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Andreas BUSCH; Nils JÖNSSON; Thomas LORENZ; Andreas SUCHAU; Anke HOLST

Mortality in successive cohorts of young baltic herring larvae

Abstract

Successive cohorts of larvae of Ruegen spring herring (*Clupea harengus* L.) were reared from naturally fertilized eggs to examine the mortality during the first 4 weeks of their life. The experimental conditions were similar to those measured in nature (Greifswalder Bodden). Mortality rates were measured as a percentage of the larval numbers present in the tank on the previous day. From hatching to the first feeding (early season larvae: age 5-9 d; late season larvae: age 4-7 d), only ca. 6.2 % of the starting population of all cohorts had died. 50 % of the starting population had died up to the time point of yolk exhaustion (early season larvae: age 14-16 d; late season larvae: age 8-14 d), although 60 to 90 % of all larvae had already fed additionally on external food up to this time and the food density was maintained at a density of more than 200 organisms l^{-1} (mixed natural zooplankton). Mortality rates amounted to 2 to 3 % d^{-1} from hatching up to the time of yolk exhaustion. During 2 to 6 days after the yolk exhaustion, higher mortality rates (ca. 10 to 40 % d^{-1}) were established for all cohorts. Afterwards, for early and late cohorts which used their yolk at temperatures < 16 °C, mortality rates decreased again (ca. 2 to 20 % d^{-1}). Ca. 3 % of the starting population of early and late cohorts were still alive after ca. 4 weeks. In contrast if larvae had used their yolk at temperatures above 16°C, all larvae had died with mortality rates of 20 to 60 % d^{-1} during a short period of 12 days. The results show that the mortality during the early larval life cannot be controlled only by external food supply. The role of internal yolk supply and the yolk use effectiveness is discussed.

Key words: Herring larvae, Mortality, Yolk supply, Yolk use efficiency, First feeding

Introduction

The variability in recruitment of marine fish stocks due to changing environmental conditions is of great importance with regard to economy and ecology. The initial search for an unifying theory of causal mechanisms determining recruitment variability centered around the critical feeding period proposed by HJORT (1914). Hjorts

concept maintains that larval survival and hence recruitment are primarily determined by food limitation in the early larval stage, i.e. during the transition from yolk sac to actively feeding larvae. This hypothesis has been modified and developed by a number of workers. The resulting hypotheses are summarized and discussed by ANDERSON (1988). He suggested to use a hypothesis, which includes temperature effects on growth and handles starvation and predation as important sources influencing the mortality. This so-called "growth-mortality hypothesis" is a reasonable framework for future studies dealing with the determination of the year-class size.

Since herring spawn according to the age composition of the population, in several batches at different times - older and bigger fishes spawn first, younger and smaller fishes later (BIESTER et al. 1978, LAMBERT 1987), the entire spawning period must be considered, when estimating the recruitment success of a fish stock. However, earlier studies have utilised laboratory experiments or short-term field experiments on one cohort or on only a small number of cohorts. The small number of cohorts represented no chronological order within a spawning period, but were composed of groups of larvae coming from different locations (see ROSENTHAL & HEMPEL 1970, KIØRBOE et al. 1985, RAID 1985, KLINKHARDT 1986, YIN & BLAXTER 1987 a, b, PEDERSEN et al. 1987, 1990).

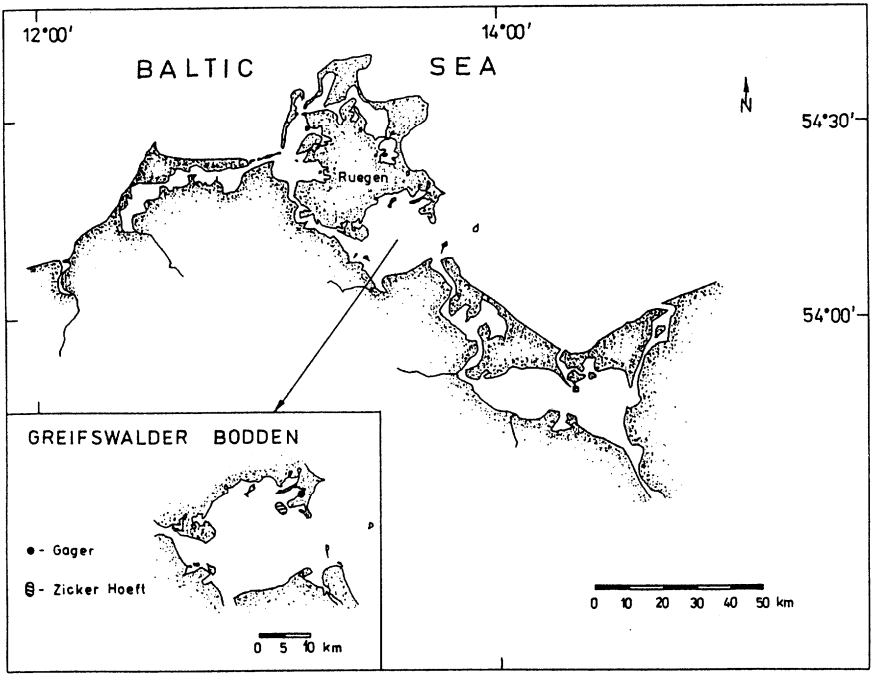

Fig. 1 Study area. Herring eggs were collected at Zicker Hoeft - a main spawning location.

In contrast to previous work this study highlights the seasonal aspect. Thus, we investigated growth and mortality of different herring larvae (*Clupea harengus* L.) cohorts at increasing temperatures during a spawning season. We concentrated on yolk nutrition and demonstrated that survival chances are mainly determined in the period before external feeding starts, namely by the yolk content of the larvae and the temperature-regulated efficiency of yolk use.

Material and methods

Larval rearing and survival

The investigations were performed between the months of February and June, 1990 to 1992, at the field station Gager on the Greifswalder Bodden (Fig. 1). Naturally fertilized eggs were used to ensure that larvae came from a large amount of females and males, and incorporated a wide range of the genetic material of the stock (see ANEER et al. 1983). Spawn was collected by divers 5 days before the hatching of the larvae, and was transferred to 55-l aquarium tanks. The tanks were fitted with an internal filter (FLÜCHTER 1964) with a turnover rate for 1 tank of 79 minutes. After hatching, larvae were subsequently placed in 140-l circular black tanks. The tanks were aerated indirectly via an external filter (turnover rate was 1 tank in 1.4 days). The stocking density was 6 to 14 larvae l^{-1}. The rearing conditions for each cohort of larvae (Table 1) were similar to those in the sea. The difference between the maintenance temperature and the temperature in the sea was 0.5 ± 1.5 °C and not significant (n = 18, α = 5 %). The salinity in the tanks was identical to that

Table 1 *Clupea harengus* larvae. Incubation and rearing conditions in the tanks in comparison with conditions in the sea. SD, standard deviation.

Year	1990			1991		1992	
Larval cohort	1. cohort	2. cohort	3. cohort	1. cohort	2. cohort	1. cohort	2. cohort
Date	1.4.-26.4.	17.4.-9.5.	29.4.-11.5.	9.4.-7.5.	22.5.-9.6.	3.4.-18.4.	8.5.-27.5.
Temperature (°C) ± SD							
* during egg incubation	9.1±1.4	7.7±1.6	9.1±1.6	6.9±2.4	10.9±1.3	5.7±2.2	10.7±0.0
* during larval rearing (from hatching to (100 % mortality)	9.6±2.6	13.3±4.4	17.0±3.5	8.6±1.8	13.0±1.7	7.5±1.4	13.4±2.4
* during the early larval period in the sea	9.0±1.0	11.1±3.1	15.1±2.6	8.6±1.6	13.1±0.8	6.8±0.8	15.0±3.4
Salinity (‰) ± SD							
* in the rearing tanks		9.75±0.25		7.25 ± 0.10		7.78 ± 0.18	
* in the sea		9.75±0.25		7.25 ± 0.10		7.78 ± 0.18	
Oxygen saturation ± SD (%)							
* in the rearing tanks		86.7±10.6		83.2 ± 3.3		93.2 ± 9.0	
* in the sea		80±20		75 ± 20		80 ± 15	

in the sea, since water was replaced daily. Salinity fluctuations were small (Table 1). The oxygen saturation fluctuated somewhat, but was generally in the range 60 - 100 %. Light was supplied by white fluorescent tubes equipped with a diffuser and situated 0.6 m above the tanks (intensity: 1400 lx). The lighting regime was 12 h light : 12 h dark, with 30 min dim light (600-800 lx) at the beginning (8.00 a.m.) and end (7.30 p.m.) of each light period. Zooplankton (tintinnids, rotifers, copepod stages; body (or cephalothorax) length: 0.11 to 0.75 mm) filtered from seawater was added to the tanks to maintain a density of more than 200 organisms l^{-1}, which is thought to be enough for the successful feeding (see SCHNACK 1972, WERNER & BLAXTER 1980, PEDERSEN et al. 1987). The presence of zooplankton in the larval gut was used as an indicator to separate the phase of pure yolk nutrition from that of additional feeding on external food. Hence it was possible to ascertain the efficiency of yolk use.

Dead larvae were counted and removed by pipette every day from the tank to assess the mortality rate. Mortality rates were measured as a percentage of the larval numbers present in the tank on the previous day.

Characterization of herring larvae

Fig. 2 shows herring larvae and explains parameters used for assessment of herring larvae during the yolk phase.

Comparisons of the yolk amounts, the duration of yolk resorption and the efficiency of yolk resorption of larvae of different cohorts during a spawning season, must start using larvae at identical developmental stages at the beginning of the experiment. However, at hatching larvae of different cohorts have different developmental stages (parameter: standard length, yolk volume; Table 2), for example as a consequence of temperature-regulated support of the hatching process by the mobil-

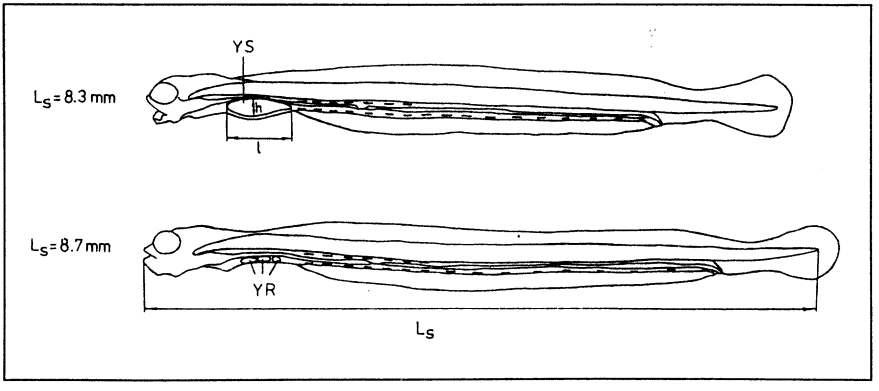

Fig. 2 *Clupea harengus.* Larvae during the yolk phase. L_S, standard length; YS, yolk sac (measurable); h, minor axis in mm; l, major axis in mm; YR, yolk remnants (not measu rable).

ity of embryos (see BLAXTER 1969). Therefore t_0 was defined as the moment, when larvae of different cohorts are comparable with each other, i.e. equal standard length, generally similar yolk volume (Table 3). It is equal to day 0 of the experiments.

The exception for the larvae of the 2nd cohort 1991 (at hatching equal and at t_0: different yolk volumes in comparison to the 1st larval cohort) could be caused by higher temperatures (> 11°C) and hence higher metabolic losses.

Experiments

1982 larvae were examined. At frequent intervals, » 30 larvae (at least 20, rarely < 20) were removed. Care was taken to sample larvae randomly from the surface, subsurface, mid-water and bottom. The larvae were put into a small glass vessel, anaesthetised with MS-222 (MS-seawater-concentration was 0.005 % at the end) and transferred to microscope slides where the water was removed except for a thin film around the larva. The whole procedure had to be completed within 5 minutes because the larvae were found to empty their gut within this period, and their gut contents would otherwise have been lost.

The dimensions of the yolk sac were measured with a microscope (magnification: 100 to 400) and the yolk volume was calculated with the formula of KLINKHARDT (1986):

$$\text{Yolk volume} = \pi / 6 * l * h^2.$$

If a larva had only yolk remnants (YR), then the yolk volume of this larva used for the calculation of the average was defined as 0. Therefore the duration of yolk sac resorption is not identical with the duration of yolk resorption. The yolk sac is exhausted, when the calculated averaged yolk volume is 0. But *yolk is exhausted* (YE), when 90 % of the larvae have no more visible yolk remnants.

Standard length of anaesthetised larvae was determined with an accuracy of 0.1 mm.

Results

Duration of yolk resorption

The results of the experiments on duration of yolk use are shown in Fig. 3 for temporally-separated cohorts of herring larvae for the years 1990 to 1992 from t_0.

The mean temperature from t_0 to YE (given as confidence intervals) for early cohorts (1st cohorts) and late cohorts (2nd and 3rd cohorts) of all three spawning periods amounts to 8.7 to 9.8 (n=57) and 12.0 to 14.3°C (n=30), respectively.

Table 2 *Clupea harengus.* Standard length (fresh) and yolk volume of larval herring of successive cohorts in 1990, 1991, and 1992 at hatching: size and yolk volume are given as 95 % confidence limits.

Year/Cohort	Hatching time	Standard length (mm)	n	Yolk volume (mm^3)	n
1990					
1. cohort	Beginning of April	7.91 - 8.16	9	0.029 - 0.043	9
2. cohort	Middle of April	6.66 - 6.86	32	0.146 - 0.231	22
3. cohort	End of April	6.65 - 6.92	22	0.118 - 0.148	22
1991					
1. cohort	Beginning of April	7.09 - 7.25	50	0.212 - 0.275	50
2. cohort	End of May	5.40 - 5.80	50	0.230 - 0.270	50
1992					
1. cohort	Beginning of April	7.10 - 7.39	51	0.146 - 0.190	51
2. cohort	Beginning of May	6.20 - 6.80	30	0.252 - 0.300	30

Table 3 *Clupea harengus.* Age, standard length (fresh) and yolk volume of larval herring of different cohorts in 1990, 1991, and 1992 at the beginning of the experiments (t_0): size and yolk volume are given as 95 % confidence limits.

Year/Cohort	Age (d) at t_0	Standard length (mm)	n	Yolk volume (mm^3)	n
1990					
1. cohort	0	7.91 - 8.16	9	0.029 - 0.043	9
2. cohort	4	7.74 - 8.06	19	0.009 - 0.048	7
3. cohort	3	7.77 - 8.08	20	0.009 - 0.031	20
1991					
1. cohort	0	7.09 - 7.25	50	0.212 - 0.275	50
2. cohort	3.5	6.95 - 7.27	20	0.055 - 0.095	20
1992					
1. cohort	0	7.10 - 7.39	51	0.146 - 0.190	51
2. cohort	1.5	7.04 - 7.32	30	0.111 - 0.159	30

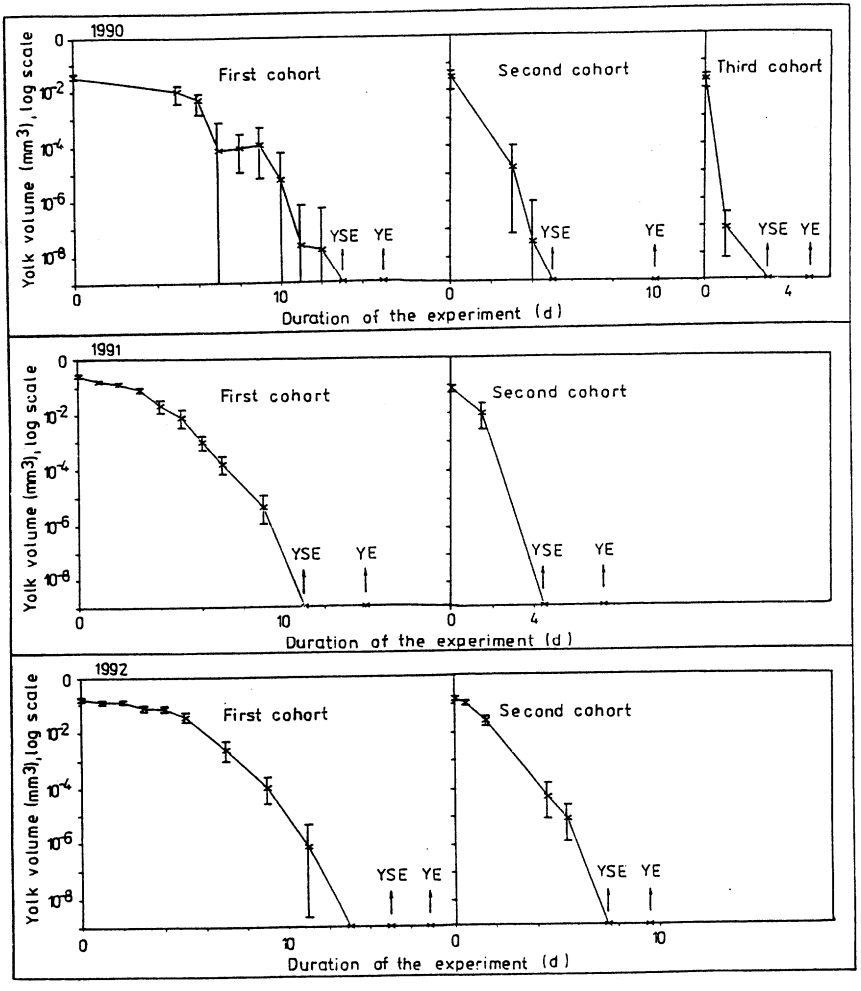

Fig. 3 *Clupea harengus*. Yolk absorption of larval herring of different cohorts during the spawning period in 1990, 1991, and 1992. Abscissa gives days since beginning of the experiments (t_0). YE, yolk exhaustion; vertical bars are 95 % confidence limits.

The larvae of early cohorts resorbed their yolk over a longer time than larvae from late cohorts: the length of the period from t_0 to YE (given as confidence intervals) is 11.5 to 19.1 days (n=3) and 4.4 to 11.6 days (n=4), respectively. Note that the confidence intervals for the duration of yolk resorption of the early and late cohorts only slightly overlap.

The duration of yolk utilization between t_0 and YE (Fig. 4) can be expressed as:

$$y = 384.2 * x^{-1.5}$$

$$r^2 = 0.97$$

where y is the time from t_0 to YE in d and x is the mean temperature throughout this period in °C.

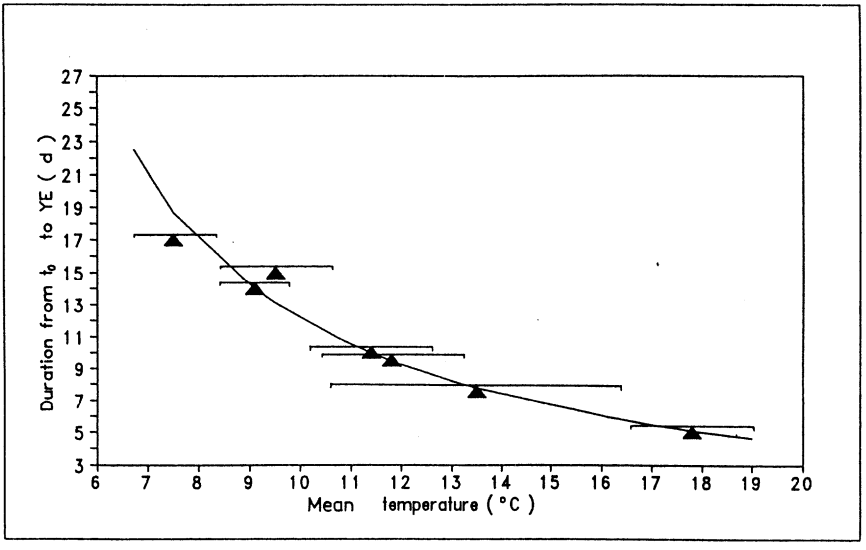

Fig. 4 *Clupea harengus*. The duration of yolk exhaustion as a function of the mean temperature throughout the period beginning at t_0 and ending at YE. Results obtained from all larval cohorts are summarized. The generated regression line shows this relationship for one averaged spawning season. Horizontal bars are 95 % confidence limits. From left to right: 1st cohort 1992, 1991, 1990, 2nd cohort 1990, 1992, 1991, 3rd cohort 1990.

Efficiency of yolk use

The yolk is almost completely exhausted by the time of first external feeding (volume of yolk remnants < 5 % of the original yolk volume at t_0, Table 4).

Accordingly, yolk use efficiency between t_0 and the moment at which the yolk volume is reduced to 5 % of the original volume, finds its expression in the increase in

Table 4 *Clupea harengus*. Timing of events during the experiments with larvae of successive cohorts in 1990, 1991, and 1992: F, first feeding; YE, yolk exhaustion.

Year/Cohort	Days from hatching to:				
	F	the moment, at which the yolk volume is smaller than 5 % of the value at t_0	YE	50 % mortality	100 % mortality
1990					
1. cohort	8	6.2	15	16	27
2. cohort	7	5	14	13	22
3. cohort	4	3.2	8	9	12
1991					
1. cohort	5	4.2	14	14	29
2. cohort	*	5.2	11	*	*
1992					
1. cohort	9	6	17	9 (*)	15 (*)
2. cohort	6	3.6	11	12	22

* no values and no sure values because of fungal infection of larvae

length correlated to a 0.001 mm^3 decrease in yolk volume (Fig. 5). The graph plotted by computer shows a trend for successive cohorts throughout the course of the season summarized for all three years:

$$y = 0.077 - 0.028 \ln x$$

$$r^2 = 0.63$$

where y is the increase in length in mm correlated to 0.001 mm^3 yolk volume decrease and x is the temperature in °C.

In the course of a season, the larvae of early cohorts below 9 °C grew between 0.009 and 0.035 mm basing on a decrease in yolk volume of 0.001 mm^3. At temperatures above 9 °C, lower yolk use efficiency leads to a smaller corresponding length increase between 0.001 and 0.012 mm for larvae of early and late cohorts. The computer graph indicates no length increment at temperatures above 16 °C correlating to 0.001 mm^3 yolk volume decrease. This value must not be representative because of the data lack.

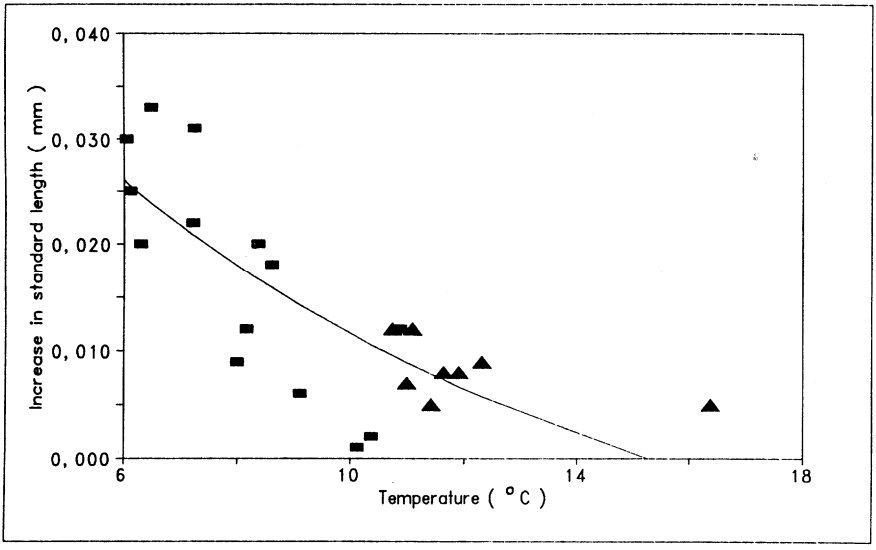

Fig. 5 *Clupea harengus*. The increase in standard length correlating with a 0.001 mm^3 yolk volume decrease throughout the period beginning at t_0 and ending at the time point, at which the yolk volume is smaller than 5 % of the value at t_0. Results obtained from all larval cohorts are summarized. For formula see text. Rectangles and triangles are measurements for early (1st) and late (2nd, 3rd) cohorts, respectively.

Mortality of larvae in the yolk phase

It is noticeable that the critical point is marked not by the beginning of external feeding, but rather by the time point of yolk exhaustion. Only 6.2 % of the hatched larvae had died up to the time of first feeding, 50 % of the hatched larvae had died up to YE (Table 4), although between 60 % (late cohorts) and 90 % (early cohorts) had already fed additionally on external food up to this moment and the food density was maintained at a value of more than 200 organisms l^{-1}. Whereas mortality rates from hatching to the first feeding time and nearly to YE remained low and constant (< 10 % d^{-1}), higher mortality rates (> 10 % d^{-1}) were established nearly from YE and the next few days.

The larval development was divided into 3 phases (see horizontal bars from left to right in Fig. 6):

1st phase: mortality rates are below 10 % d^{-1};

2nd phase: mortality rates are above 10 % d^{-1};

3rd phase: mortality rates are below the values established at the 2nd phase.

If larvae had used their yolk at temperatures below 16°C, then ca. 3 % of the larval starting population survived. The 3rd phase followed with lower mortality rates than in

the 2nd phase (Fig. 6 A to D). The daily mortality rates show nearly no significant differences when comparing the values of early and late cohorts.

However, if larvae had used their yolk at temperatures above 16°C, then all larvae died within a short period without a 3rd phase (Fig. 6 E).

With consideration of all results, survival chances of early cohorts are primarily determined by yolk supply at temperatures £ 9 °C. Moreover survival chances at higher temperatures were determined by slight decreasing efficiency of yolk use (especially late cohorts).

At temperatures above 16°C yolk use efficiency is too small, therefore yolk supply is not sufficient for larval recruitment (3rd cohort 1990).

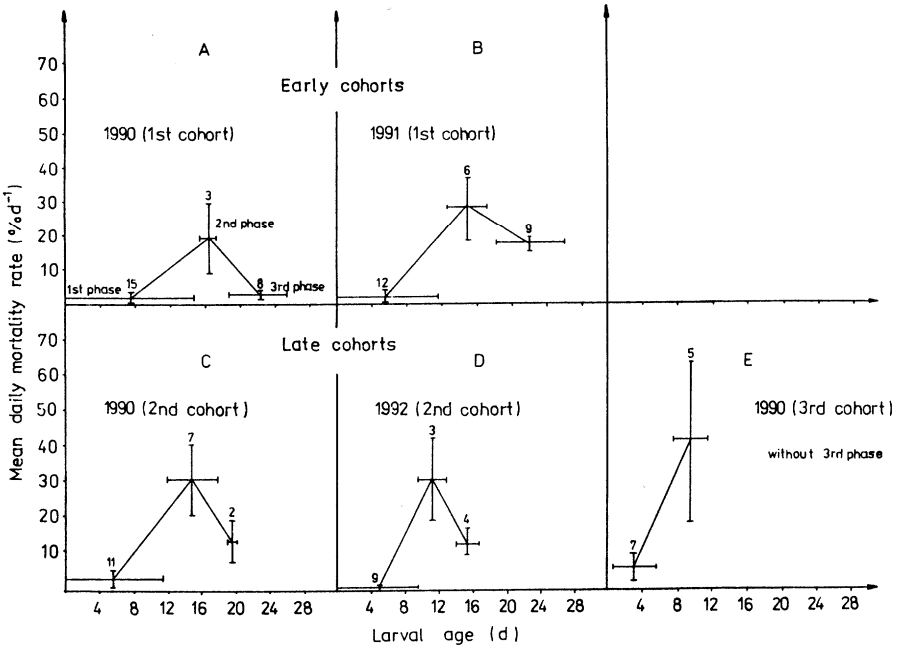

Fig. 6 *Clupea harengus.* Mean daily mortality rates of early (A, B) and late herring larvae cohorts (C, D, E) during the three different phases (explanation see text). Vertical bars are 95 % confidence limits. Horizontal bars mark the extent of phases 1, 2, and 3 (from left to right in the graphs). The figures above the maximum values represent the sample numbers. Investigations were not performed for the 2nd cohort 1991, and the 1st cohort 1992 had a fungal infection.

Discussion

Earlier work had determined the transition from yolk nutrition to external feeding as a critical phase (HJORT 1914, SINCLAIR & TREMBLAY 1984, FORTIER & LEGGETT 1984, 1985, RAID 1985, HOUDE 1989). In addition to the ability and readiness of the larvae to use external food (BLAXTER 1969, ROSENTHAL 1969, ROSENTHAL & HEMPEL 1970, BEYER 1980, JOHNSTON & WILDISH 1982, GIBSON 1988, GIBSON & EZZI 1992, BUSCH 1996), there must be sufficient food of the correct size and species composition available (OJAVEER & SIMM 1975, BEYER & LAURENCE 1981, KIØRBOE & JOHANSEN 1986, KIØRBOE et al. 1988, FORTIER & GAGNÉ 1990).

However, the results of this investigation have shown that the development of the mortality rate up to the point of complete yolk resorption is not only controlled by external food supply. Up to the end of the yolk phase, 50 % of the starting population had died in all cohorts (larval age: 8 to 18 days), although between 60 % (late cohorts) and 90 % (early cohorts) had already fed additionally on external food up to this moment (BUSCH 1993) and the food density has ever been maintained at a value of more than 200 organisms l^{-1} (mixed natural zooplankton: from small naupliar stages and tintinnids with a length of 0.11 mm to big adult copepods with a cephalothorax length of 0.75 mm). YIN & BLAXTER (1987 a, b) came to the same results, but no external food was supplied by them.

When yolk was exhausted, larvae were subjected for a subsequent, short period to higher mortality rates with different survival success, although meanwhile all larvae fed on enough external food. It is a doubtless fact, that this mortality development can have different causes e.g. larval constitution, food density, food composition etc. However, survival chances are greater, when the yolk supply was utilized with greater effectiveness in growth, i.e. at temperatures below 16°C. The larvae of early cohorts showed a greater length increment than those of later cohorts correlating to 0.001 mm^3 yolk volume decrease. However, this difference must not have any significance since the correlation coefficient (r^2) is only 0.63, so that the main influence of increasing temperature during the spawning season (March to May) is to shorten the yolk phase. As a consequence of the higher rate of yolk use (decrease of yolk volume d^{-1}), larvae of later cohorts grew quicker (0.25 to 0.38 mm d^{-1}) than those of earlier cohorts (0.11 to 0.17 mm d^{-1}) in the period before feeding on external food sources had begun. At the time of first feeding, all larvae had a standard length of 8.3 to 8.6 mm. The morphological and functional developmental stage (mouth opening, esophagus opening, gut function etc.) which has been reached at this length is the prerequisite for switching from internal to external feeding (for data see BUSCH 1996, and also BLAXTER 1969, ROSENTHAL 1969, ROSENTHAL & HEMPEL 1970, JOHNSTON & WILDISH 1982, KIØRBOE et al. 1985).

In contrast, if larvae had resorbed their yolk substance at temperatures above 16°C (at the end of the spawning period), the efficiency of yolk use was so low that successful recruitment was not possible from the yolk supply available. We assume that higher metabolic costs especially for respiration must have resulted in incomplete larval growth and development. The larval growth was stoped. Larvae starved. As an example, the larvae of the 3rd cohort of 1990 can be considered. In this case, mortality was 100 %. OJAVEER & SIMM (1975) stated as upper temperature limit 16

to 17°C for the spawning in the Gulf of Riga. YIN & BLAXTER (1987 b) recorded upper lethal temperatures of 21 to 23.5°C and 20.5 to 23 °C for yolk sac larvae of Clyde and North Sea populations, respectively. At temperatures of over 16°C, yolk sac larvae are rarely found in the Greifswalder Bodden.

The most widely accepted suggestion of the ecological significance of the yolk sac stage is that a large yolk supply of the newly hatched larvae increases the time to the point-of-no-return, and is, therefore an adaptation to a harsh environment and a poor food supply in the larval nursery area (KIØRBOE et al. 1985). Our study shows, that in the Greifswalder Bodden herring larvae of earlier cohorts are provided with yolk for a longer period than those of later cohorts. Results from BRENNING & KELL (1990) and SUCHAU (1992) reveal that the early larvae "grow into" a zooplankton community (potential prey community) whose population density is continuously increasing with time: from ca. 50 organisms l^{-1} (beginning of april) to ca. 200 organisms l^{-1} (beginning of may). Therefore, they can practice at catching prey, but they do not need external food. In contrast, larvae of late cohorts are growing at a time when the zooplankton populations have reached their peak abundance and when zooplankton densities start to decrease again: from ca. 300 organisms l^{-1} (between the middle and the end of may) to ca. 200 organisms l^{-1} (end of june). The temperature-accelerated yolk use is no disadvantage, because the zooplankton population is much more dense and so less searching is required to find a prey item. By means of their fast and nearly equally effective yolk use, these larvae can compensate for their smaller hatching size, as opposed to larvae of earlier cohorts, and switch to external feeding within a shorter period.

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Authors

Dr. Andreas Busch
Dr. Nils Jönsson
Thomas Lorenz
Andreas Suchau
Anke Holst

University of Rostock
Department of Biology
Zum Laakkanal 20
D-18109 Rostock, Germany