Vol. 24: 15–21, 1985 | MARINE ECOLOGY – PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published July 11

Feeding behaviour and swimming activity of larval herring *(Clupea harengus)* in relation to density of copepod nauplii

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ABSTRACT: Prey organisms of fish larvae vary in density, both temporally and spatially. Do fish larvae respond behaviourally to variation in food density? The responses of larval herring *Clupea harengus* L. to different densities of copepod nauplii (5 to 360 nauplii l^{-1}) were studied in laboratory experiments. Larval feeding rate increased as food availability increased until an asymptote was reached. At low food densities, larval swimming activity was ca 100 % higher than at the highest food concentrations; a change in larval swimming mode within the range of food densities was also noted. The water volume searched by the larvae, calculated on the basis of rate of feeding attacks, showed a pronounced increase when food density declined, partly due to the increased swimming activity but also as a result of an increase in distance of reaction to food particles. The adaptive significance of these behavioural changes is discussed.

INTRODUCTION

Larvae of herring *Clupea harengus* L. are planktonic predators, mainly feeding on copepodites and copepod nauplii. The density of larval prey varies temporally and spatially; this paper addresses the questions (1) do herring larvae exhibit behavioural adaptations to a varying food environment; (2) to what degree do potential behavioural changes influence larval growth and vulnerability to predators?

A number of studies on the feeding behaviour of larval herring and other larval fish have been carried out, often with the goal of estimating the minimum food concentration at which larvae can grow and survive in the sea (e.g. Rosenthal & Hempel 1970, 1971, Blaxter & Staines 1971, Hunter 1972, Solberg & Tilseth 1984). These studies have provided important information on modes of swimming, searching and attack behaviour, swimming speeds, etc. However, further insight into the relation between larval feeding behaviour and food density is needed in order better to understand the ecology of larval fish.

The effect of varying prey densities on larval growth and survival is expected to be most pronounced at low concentrations of food availability. Therefore, interest is focused on potential behavioural adaptations in the lower range of food densities experienced by larvae in nature. The aim of this study is to look for such behavioural adaptations in herring larvae by analysing the behavioural components of the functional response over the range of food densities herring larvae naturally experience in the sea. The functional response is defined as the change in prey consumption rate with prey density (cf. Holling 1963). In the present study on herring larvae, important components of the functional response, i.e. attack rate, swimming activity and reaction distance were studied in relation to the density of prey organisms in laboratory experiments.

MATERIAL AND METHODS

Three experimental series were run between November 1983 and January 1984. The larvae were obtained from 2 sources. Larvae in the first 2 experiments were of the Baltic stock (autumn spawners); larvae from winter spawning Downs herring were used in the third experiment. We followed the fertilization and incubation procedure described by Munk & Rosenthal (1983). Incubation temperature was 8.2 °C ± 0.1 C°. Constant illumination was applied during incubation. After 14 d, hatching was stimulated by darkening of the incubation tank, and 800 of the larvae which hatched during the following 16 h were transferred to a 800 l stock tank.

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Larvae were fed copepod nauplii *(Acartia tonsa)* cultivated in the laboratory as described by Støttrup & Munk (1983). Copepod eggs were siphoned daily from the cultivation tank and nauplii were grown to an age of 6 d at 16 °C (Stage 3 to 5, body length ca 150 µm, mean dry weight 0.17 µg) before they were used for feeding.

Experimental tanks were cylindrical (diameter = 50 cm), made of black polyethylene, and contained 172 l of 27 ‰ sea water. Five water-jets placed in the water column mixed the water mass and circulated the water column (0.7 cm s^{-1} current speed at tank wall), thus ensuring an even distribution of nauplii in the tank. Tanks were double-walled, and cooling water in the wall kept the temperature at 8.3 °C ± 0.1 C°. Light from cool-white fluorescence tubes increased from zero to 1000 lux (at water surface) or decreased from 1000 lux to zero in 30 min in order to simulate sunrise and sunset. The feeding day had a length of 14.5 h.

In the first 2 experiments, 6 tanks were kept at nominal nauplii densities of 7.5, 15, 30, 60, 120 or 360 n l^{-1} (in the second series an additional experiment with no nauplii was performed after termination of the other tank experiments). In the third experimental series 4 tanks were kept at nominal nauplii densities of 0, 5, 7.5 and 12.5 n l^{-1}. The density of nauplii in the stock tank was kept at 120 n l^{-1}. One day prior to experiments, larvae were added carefully to the experimental tanks. Larval densities were varied according to nauplii densities in order to ensure approximately the same percent grazing impact: 0.05 larvae l^{-1} (5 to 15 n l^{-1}), 0.07 larvae l^{-1} (30 + 60 n l^{-1}) or 0.12 larvae l^{-1} (0 + 120 + 360 n l^{-1}). Larval age and size at the start of experiments are given in Table 1.

Each morning, water samples for nauplii counts were siphoned through glass tubes placed at 2 depths in the tank. Sample size was regulated to a total count of 40 to 120 nauplii $sample^{-1}$. Nauplii were then added and the density was checked following the same procedure. Deviations of up to 20 % from the nominal density were accepted (Table 2). Nauplii density declined by ca 25 % during the 24 h between adjustments of concentrations. No accumulation of copepod nauplii in the tanks was observed, neither vertically nor horizontally.

Observations of larval feeding behaviour were carried out 2 to 3 times every day within 6 h of nauplii density adjustment. Each time 10 to 20 free-swimming larvae were observed for about 1 min each. Observations on frequency and length of swimming periods, aiming posture and feeding attacks (forward dart after S posture) were recorded on a computer (at $\frac{1}{16}$ s computer accuracy) by use of a portable 5-finger keyboard. For measuring attack success, a spotlight was used to examine visually the larval foregut for swallowed nauplii. After 4 d, the remaining larvae were counted, measured to standard length, dried for 24 h at 55 °C, stored in a dessicator and weighed within 1 mo.

Table 1. *Clupea harengus.* Characteristics of larvae used at onset of experiments

Experiment no.	Spawning stock	Age at start (d after hatching)	Standard length (mm) $\bar{X}$	S	Dry weight (µg) $\bar{X}$	S
Series I	Baltic autumn	9	11.3•	–	152•	–
Series II	Baltic autumn	13	11.9	0.5	161.3	35.3
Series III	Downs	13	12.6	0.6	228.5	42.0

• Estimated

Table 2. Nominal and actual densities of *Acartia tonsa* nauplii in experimental tanks immediately before and after addition of nauplii. In Series III, density was not checked after food addition

Nominal density (no l^{-1})	Series I Before control $\bar{X}$	SD	After control $\bar{X}$	SD	Series II Before control $\bar{X}$	SD	After control $\bar{X}$	SD	Series III Before control $\bar{X}$	SD
5									3.4	1.4
7.5	5.0	1.4	7.6	1.1	4.3	1.8	8.9	1.2	4.7	3.4
12.5									8.8	3.5
15	9.8	4.8	15.2	1.3	11.0	1.2	17.7	3.2		
30	18.4	4.5	27.1	2.0	23.5	8.4	28.6	5.2		
60	41.2	9.7	58.0	10.6	35.4	13.9	61.5	9.6		
120	89.0	26.9	136.8	1.6	89.0	33.1	128.4	18.4		
360	255.3	56.6	327.3	24.8	306.3	85.2	360.5	36.6		

RESULTS

Herring larvae were influenced by experimental conditions, i.e. by being placed in an unusually restricted environment. Even though experimental conditions were designed to make the environment less stressful for the larvae (gradual change in light intensity, circulating water current etc.), we still found larvae swimming against the tank wall for a significant part of the time (up to 50 %). In free-swimming larvae, however, no indications of stress were observed. The larvae were seen to alternate between different types of swimming behaviour as described by Rosenthal & Hempel (1970). These authors distinguished 3 types of swimming behaviour, 'abrupt swimming', 'normal swimming', and 'slow meandering'. They defined abrupt swimming as movements of very short duration (< 0.5 s), often connected with a shift in orientation; slow meandering, as long periods of movement with an undulation of high amplitude; and normal swimming, as intermediate between these 2 types with no clear boundaries.

Intermittently, we observed a single larva suddenly making a 'sprint', crossing the tank several times within a few seconds. Such very high activity levels, with fast starts and a steady burst of swimming have been described by other authors (Batty, quoted in Blaxter & Hunter 1982 for herring, and Hunter 1972 for anchovy) and may be important in escape and attack situations (Webb & Corolla 1981).

Larval behavior changed as a function of nauplii density. The changes, described in the following sections, have been tested for significance using an unbalanced ANOVA in the 'Statistical Analysis System' (SAS Institute Inc. North Carolina). Except for duration of aiming postures, all observed behaviour changes were significant ($p < 0.02$) in the food density range 7.5 to 30 nauplii l^{-1} (unsatiated larvae only) and highly significant ($p < 0.009$) when comparing behaviour in the whole range of food densities offered. Differences between replicate series were insignificant (except duration of aiming postures), and no correlation to time of day was found.

Attack rate

Prey catching behaviour of herring larvae has been thoroughly described by Rosenthal (1969). Upon sighting a prey object the larva bends its body in an aiming posture and subsequently darts forward against the prey by straightening its body.

Mean values of observed attack rates are shown in Fig. 1 as a function of nauplii density. The rate increased from 0.1 attacks min^{-1} in experiments at the nominal 0 n l^{-1} to ca 0.9 attacks min^{-1} at 30 n l^{-1}. No further increase in attack rate was found when nauplii density was raised above 30 n l^{-1}. Feeding attacks in experiments 0 n l^{-1} were directed against detritus. This type of feeding was insignificant when alternate food (nauplii) was present; detritus was found only in stomachs of larvae reared without nauplii.

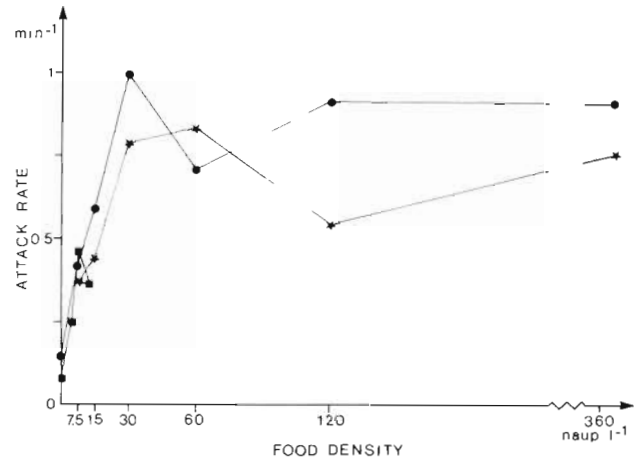

Fig. 1. *Clupea harengus*. Rate of feeding attacks of larvae plotted against density of copepod nauplii. Points represent means of observations at nominal food density. Series I (★), Series II (●), Series III (■)

Feeding success (percentage of attacks which lead to ingestion) increases as a function of age (Rosenthal 1969). Feeding success of larvae in the stock tank was recorded in the middle of experimental Series I and II. In the first period 40 % success was found, in the second ca 60 %. In experiments with larvae from other herring stocks feeding success was independent of food density in the range 7.5 to 120 n l^{-1} (Kiørboe & Munk unpubl.).

Handling time and digestive capacity

Subcomponents of handling time are time for pursuit and consumption of prey, and time for a digestive pause. Time for prey pursuit is represented by the duration of aiming postures (Table 3). The postures lasted for about 1.1 s in Series I but only 0.9 s ($p < 0.008$) for the slightly older larvae in Series II and III. No correlation to food density was found. The proportion of aiming postures that end with an attack, however, depends on prey density (Table 3). At prey densities below 15 n l^{-1} about 40 % of the aiming postures are followed by an attack, increasing to 70 % with increasing food density. Therefore, the time used for pursuit per prey attacked decreases from about 2.5 s at low, to about 1.5 s at high prey densities; the time used is very short and the differences are of limited importance.

Table 3. *Clupea harengus.* Mean and standard deviation of observations on feeding behaviour and swimming activity of larvae

Series	Nauplii density (no l^{-1} nominal)	Attack rate (min^{-1})		Attack posture				Attack	Swimming		
				Rate (min^{-1})		Duration (min)		%	Proportion of obs. time (%)		Duration (min)
		$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	$\bar{X}$	SD	$\bar{X}$
I	7.5	0.37	0.26	1.09	0.50	1.20	0.18	34	77	8	2.1
	15	0.44	0.34	0.77	0.59	1.05	0.29	57	66	15	1.5
	30	0.79	0.40	1.55	0.80	1.01	0.19	51	58	16	1.1
	60	0.83	0.53	1.40	0.79	1.00	0.23	59	56	17	1.2
	120	0.54	0.30	0.88	0.44	1.33	0.33	61	36	8	0.6
	360	0.92	0.47	1.42	0.73	0.88	0.17	65	38	12	0.6
II	0	0.15	0.11	0.32	0.22	–	–	47	46	12	1.0
	7.5	0.42	0.22	1.07	0.34	0.80	0.20	39	74	8	1.9
	15	0.59	0.28	1.10	0.42	0.96	0.19	54	68	11	1.4
	30	0.99	0.36	1.70	0.78	0.73	0.16	58	70	12	1.6
	60	0.71	0.27	1.11	0.46	0.88	0.40	64	46	13	0.8
	120	0.92	0.44	1.30	0.49	0.93	0.15	71	41	5	0.7
	360	0.91	0.38	1.31	0.64	0.84	0.14	70	34	10	0.6
III	0	0.09	0.06	0.13	0.07	–	–	69	45	11	1.0
	5	0.25	0.20	0.87	0.70	0.94	0.27	29	75	10	2.6
	7.5	0.46	0.17	1.16	0.60	1.13	0.20	40	77	10	2.3
	12.5	0.37	0.23	0.83	0.42	0.93	0.24	45	54	9	0.9

The digestive pause is also of short duration. We often observed a feeding process leading to prey consumption to be immediately followed by another prey attack. Thus, total handling time is of negligible duration, and does not limit feeding rate.

Gut capacity and digestion rate determine the upper limit to the consumption rate. At a full stomach, digestion rate can be estimated from the satiated attack rate: if we use a mean capture success of 50 % and assume 50 % of the time spent at the tank wall, maximum attack rate (0.9 attacks min^{-1}) corresponds to 0.23 prey consumed min^{-1} and a digestion rate of ca 4 min $prey^{-1}$.

Time spent swimming

The activity of the larvae, expressed as time spent swimming as percentage of total time, is shown in Table 3 and Fig. 2. Larval activity was highest at 5 to 15 nauplii l^{-1}; it decreased at both higher and lower (zero) densities. The activity decreased to about 35 % at 120 nauplii l^{-1}, and remained the same at 360 nauplii l^{-1}. At nauplii density zero, the larvae showed a similarly low activity.

When inactive, herring larvae sink. Sinking rate is about 0.3 cm s^{-1} (Blaxter & Ehrlich 1974). Therefore, a certain activity is necessary for the larvae to remain in the water column. The leveling out of swimming activity to about 35 % at the highest nauplii densities suggests a minimum activity of this magnitude. Mean length of swimming periods decreased from about 2 s

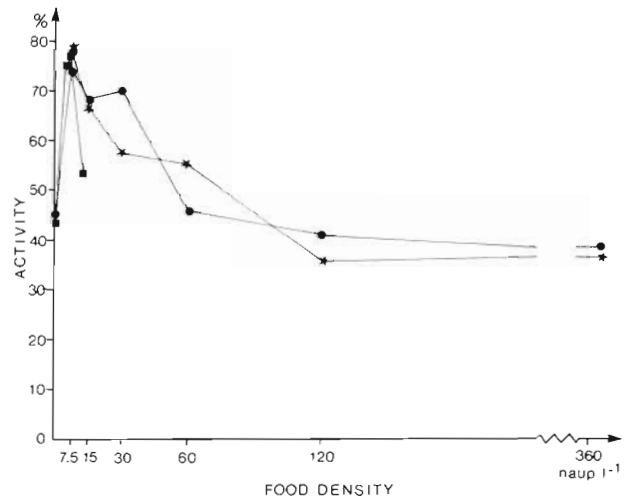

Fig. 2. *Clupea harengus.* Swimming activity of larvae (in percent of total time observed) plotted against density of copepod nauplii. Points represent means of observations at the nominal food density. Series I (★), Series II (●), Series III (■)

at the lowest densities to about 0.5 s at the highest (Fig. 3). Length of resting periods was more constant, increasing from 0.7 s at the lowest to 1 s at highest food densities. Thus, length of swimming periods and percent activity are closely correlated (compare Fig. 2 & 3). At zero prey density, the larvae exhibited a unique behavioural pattern: both long periods of activity (mean 1.0 s) and long inactive periods (mean 1.2 s) were found.

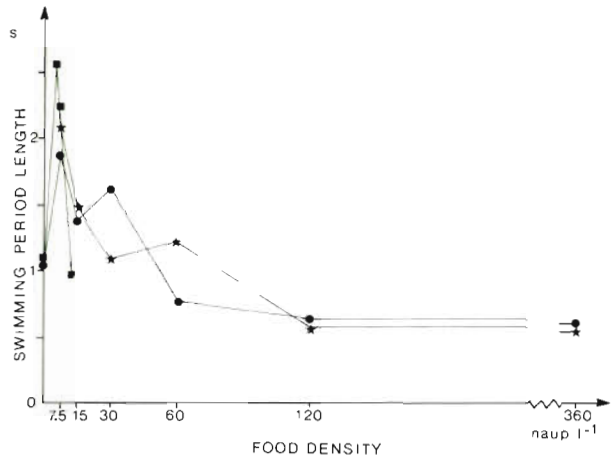

Fig. 3. *Clupea harengus*. Length of swimming activity sustained by larvae against nominal density of copepod nauplii. Series I (★), Series II (●), Series III (■)

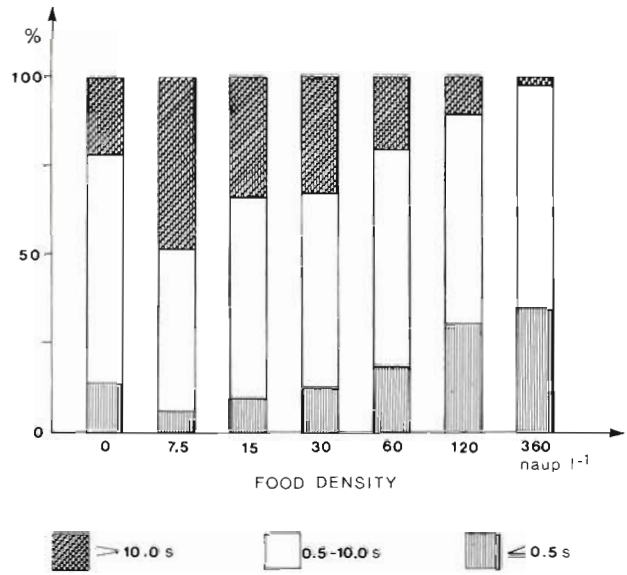

Fig. 4. *Clupea harengus*. Distribution of time spent bursting (≤ 0.5 s), meandering (> 10.0 s) and at intermediate mode of swimming (0.5 to 10.0 s) by larvae at different nominal nauplii densities. Data from Series II. 100 % = total time spent swimming

These changes could also be described as an increase in abrupt and a decrease in meandering larval swimming mode as a function of increasing nauplii concentration (Fig. 4). In this figure, swimming periods of less than 0.5 s are defined arbitrarily as abrupt swimming, and periods of more than 10 s as slow meandering (cf. Rosenthal & Hempel 1970).

Search volume and distance of reaction

Search volume is the volume of water searched per unit time. For unsatiated larvae it can be calculated as the rate of attacks or aiming postures divided by prey density, and it equals 36 to 54 cm^3 min^{-1} and 55 to 154 cm^3 min^{-1}, respectively. It consists of 3 components: swimming activity, swimming velocity (i.e. velocity of the head) and distance of perception/reaction. The outer boundary of larval 'reactive perceptual field' is set by the maximum distance at which it will react by attacking the prey (reactive distance) whereas the outer boundary of a 'perceptual field' is set by the maximum distance at which the larvae can notice the prey (perceptive distance). The observed rates of attacks and aiming postures indicate the magnitude of these fields. Reactive and perceptive distances can be calculated from search volume, based on rate of attacks or aiming postures, respectively. In the calculations swimming velocity is set to 1 cm s^{-1} (range measured by Rosenthal & Hempel 1970: 0.8 to 1.1 cm s^{-1}) and a half-circular field of vision above the head is assumed (Rosenthal & Hempel 1970; Table 4). Both distances increased when food densities decreased from 30 to 7.5 nauplii l^{-1}. Similar calculations are not valid for satiated larvae; here calculated search volume, as well as reactive and perceptive distance will approach zero at increasing prey densities.

DISCUSSION

Attack rate in herring larvae increased with increasing prey density but at a decelerating rate until an asymptote was reached. This type of response is common among predators (e.g. review by Murdoch &

Table 4. *Clupea harengus*. Average search volume and distance of reaction of larvae at different densities of nauplii (calculations explained in text)

Nauplii density no l^{-1} nominal	Search volume		Distance of reaction	
	From attacks (cm^3 min^{-1})	From aiming postures (cm^3 min^{-1})	From attacks (mm)	From aiming postures (mm)
5–7.5	54	154	8.7	14.7
12.5–15	39	63	8.1	10.3
30	36	55	7.7	9.5

Oaten 1976), and has also been found in other species of larval fish (e.g. Laurence 1977, Houde & Schekter 1980). The response resembles the Holling type II response (Holling 1959a), but attack rate is limited by factors other than handling time.

Herring larvae respond to low food densities by searching an increasing water volume for food particles. This is done in 2 ways: by increasing swimming activity and, to some degree, by increasing reactive distance at low food densities.

The variation in perceptive distance is somewhat unexpected. However, from direct observations on the distance of perception Rosenthal & Hempel (1970) showed that this was higher by 20 to 30 % when larvae were meandering than when they exhibited abrupt swimming. We found that the mode of swimming changed from meandering to abrupt swimming with increasing prey density (Fig. 4), and this can roughly explain the observed variation in perceptive distance. This variation is therefore primarily a consequence of changed mode of swimming. Our calculated perception distance for larvae at 7.5 nauplii l^{-1} (1.47 cm) is quite close to the mean distance of perception at meandering (1.36 cm for 12 mm larvae) reported by Rosenthal & Hempel (1970).

The volume of water searched has been estimated for herring larvae by other authors from estimates of perceptive distance, swimming velocity and swimming activity, and quite different results have emerged. Blaxter (1966) estimated 1.5 l h^{-1} for 12 to 14 mm larvae, Blaxter & Staines (1971) about 0.25 l h^{-1} for 14 d old larvae, and Rosenthal & Hempel (1970) 3 to 4 l h^{-1} for 9 to 13 d old larvae. Thus, estimates for similar-sized herring larvae vary over more than 1 order of magnitude.

Our estimate of search volume, based on aiming postures (i.e. perceptive distance), is in the range of 3 to 10 l h^{-1} depending on prey density (Table 4). The discrepancy between our estimate and that of Rosenthal & Hempel (1970) appears to be due primarily to differences in larval activity. In the present study unsatiated larvae exhibited higher swimming activity than mostly observed for laboratory-reared larvae (e.g. Westernhagen & Rosenthal 1979 [39 %]). The activity was similar to activity of larvae observed in the field (Westernhagen & Rosenthal 1979 [50 %]).

Whereas search volume obviously depends on prey density, instantaneous rate of prey discovery (*sensu* Holling 1959b) is constant and independent of prey density. It can be estimated both from the disk equation and the Ivlev equation (Houde & Schekter 1980), when based on prey-attack rates rather than prey consumption rates (Fig. 1). Present estimates for all 3 series are about 100 ml min^{-1} (Holling-equation), and 65 ml min^{-1} (Ivlev-equation) comparable to the search volume at the lowest prey density (Table 4). The instantaneous rate of prey discovery in herring larvae is, thus, somewhat smaller than the rates estimated by Houde & Schekter (1980) for similar-sized larvae of 3 species of subtropical marine fish (140 to 370 ml min^{-1} for 200 µg dw larvae). This difference may be partly due to the difference in temperature (8° *vs* 20 to 26 °C).

A potential effect of decreased swimming activity at high prey densities is an increased probability of the larvae staying in areas with high food concentrations. Larval food, e.g. copepods and copepod nauplii, is patchily distributed in the sea, both on a small (dm to m) scale (Owen 1981) and large (m to km) scale (e.g. Arthur 1977, Greenblatt 1982). Within these scales of patchiness, the observed behaviour may be advantageous, depending on the timelag between changes in prey density and in behaviour. Utilization of a fine-grained patchiness demands a nearly instantaneous behavioural response, e.g. mediated by the eye. Hunter & Thomas (1974) found that larval anchovy had a tendency to stay in artificial food patches (5 to 10 cm in diameter), by instantly decreasing their swimming speed and adopting frequent shifts of direction, when entering a patch. In herring we found the abrupt swimming mode to increase at high food concentrations (Fig. 4). Abrupt swimming is usually connected to shifts in swimming direction. Thus the response of herring larvae to food concentration resembles that observed for anchovy larvae. However, the scale of patchiness that can be utilized by larval herring remains to be tested. If the behavioural response is mediated by the gut rather than the eye, which is believed to be more generally the case in fishes (Dill 1983), a significant time-lag may be expected.

Several authors have used laboratory estimates of search volume in combination with estimates of calorific requirements of growing larvae, or laboratory measured growth and survival rates, to predict the minimum concentration of food necessary for growth and survival of fish larvae in nature (e.g. Rosenthal & Hempel 1971, Houde 1978, Werner & Blaxter 1980). In most cases, predicted minimum prey densities are higher than average food densities in the sea. However, in the present experiments larval feeding rate satiated at comparatively low nauplii concentrations (~ 5 µg dw l^{-1}). Also, in our experiments, where a homogenenous distribution of food particles was ensured, herring larvae were able to initiate exogenous feeding at food densities in the lower range of those experienced by larvae in the sea (Kiørboe et al. 1985) and to grow at a rate similar to that in nature at comparable food densities (Kiørboe & Munk unpubl.). Thus, plankton patchiness is apparently not necessary for herring larvae to grow and survive in the sea.

It has been suggested that larval mortality due to

predation may increase at low food concentrations since decreased growth may delay metamorphosis and, thus, increase the length of the period of high vulnerability to predators (e.g. Houde & Schekter 1980). Such an interplay between food concentration and predation mortality may also be mediated in a more direct way. Most larval predators are visual hunters. The probability of sighting a larva may, therefore, increase with larval activity. Also, if larvae are more active, they will have a higher probability of encountering predators because the probability of contact will increase with activity rate of both predator and prey. Consequently, predator vulnerability of herring larvae is expected to increase with decreasing food density, and a higher mortality rate due to predation may be predicted when larval food is scarce.

Acknowledgements. We thank M. Lermark and N. J. Pihl for technical assistance, Dr. E. Houde for critically reading our manuscript, and Dr. K. Richardson for correcting our English.

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This paper was presented by Dr. K. Sherman; it was accepted for printing on March 29, 1985