimated.

Larval drift can be expressed as distance covered per increment of larval length from a calculation which is independent of cohort separation. If larvae originate from the same spawning ground and their drift speed and growth rate are constant, we would expect larval size to increase linearly along a line from the spawning ground in the direction of the drift and to find equal sized larvae at the same geographical position irrespective of the time of sampling. Nothing is said about the numbers of larvae along the line, thus this does not contradict the hypothesis concerning the existence of a number of cohorts.

Calculations have been made taking series of samples running north-south through the concentration centers in the total distribution of larvae in 1984. For each survey period, the mean length of larvae is regressed against the distance from an arbitrary point, zero. The difference between the linear regressions from each survey is insignificant ($p > 0.1$) and data are pooled. Data are fairly well described by the linear regression ($n = 27$, $r^2 = 0.82$). Thus, the assumptions of linearity and equal sized larvae at similar geographic positions in every survey period seem reasonable. Drift speed is calculated to $30 \text{ km} \cdot \text{mm}^{-1}$. With a growth rate of $0.15 \text{ mm} \cdot \text{d}^{-1}$ this equals to $4.4 \text{ km} \cdot \text{d}^{-1}$.

The regression could be used to 'back calculate' to the position of hatching, i.e. the spawning ground. A hatching length of 6.7 mm is used, and the latitudes of emergence of these larvae are predicted to be 57.25 N. This is in accordance with our observation of very high densities of small larvae ($6000 \text{ larvae} \cdot \text{m}^{-2}$) at 57.15 N, 00.40 W on survey 1 in 1984.

Discussion

Spawning grounds

The Buchan area is a well-known spawning site for herring and high abundances of larvae have been recorded here since 1951 (Saville 1971). However, the extent of spawning has varied during this period. In the fifties, these spawning grounds were considered to be the largest in the North Sea but, from the early sixties, their importance started to decline while spawning on grounds in the Orkney-Shetland area became increasingly important. The Buchan area remained relatively unimportant through the seventies and the observation of significant numbers of

larvae reported here indicates a recovery of these spawning grounds. Preliminary results from surveys in 1985 indicate that spawning in the area has increased even further.

In 1965 and 1967 Hempel & Schnack (1971) investigated patches of herring larvae with extensions resembling the ones found in 1983 and 1984. Comparisons of distribution centers and larval sizes reveal that spawning places and spawning times have not changed significantly during the intervening period.

Larval cohorts

In Hempel & Schnack's 1965 investigation, pronounced polymodality in the length distribution of larvae was found and they suggested that spawning had taken place in two 'waves' separated in time.

Polymodality of size distributions in samples of herring larvae has also been reported elsewhere (e.g. Townsend & Graham 1981, Henderson *et al.* 1984) and special attention has recently been given to the ecological cause of this phenomenon (Ware & Henriksen 1978, Lambert & Ware 1984).

Lambert (1984) hypothesized that discrete spawning is a part of the reproductive strategy of herring. He applied the concept of 'feeding range' (Jones & Hall 1974), which refers to the size range of food organisms that can be eaten by a predator of a given size. The spacing between cohorts should tend to minimize intraspecific competition by allowing each cohort a virtually independent food supply.

When interpreting data of the type presented here, the existence of cohorts must be taken into account. Mean length estimates, for example, can be significantly biased when cohorts are not separated (see example in Nichols *et al.* 1985) and the distribution of larvae is easier interpreted when the distribution of cohorts is identified. A series of assumptions were made when interpreting larval distribution according to theory of diffusion. A brief discussion of these will be given in the following.

Larval dispersion

In the interpretation of larval dispersion, the most simple process was assumed. This was based on three main assumptions: point release of larvae (in time and space), horizontal homogeneity and vertical isotropy.

The assumption of discreteness of spawning and subsequent hatching in time and space are supported by a number of investigations on herring spawn: Aneer *et al.* (1983) observed the spawning behaviour of herring in a Swedish fjord and found that the entire spawning stock released their gametes in one day and over a relatively small area. Dempsey & Bamber (1983) were able to define the spawning grounds of herring in the Blackwater Estuary, Essex. They found herring eggs from two spawnings, a week apart, and separated in two distinct patches. The period of hatching from natural spawn is probably fairly short. Hourston *et al.* (1981) investigated hatching from natural spawn and, at 8°C, the major part (60-90%) of the larvae were released over a period of 2-3 days. When taking into account that we found relatively small areas with very high numbers of larvae, the assumption of discreteness of larval release in time and space seems reasonable.

Horizontal homogeneity implies that the watermasses in which larvae are dispersed do not differ in characteristics. As described by Richardson *et al.* (1986a) this is certainly not the case in the Buchan area. On the contrary, larvae are situated at the border (in a thermal front) between two different water masses; one mixed with respect to temperature and the other exhibiting a thermally stratified water column.

As a consequence of horizontal homogeneity, the diffusion coefficient is assumed to be constant. However, it will to some degree depend on the scale of mixing (Nihoul 1975a).

Concerning vertical isotropy, Nihoul (1975b) reported that turbulence in stratified water columns is highly intermittent and sporadic and that complete isotropy may not be expected for vertical scales larger than a few meters. Munk *et al.* (in prep.) investigated the vertical distribution of larvae in the area and found the main part of larvae in the size range 7-9 mm to be confined to a water layer between 10 and 30 meters, i.e. above the thermocline (see Richardson *et al.* 1986a). Thus, the negligence of the vertical component in the model of diffusion may be justified in the case of small larvae. It may, however, not be so for larger larvae which show vertical migrations throughout the water column (Munk *et al.*, in prep.). The vertical component will probably increase in importance with the size of the larvae, i.e. larvae may begin as they grow to acquire an active influence on their dispersion/drift. This possible 'active' dispersion has been shown by investigators working in estuaries (Graham 1972, Fortier & Leggett 1982). Iles & Sinclair (1985) suggest, in a discussion of herring larval distributions off the Yorkshire coast, that active behaviour (i.e. vertical migration) of herring larvae in that region could explain the distributional patterns observed.

Thus, we may expect the hydrographic and biological processes that lie behind the observed distribution of larval cohorts to be more complex than we acknowledge in the present interpretation of data.

Heath & MachLachlan (1985) have also interpreted the dispersion of a patch of herring larvae in relation to theories of diffusion. They found that their data on the distribution of newly hatched larvae were fairly well described by a Gaussian distribution and give estimates on lateral diffusion coefficients and current shear that are in the same order as those found in the present studies.

We made two independent estimates of drift of larvae in the area in 1984; one to be based on the movement of the centres of the cohorts and one on the observed increase in larval mean length to the south. There is a reasonable agreement between the two estimates (3.4 and 4.4 km per day). Drift speeds of larval herring patches of 2-3 km per day (Wright & Lough (1979), Georges Bank), 2.8 km per day (Heath & MachLachlan (1985), west of Scotland) and 3.8 km per day (Nichols *et al.* (1985), off Whitby) have been reported. The area off Whitby is close to the Buchan area and measurements are made in the same time period as in the present study.

Current shear and, consequently, tidal currents are estimated to be directed south-southwest. Net movement of the cohort of 9-11 mm larvae was in the direction south-southeast. The larval cohorts appeared to move along the thermal

front in the period of investigation (see Richardson *et al.* 1986a). Whether this is based on some sort of retention mechanism (cf. Iles & Sinclair 1982) cannot yet be evaluated. Interestingly, larvae appear to be concentrated passively or actively in the area with highest copepod production rates (Kiørboe & Johansen 1986).

Larval growth

Estimates of growth rate of herring larvae in the field range from 0.05 to 0.5 mm · d⁻¹ (see f.ex. review in McGurk 1984). In some cases, growth estimates are based on age determination of larvae by use of otolith analysis (e.g. Townsend & Graham 1981, Graham *et al.* 1984). However, for the most part they are based on an estimation of change in larval mean length through time (e.g. Briemann 1983). The interpretation of length distributions of larvae is important when defining a larval mean length. For example, if cohorts are combined in the calculation of a mean larval size, significant bias can result. Nichols *et al.* (1985) found unrealistically low growth (0.1 mm per day) when using mean length from total abundances of larvae. However, when using a method based on cohort analysis, they reach figures in the range 0.15-0.24 mm per day.

Some investigations reveal that growth rate could change significantly with larval age (e.g. Henderson *et al.* 1984). However, the investigations are made over fairly long periods in which neither temperature nor food concentration can be expected to be constant.

Thus, the age-component in larval growth rate changes is difficult to deduce. In this respect, measurements made on individual cohorts growing in the same area at the same time is a valuable tool for evaluating the age component in larval growth rate. Our findings of approximately a doubling in growth in length from 8 mm larvae to 15 mm larvae emphasize the importance of that factor.

Kiørboe & Munk (1986) have related growth estimates for small larvae (8 to 10 mm) to ambient food concentration. They found that part of the difference between estimates could be explained by differences in food concentration. The measured food concentration in the Buchan area in 1984 (Kiørboe & Johansen 1986) and the present estimate of growth rate of small larvae are in agreement with their findings, and it would appear that food supply limited larval growth rate.

Larval abundance and mortality

The confidence intervals for the abundance estimates are broad and, in some cases, a regression was not possible (Table 1). estimates indicate, however, that cohort sizes in both years were of the same order of magnitude.

The time series of abundance estimates for cohort 2 in 1984 has been used to calculate the mortality rate of these larvae over the study period. We found a mortality of 8% · d⁻¹ with a 95% confidence interval ranging from 4.5% to 11.5% · d⁻¹.

Mortality estimates in the literature range from 1 to 40% · d⁻¹ (McGurk 1984). Many of the estimates made are based on assumptions concerning larval dispersion. Graham & Chenoweth (1973) estimated the mortality of newly hatched larvae

with the assumption that the input from new hatchings and the decline in numbers at a station due to dispersion counter-balanced each other. They considered the estimate of $29\% \cdot d^{-1}$ to be maximal. Das (1968) assumed that dispersion was reduced due to the relative isolation of the area of investigation (Bay of Fundy) and arrived at a mortality figure of $8.5\% \cdot d^{-1}$. Dragesund & Nakken (1971) found from drogue-movement that drift and dispersion were negligible and, from data on larval growth, he calculated a mortality of $37\% \cdot d^{-1}$. Other methods of calculating mortality are based on contouring larval patches (e.g. Dragesund & Nakken 1973). In these cases, a good bit of personal interpretation is necessary and the methods suffer from difficulties in defining the boundary conditions.

Thus, although models relating to dispersion and drift suffer from simplification, we believe that such models are crucial to the interpretation of larval mortality rates.

In the last few years, several programs for the investigation of larval herring patches have been started up and valuable information pertaining to the early life of herring larvae is already accumulating.

In the present investigation, we have attempted to use different methods to deduce some of the underlying processes taking place in the larval patch and to validate simple hypotheses. With the new information being collected the employed methods and the estimates given are being re-evaluated with the hope that further refinement can take place.

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