Marine Biology 96, 459–468 (1987)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Escape speeds of marine fish larvae during early development and starvation

M. C. Yin* **and J. H. S. Blaxter**

Scottish Marine Biological Association, Dunstaffnage Marine Research Laboratory; Oban PA34 4AD, Argyll, Scotland

Abstract

Response rates to tactile stimulation and subsequent escape speeds were measured using a video-recording system during early development and starvation of fish larvae. The species studied included the yolk-sac larvae of Clyde and Baltic herring (*Clupea harengus* L.), cod (*Gadus morhua* L.), flounder (*Platichthys flesus* L.) and older larvae of Clyde herring. The proportion of larvae responding (response rate) was initially about 20 to 25% in herring and 35 to 40% in cod and flounder using a probe, but about 70 to 80% using the sucking action of a pipette in all species except flounder. Both response rates and escape speeds (mean and maximum) tended to peak 1 to 2 d before the PNR (point-of-no-return, when 50% of larvae are too weak to feed), then decreased slowly during further starvation. An inter-species comparison showed that the highest recorded mean escape speeds (measured over a period of 200 ms) and highest maximum escape speeds (over 20 ms) ranged from 5.7 to 8.6 BL/s (body lengths/s) and 12.1 to 16.1 BL/s, respectively. The larvae made directional responses away from the stimulus only when they developed and reached the feeding stage.

Introduction

Many workers have investigated changes in the morphology and feeding behaviour of marine fish larvae during early development and starvation (see Yin and Blaxter, 1986, 1987a for a summary). A few papers have dealt with swimming behaviour, tolerance to environmental conditions and buoyancy during starvation (Laurence, 1972; Wyatt, 1972; Blaxter and Ehrlich, 1974; Yin and Blaxter 1987b), but there is no work on escape behaviour during starvation even though it must be important in predator avoidance (Webb, 1981; Webb and Corolla, 1981). Since starvation and predation account for most of the mortality during the early life history of many fishes, it is crucial to investigate how these two factors interact.

The present research, being part of a programme to determine the viability of larvae of marine fish during early development and starvation, investigates the changes in escape speeds following startle responses induced by tactile stimuli in four species. The stimuli were considered to be an adequate simulation of what might be experienced by larvae touched by a predator, for example the mouth parts of a crustacean or suction feeder. The main aim of the investigation was to check whether escape performance declined gradually during starvation or whether there was a sudden reduction of escape ability near the end of the starvation period. Yolk-sac larvae of Clyde and Baltic herring, cod and flounder and older larvae of Clyde herring were used.

Materials and methods

Yolk-sac larvae of Clyde and Baltic herring (*Clupea harengus* L.); cod (*Gadus morhua* L.) and flounder (*Platichthys flesus* L.) were hatched and the older Clyde herring larvae were obtained as described by Yin and Blaxter (1987a). Yolk-sac larvae after hatching, and older larvae after a period of feeding, were held in 25-litre circular tanks and deprived of food for varying periods of time until the experiments were performed. The rearing temperature, larval length and survival times are given in Tables 1 and 2.

Experiments were conducted in an air-conditioned room, at 9° to 10 °C, under a fluorescent room light of 150 lux (≡ 75 μW/cm) intensity. For each experiment, about 20 larvae were transferred every second day from the holding tank into a Perspex dish, 11.5 cm in diameter by 4 cm deep. Care was taken to sample the larvae from

---

* Permanent address: Shanghai Fisheries University, Shanghai, People's Republic of China

Table 1. *Clupea harengus, Gadus morhua* and *Platichthys flesus.* Timing of events during early development and starvation of larvae. Times to reach first feeding, yolk exhaustion (YE) for yolk-sac larvae, and to reach PNR (point-of-no-return) and 50 and 100% mortality (mort) for both yolk-sac and older larvae were obtained from Yin and Blaxter (1987 a)

Species	Days from hatch to:					Rearing temp. (°C±SD)
	first feeding	YE	PNR	50% mort	100% mort	
Yolk-sac larvae						
Clyde herring	6	8	12	20	22	7.5±0.5
Baltic herring	3	5	8	14	16	9.2±0.6
Cod	5	7	11	14	16	6.9±0.4
Flounder	6	7	10	12	13	9.5±0.8
	Days from initial starvation to:					
Older larvae	PNR	50% mort	100% mort			
Clyde herring	6	10	12			9.6±0.7
36 d[a]	7	10	13			10.5±0.3
60 d[a]						

[a] Age in days post-hatching

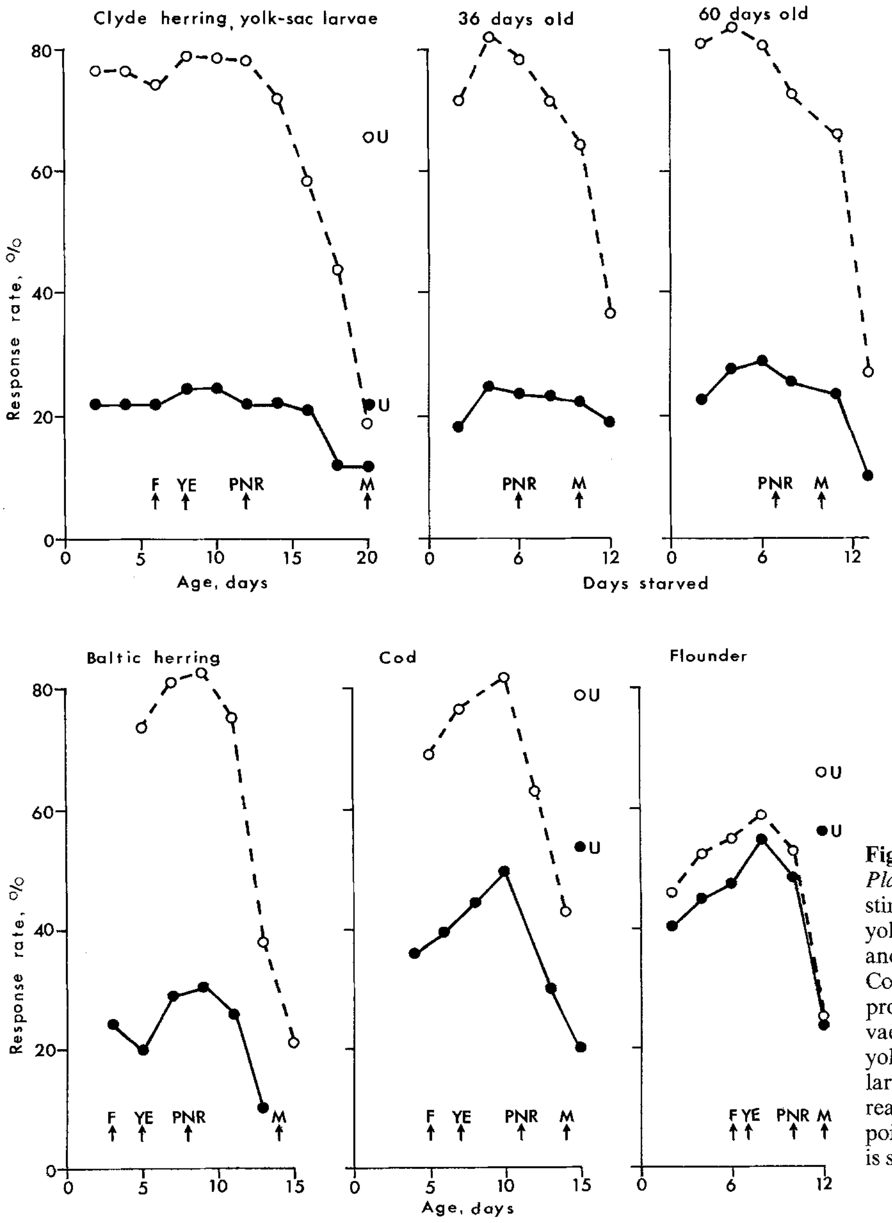

Fig. 1. *Clupea harengus, Gadus morhua* and *Platichthys flesus.* Startle response rates to tactile stimuli during early development and starvation of yolk-sac larvae of Clyde and Baltic herring, cod and flounder and older larvae of Clyde herring. Continuous line represents responses induced by probe; dashed line, by pipette. U: unstarved larvae, in comparison with starved ones. Age for yolk-sac larvae, is in days post-hatching; for older larvae, as days since onset of starvation. Time to reach initial feeding (F), yolk exhaustion (YE), point-of-no-return (PNR) and 50% mortality (M) is shown (from Yin and Blaxter, 1987 a)

Table 2. *Clupea harengus, Gadus morhua* and *Platichthys flesus.* Total fresh length (cm) during early development and starvation of larvae measured from video screen. For comparison, at end of starvation period, lengths of some unstarved larvae (U) are also presented. For 36 and 60 d-old Clyde herring larvae, measurements were taken on the first day starved. Age is in days post-hatching

Species	Age (d)	Total length (mean ± 95% CL)	*N*
Clyde herring	2	0.91 ± 0.03	11
	4	0.94 ± 0.03	11
	6	0.97 ± 0.03	24
	8	1.00 ± 0.03	10
	10	1.02 ± 0.04	13
	12	1.03 ± 0.03	16
	14	1.04 ± 0.03	15
	16	1.04 ± 0.04	15
	18	1.04 ± 0.03	13
	20	1.03 ± 0.03	10
	20 (U)	1.34 ± 0.03	21
	36	1.45 ± 0.08	13
	60	1.90 ± 0.11	19
Baltic herring	1	0.72 ± 0.04	17
	3	0.80 ± 0.03	12
	5	0.83 ± 0.04	13
	7	0.86 ± 0.03	16
	9	0.88 ± 0.02	16
	11	0.87 ± 0.03	14
	13–15	0.87 ± 0.04	12
Cod	2	0.46 ± 0.02	12
	4	0.47 ± 0.02	10
	6	0.49 ± 0.02	15
	8	0.50 ± 0.02	11
	10	0.53 ± 0.02	10
	13–15	0.53 ± 0.02	20
	14 (U)	0.58 ± 0.02	18
Flounder	2	0.31 ± 0.01	10
	4	0.37 ± 0.02	10
	6	0.42 ± 0.01	11
	8	0.43 ± 0.01	10
	10	0.42 ± 0.01	12
	12	0.41 ± 0.01	10
	13 (U)	0.46 ± 0.01	20

all depths of the holding tank. The larvae were observed by a television camera using transmitted illumination from a strobed infra-red light-emitting diode positioned under the dish (see Batty, 1983, for details). The larvae were watched on the viewing screen of the camera and recordings made on videotape at a rate of 50 frames/s. After 5 min acclimation time, the larvae were stimulated either by touching them with a fine probe, 0.02 cm in diameter, or by following and attempting to suck them into a glass pipette, 0.15 cm in diameter. Although it was not possible to identify individual larvae, an attempt was made to use all the larvae in the dish and to avoid repeated stimulation of the same individuals with the consequent danger of habituation. The experiment was stopped after 40 or 50 encounters over a 10 to 15 min period.

Video-recordings were analysed frame-by-frame. Some larvae showed a very sharp flexion of the body following stimulation (see Weihs, 1973; Blaxter and Batty, 1985; Eaton and Nissanov, 1985; Eaton and DiDomenico, 1986). These startle or C-responses were completed over 1 to 2 frames (20 to 40 ms). The proportion of larvae responding in this way gave the response rate. Following a startle response, escape speeds were measured in several ways using the methods of Bailey and Batty (1984). The *effective* mean speed was calculated over 10 frames (200 ms) by measuring the straight-line displacement of the snout of the larvae between Frame 1 and Frame 10. For comparison, in some experiments the "*true*" mean speed was estimated by aggregating the displacements of the snout frame-by-frame over the first 10 frames. The *maximum* speed was also calculated from the maximum displacement of the snout between any pair of consecutive frames between Frame 3 and Frame 10. The first two frames, during which the startle flexion took place, involved considerable lateral movement of the head and were not used for this purpose.

Results

Startle response rates

Larvae of all species and different stages of development used, and starving larvae showed startle responses (Fig. 1). In general, the response rates increased somewhat during early starvation and remained level until near the point-of-no-return (PNR, when 50% of larvae, although still alive, are no longer strong enough to feed; Blaxter and Hempel, 1963). After the PNR, the response rates declined slowly.

It is clear that the larvae were much more responsive to the pipette than to the probe. The initial response rates were about 20 to 25% in herring and 35 to 40% in cod and flounder using the probe, but about 70 to 80% using the sucking action of a pipette in all species except in flounder, where the rates using probe or pipette were similar (see Fig. 1). A Mantel-Haenszel test (Mantel and Haenszel, 1959; Mantel, 1963) showed the pipette:probe differences to be statistically significant ($P < 0.001$) for all but the flounder larvae. This might be explained by the small size of the flounder, which were sometimes sucked into the pipette before the response occurred. Response rates to the pipette were similar for all cases (except the flounder) at comparable stages of development, but the cod and flounder larvae appeared more responsive to the probe than the herring and there was also a significant difference between the response rates of the different species ($P < 0.001$, Mantel-Haenszel test).

Maximum escape speeds

Maximum escape speeds during early development and starvation for both yolk-sac and older larvae are shown in

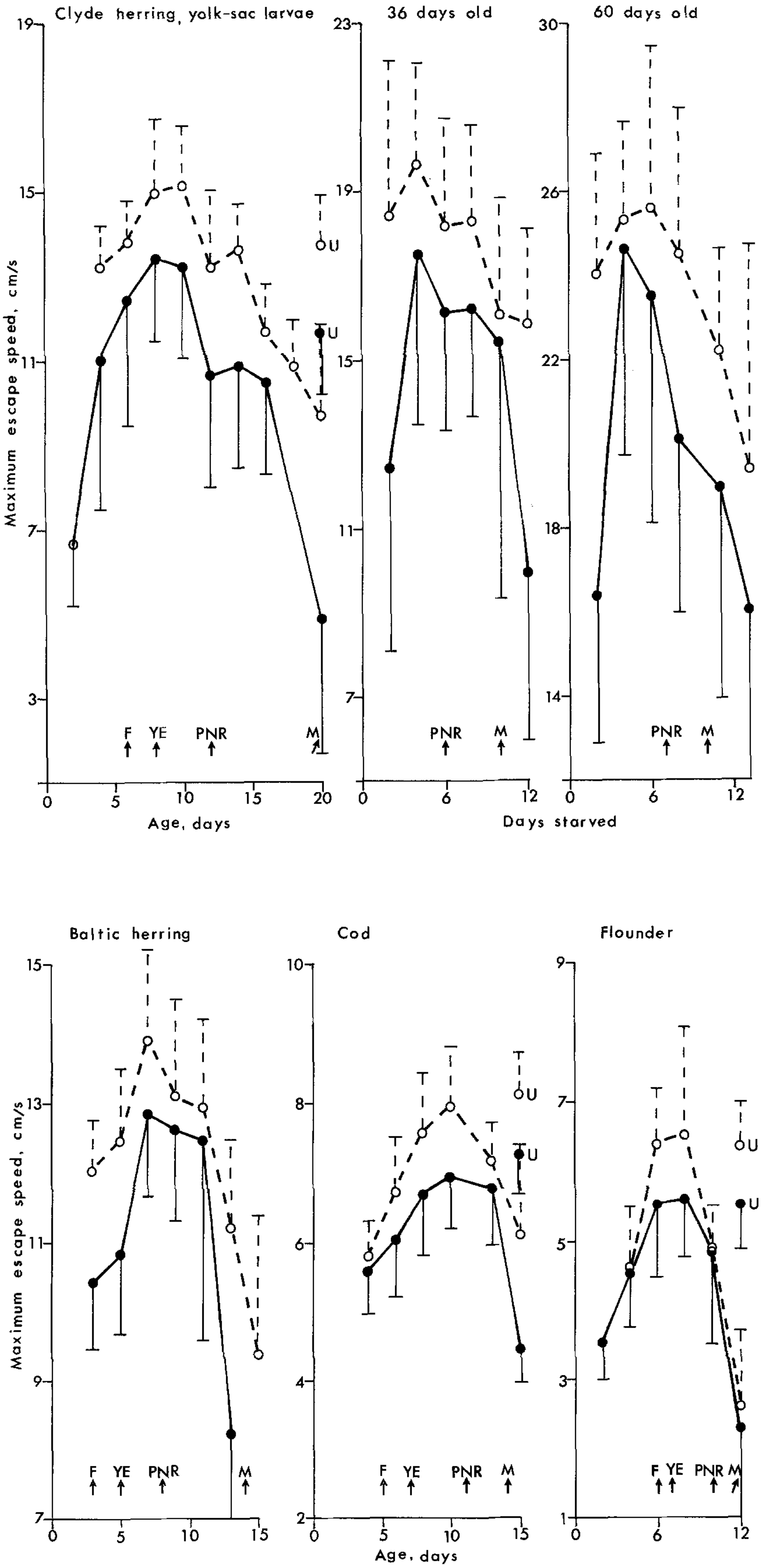

Fig. 2. *Clupea harengus*, *Gadus morhua* and *Platichthys flesus*. Changes in maximum escape speed during early development and starvation of larvae. Vertical bars are 95% confidence limits (for clarity only one side is shown). For converting cm/s to BL/s use Table 2. Other details as in legend to Fig. 1

Fig. 2. The pattern of the change in maximum escape speeds was very similar in all experiments. In yolk-sac larvae, the speeds rapidly increased from hatching and reached a peak at the same time as the response rates, i.e., 1 to 2 d before the PNR. In 36 and 60 d-old larvae of Clyde herring, the maximum escape speeds remained level for 7 to 8 days after the onset of starvation. After the PNR, the speeds in both yolk-sac and older larvae dropped but still remained quite high until the larvae became moribund, when the speeds declined dramatically.

For a comparison between species, the highest maximum escape speeds observed are given in Table 3. In general, those induced by the pipette were only about 1 to 2 cm/s higher than those induced by the probe. It is clear that the speeds varied with species. This might be caused by differences in body form or by size. If the speeds are recalculated as specific speeds (body lengths/s, BL/s) the differences between species are much lower. For example, the highest maximum escape speeds induced by pipette were 15.2 cm/s (14.9 BL/s), 13.9 cm/s (16.1 BL/s), 8.0 cm/s (15.1 BL/s) and 6.5 cm/s (15.1 BL/s) for the yolk-sac larvae of Clyde and Baltic herring, cod and flounder respectively.

Similarly, the effect of growth on the speeds was very marked if expressed as cm/s, e.g. the highest maximum escape speeds were 15.2, 19.6 and 25.6 cm/s for yolk-sac, 36 and 60 d-old larvae of Clyde herring respectively, but there were no noticeable differences, and even a slight decrease, when specific speeds were used (Table 3).

Mean escape speeds

Changes in mean escape speeds induced by pipette or by probe during early development and starvation varied in a similar fashion to the maximum escape speeds, with a peak before the PNR (Fig. 3). The peak mean escape speeds are also given in Table 3. In general, the mean escape speeds of all species were about one half of the maximum escape speeds and there was only a small difference between responses induced by use of the pipette or probe.

Table 3. *Clupea harengus, Gadus morhua* and *Platichthys flesus.* Highest escape speeds (cm/s) during progressive starvation (BL/s given in parentheses). Speeds are means ± 95% confidence limits

	Probe		Pipette	
	max.	mean	max.	mean
Yolk-sac larvae				
Clyde herring	13.5±2.1	6.6±1.9	15.2±1.3	7.3±1.0
	(13.2±2.1)	(6.5±1.9)	(14.9±1.3)	(7.2±1.0)
Baltic herring	12.9±1.2	6.0±0.7	13.9±1.3	6.5±1.0
	14.9±1.4	(6.9±0.8)	(16.1±1.5)	(7.5±1.2)
Cod	6.9±0.7	3.6±0.5	8.0±0.8	4.3±0.5
	(13.2±1.3)	(7.2±1.0)	(15.1±1.5)	(8.6±1.0)
Flounder	5.6±0.9	3.0±0.6	6.5±1.5	3.5±0.9
	(13.0±2.1)	(6.9±1.4)	(15.1±3.5)	(8.1±2.1)
Older larvae, Clyde herring				
36 d-old	17.6±4.1	8.2±2.3	19.6±2.4	10.0±1.4
	(12.1±2.8)	(5.7±1.6)	(13.5±1.6)	(6.9±1.0)
60 d-old	24.7±4.9	12.7±2.9	25.6±3.9	14.5±1.5
	(13.0±2.6)	(6.7±1.5)	(13.5±2.0)	(7.6±0.8)

Mean escape speeds were also measured by aggregating the displacement distances frame-by-frame over the ten frames in the pipette experiments (Fig. 4). A comparison of the results with those in Fig. 3 should give an estimate of how straight the escape paths were. The pattern of change in speed was very similar to the previous measurements, but the speeds measured were higher by 2 cm/s for both yolk-sac and older larvae of herring, 1 to 1.5 cm/s for cod and 1 cm/s for flounder larvae when compared with speeds calculated by straight-line displacements.

Changes in mean escape speeds during an escape movement

Changes in mean escape speeds frame-by-frame during an escape movement (10 frames = 200 ms) are shown in Fig. 5. The relationship of speed with time in all cases was parabolic. After the initial flexion of the body during the first 1 to 2 frames, the larvae accelerated, the mean speed reaching a peak at Frames 4 to 5. The displacement distances during the first five frames were about 0.9 to 1.2 BL for all species (0.9 to 1.0 for Clyde herring, 1.1 for Baltic herring, 1.2 for cod and 1.05 for flounder). Subsequently, speeds decreased as most larvae started to glide, but there were still some larvae (about 10% or more) which did maintain very high propulsive speeds (about 17.5 to 22.5 BL/s) up to Frames 6 to 8. The speed over the ninth to tenth frame was still 2.0 to 2.3 times the maximum cruising speed in older Clyde herring larvae, 1.6 to 1.8 times in yolk-sac herring and flounder larvae and 1.2 times in cod larvae (unpublished data of the authors). In other words, the effect of the startle response was still evident after 9 frames (180 ms) in herring and flounder larvae.

Directionality

The initial startle turn could be classified into away from (A) or towards (T) the stimulus or (A/T) if the larval body axis was aligned with the stimulus (Blaxter and Batty, 1985). From Table 4, it can be seen that over all species and different stages of development and starvation many more larvae turned away from the stimulus than turned towards it. The pooled results were statistically significant ($P < 0.01$, chi-square test) in all species except the flounder, in which the directionality in response to the pipette only was significant, but at the $P < 0.05$ level.

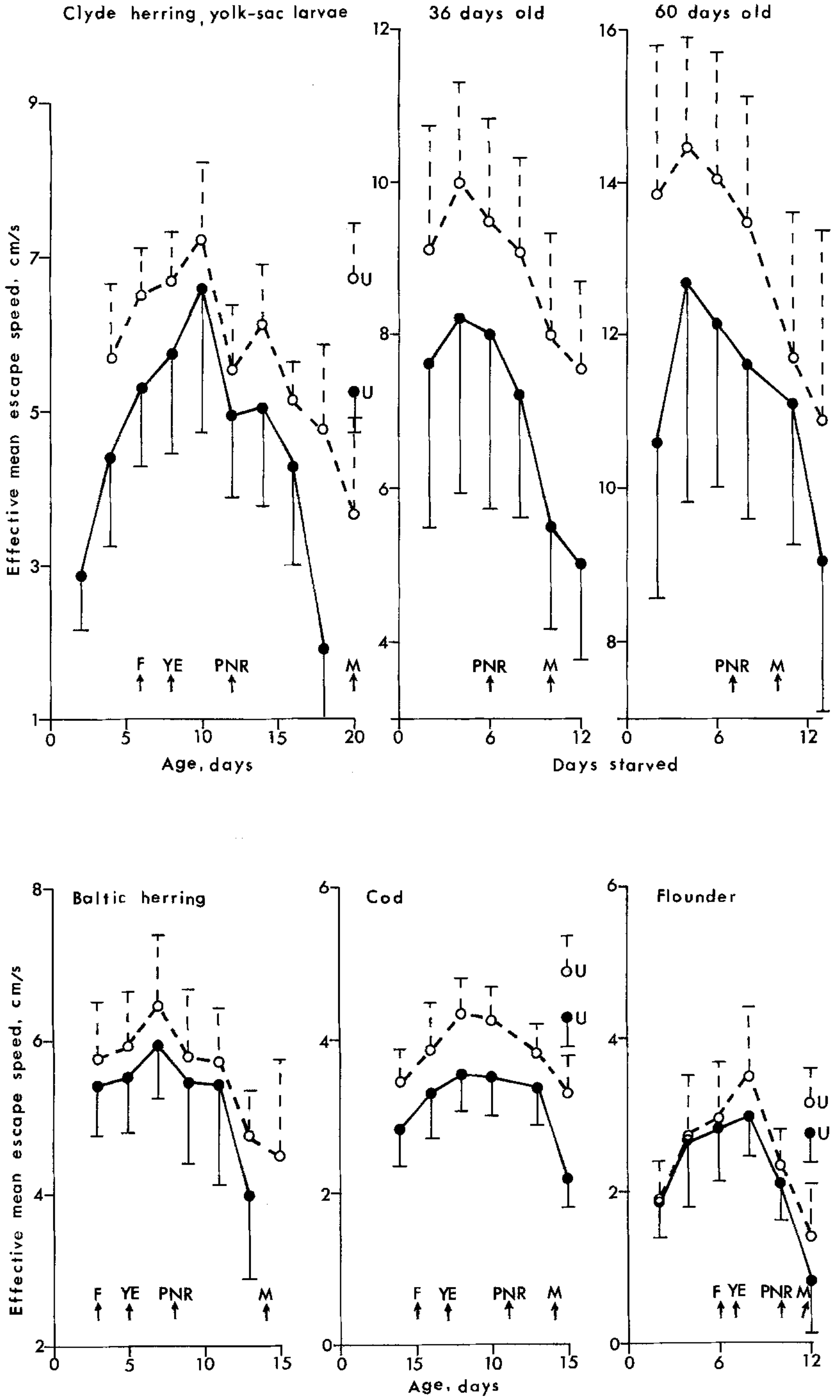

Fig. 3. *Clupea harengus, Gadus morhua* and *Platichthys flesus.* Changes in effective mean escape speed during early development and starvation of larvae. Vertical bars are 95% confidence limits (for clarity only one side is shown). For converting cm/s to BL/s use Table 2. Other details as in legend to Fig. 1

The ability of larvae to make directional turns tended to increase with the development of larval organs. In yolk-sac larvae of herring and cod, the chi-square tests showed that the difference in the A's and T's was significant only when the larvae developed and reached the feeding stage (see Table 4). A Mantel-Haenszel test on all the directional data showed that there were no significant differences in directionality between species, stimulus types, or during starvation.

Discussion

During starvation there was a tendency for the response rate and mean and maximum swimming speeds to peak shortly before the PNR. Subsequently, there was a fairly rapid decline in responsiveness at a time when death was inevitable from starvation, if not from predation. It seems an appropriate adaptation that escape performance should

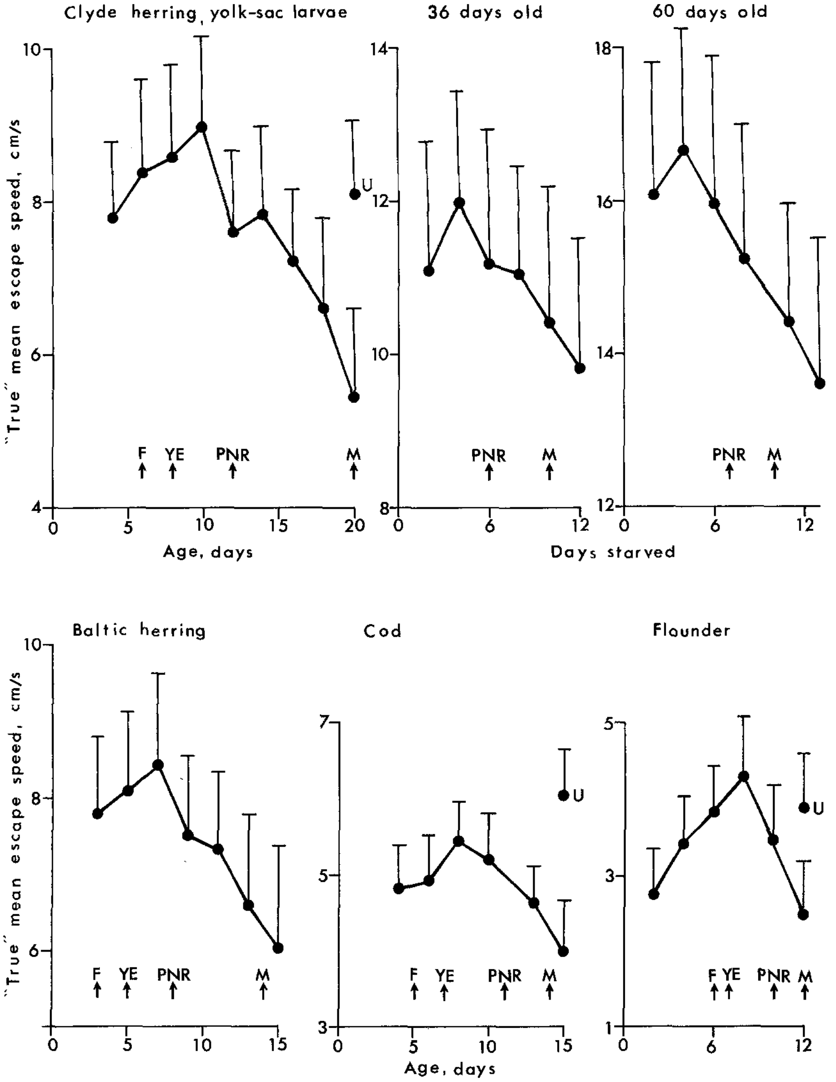

Fig. 4. *Clupea harengus, Gadus morhua* and *Platichthys flesus.* Changes in "true" mean escape speed induced by pipette during early development and starvation of larvae. Vertical bars are 95% confidence limits (for clarity only one side is shown). For converting cm/s to BL/s use Table 2. Other details as in legend to Fig. 1

remain constant (or even increase) during most of the period when the larvae are still viable. Somewhat similar results were obtained by Blaxter and Ehrlich (1974), who found that herring and plaice larvae maintained their vertical migration activity during starvation up to the PNR. Yin and Blaxter (1987a) also found that several marine species increased their first-feeding ability if offered food after limited periods of starvation at the end of the yolk-sac stage. Wyatt (1972) reported that suboptimal food concentrations increased the activity level of plaice larvae. The underlying "strategy" during starvation therefore seems to be to maintain activity and responsiveness in spite of the high energetic cost.

The response rates induced by probe in herring larvae at the feeding stage obtained in this study were 20 to 22%, similar to the results reported by Bailey and Batty (1984), but about 35 to 40% in cod and flounder larvae. The response rates induced by pipette, however, were much higher than those by probe in all species except flounder. It seems that response rate depends on both the type of stimulation (the pipette being larger) and the species.

Bailey and Batty (1984) did not find a consistent difference in the escape speeds of herring, cod, flounder or plaice larvae stimulated by a probe or the sting of a medusa. On the other hand Blaxter and Batty (1985) found, in herring larvae, specific escape speeds of 5.8 BL/s to tactile stimulation, 10.1 BL/s to the sting of a medusa and 11.6 BL/s in response to an acoustic stimulus. The mean escape speed of northern anchovy larvae was described by a regression of speed on larval length (L), viz. Speed = 4.53 L + 2.73 cm/s after visual stimulation (Webb, 1981). In our experiments, the escape speeds (maximum and mean) induced by probe for herring, cod and flounder larvae during early starvation were similar to the results measured by Bailey and Batty (1984) using a similar video system, but the speeds were somewhat lower than those induced by pipette. The maximum escape speeds of 13 to 16 BL/s induced by pipette at 9° to 10 °C obtained in this study are very low compared with Fuiman's (1986) results of 50 to 64 BL/s on zebra danios (*Danio [Brachydanio] rerio*) and Swain's (1986) results of 38 to 53 BL/s on sticklebacks (*Gasterosteus aculeatus*) stimulated by electric

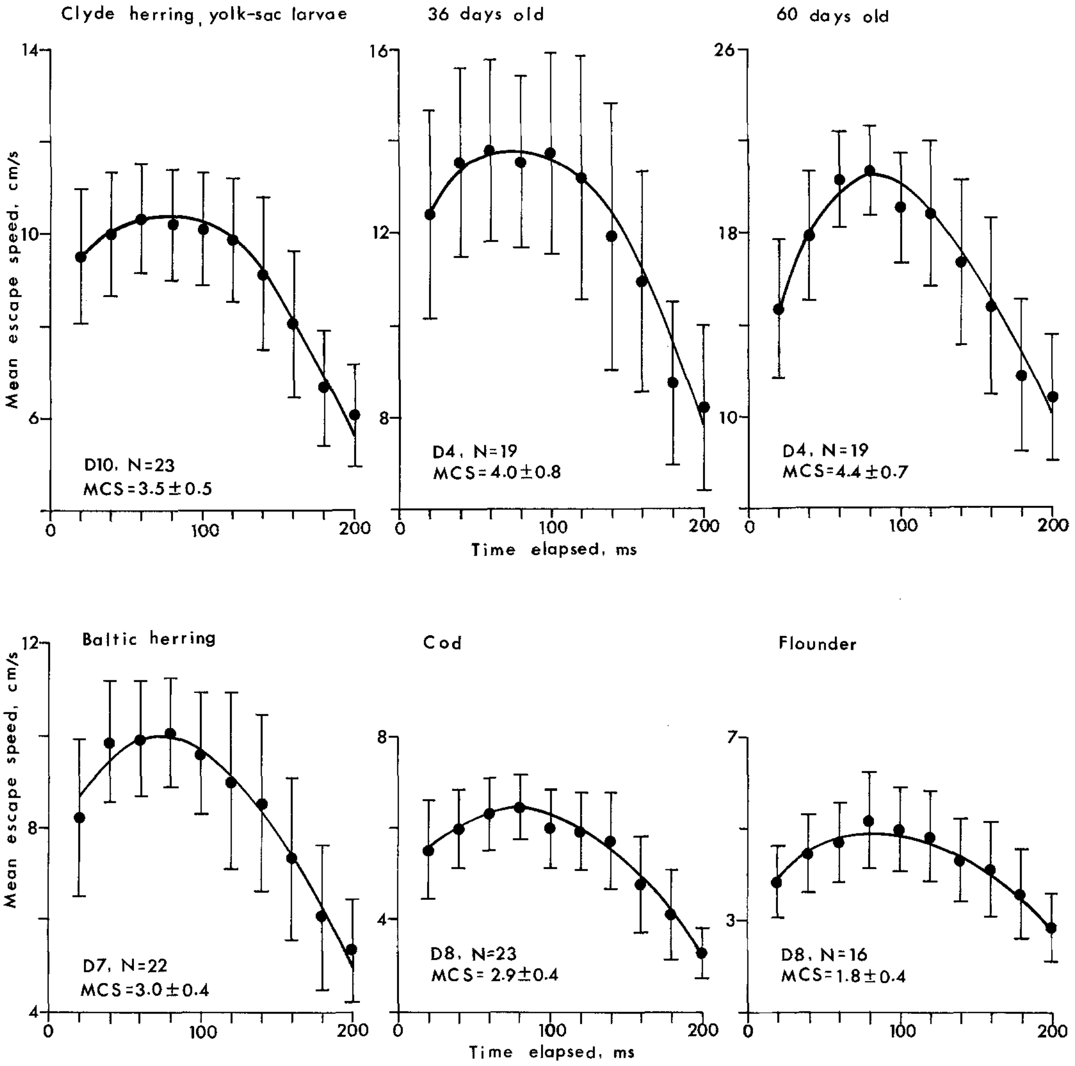

Fig. 5. *Clupea harengus, Gadus morhua* and *Platichthys flesus.* Changes in mean escape speeds frame-by-frame during an escape movement (10 frames = 200 ms) of larvae. Vertical bars are 95% confidence limits. Abscissae give time elapsed since start of response. D and N: day examined and number of larvae measured; e.g. D8 = Day 8 post-hatching for yolk-sac larvae, D4 = Day 4 from start of starvation for older larvae. MCS: maximum cruising speed (cm/s), as mean ± 95% confidence limits, from authors' unpublished data. For converting cm/s to BL/s use Table 2

shock, even allowing for the much higher temperatures they used. These authors used cine-filming with a high framing rate and these very high specific speeds were maintained for very short periods which could not have been observed by our video system. Although such short-term high specific speeds might be inadequate for escaping a pursuit predator, they might be of value if the larva attempted escape by "dodging" movements out of the predator's path.

Blaxter and Batty (1985) reported that herring larvae 19 to 36 mm long did not make directional responses to acoustic stimuli until the head lateral line, and its coupling with the bulla, had developed. It is clear from the present results that much smaller herring larvae can make directional escape responses from tactile stimuli. It is not possible, however, to draw any firm conclusions about the sense organs involved in these tactile responses. Probes or pipettes could stimulate the free neuromast system, known to be present, or putative tactile receptors, or they could cause sufficient movement of the larval body to stimulate the inner ear. Zebra danios can still show a startle response when touched, even after removal of the otoliths (Eaton and DiDomenico, 1986) suggesting nervous pathways from peripheral receptors to the Mauthner cells. It seems likely that such pathways exist in the species we used.

Acknowledgements. M. C. Yin, whose stay was originally financed by the Chinese Government and the British Council, wishes to thank the Director of the Dunstaffnage Marine Research Laboratory for providing facilities and supporting an extension of his stay to complete this work. The authors wish to thank Dr. L. A. Fuiman and Dr. R. S. Batty for commenting on the manuscript and Dr. R. S. Batty for computing the Mantel-Haenszel statistical tests.

Table 4. *Clupea harengus, Gadus morhua* and *Platichthys flesus.* Numbers of larvae turning away from (A), towards (T) and aligned with (A/T) the point of stimulation (probe or pipette) during early development and progressive starvation. Chi-squared tests are given for A's vs T's; asterisks indicate those significantly different from a 50:50 distribution at * $P<0.05$, and ** $P<0.01$. Age is in days post-hatching for yolk-sac larvae, and days from onset of starvation for older Clyde herring larvae

Species	Age (d)	Probe				Pipette			
		A	T	A/T	χ^2	A	T	A/T	χ^2
Yolk-sac larvae									
Clyde herring	2	6	8	1	0.29	9	6	8	0.60
	4	4	4	2	0.00	10	7	6	0.53
	6	5	3	3	0.50	11	8	4	0.47
	8	11	2	2	6.23*	14	5	4	4.26*
	10	8	2	2	3.60	17	4	5	8.04**
	12	5	1	2	2.67	13	6	3	2.58
	14	4	2	2	0.67	14	8	4	1.63
	16	6	4	0	0.40	12	7	5	1.31
	18	4	2	0	0.67	5	7	3	0.33
	20	4	3	2	0.14	3	5	4	0.50
	Pooled	57	31	16	7.68**	108	63	46	11.84**
Baltic herring	3	7	6	1	0.08				
	5	5	1	1	2.67	17	6	5	5.26*
	7	9	2	2	4.45*	15	4	3	6.37*
	9	10	4	1	2.57	19	4	2	9.78**
	11	5	2	0	1.28	16	7	5	3.52
	13	6	3	0	3.00	16	10	1	1.38
	15					6	3	1	1.00
	Pooled	42	18	5	9.60**	89	34	17	24.59**
Cod	4–5	12	8	3	0.80	16	8	3	2.67
	6–7	12	5	2	2.88	15	4	4	6.36*
	8	14	5	1	4.26*				
	10	14	6	1	3.20	18	5	4	7.34**
	12–13	11	5	2	2.25	17	9	1	2.46
	14–15	6	4	1	0.40	6	5	4	0.09
	Pooled	69	33	10	12.71**	72	31	16	16.32**
Flounder	2	10	7	2	0.53	10	6	1	1.00
	4	8	5	4	0.69	9	5	6	1.14
	6	7	3	9	1.60	8	3	5	2.27
	8	6	4	6	0.40	9	4	3	1.92
	10	5	4	8	0.11	9	6	1	0.60
	12	1	2	1	0.33	3	2	5	0.20
	Pooled	37	25	30	2.32	48	26	21	6.54*
Older larvae									
Clyde herring	36 (2)[a]	8	0	0	8.00**	16	3	1	8.89**
	(4)	7	1	0	4.50*	16	6	3	4.55*
	(6)	5	1	0	2.67	15	7	1	2.90
	(8)	7	2	1	2.78	9	3	1	3.00
	(10)	6	2	1	2.00	13	6	1	2.58
	(12)	7	4	1	0.82	9	4	1	1.92
	Pooled	40	10	3	18.00**	78	29	8	22.44**
	60 (2)	10	1	1	7.36**	20	5	1	9.00**
	(4)	9	1	2	6.40*	17	6	4	5.26*
	(6)	7	2	2	2.78	14	5	3	4.26*
	(8)	11	5	1	2.25	14	7	4	2.33
	(11)	12	7	2	1.32	14	9	3	1.09
	(13)	6	3	1	1.00	3	1	1	1.00
	Pooled	55	19	9	17.51**	82	33	16	20.88**

[a] Values in parentheses: no of days starved

Literature cited

Bailey, K. M. and R. S. Batty: Laboratory study of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring: development and vulnerability to capture. Mar. Biol. *83*, 287–291 (1984)

Batty, R. S.: Observations of fish larvae in the dark with television and infra-red illumination. Mar. Biol. *76*, 105–107 (1983)

Blaxter, J. H. S. and R. S. Batty: The development of startle responses in herring larvae. J. mar. biol. Ass. U.K. *65*, 737–750 (1985)

Blaxter, J. H. S. and K. F. Ehrlich: Changes in behaviour during starvation of herring and plaice larvae. *In:* The early life history of fish, pp 575–588. Ed. by J. H. S. Blaxter. Berlin: Springer-Verlag 1974

Blaxter, J. H. S. and G. Hempel: The influence of egg size on herring larvae. J. Cons. perm. int. Explor. Mer *28*, 211–240 (1963)

Eaton, R. C. and R. DiDomenico: Role of the teleost escape response during development. Trans. Am. Fish. Soc. *115*, 128–142 (1986)

Eaton, R. C. and J. Nissanov: A review of Mauthner-initiated escape behaviour and its possible role in hatching in the immature zebrafish, *Brachydanio rerio*. Envir. Biol. Fish. *12*, 265–279 (1985)

Fuiman, L. A.: Burst-swimming performance of larval zebra danios and the effects of diel temperature fluctuations. Trans. Am. Fish. Soc. *115*, 143–148 (1986)

Laurence, G. C.: Comparative swimming ability of fed and starved larval large mouth bass (*Micropterus salmoides*). J. Fish. Biol. *4*, 73–78 (1972)

Mantel, N.: Chi-square tests with one degree of freedom, extensions of the Mantel-Haenszel procedure. J. Am. statist. Ass. *58*, 690–700 (1963)

Mantel, N. and W. Haenszel: Statistical aspects of the analysis of data from retrospective studies of disease. J. natn. Cancer Inst. *22*, 719–748 (1959)

Swain, D. P.: Adaptive significance of variation in vertebral number in fishes: evidence in *Gasterosteus aculeatus* and *Mylocheilus caurinus*, 198 pp. Ph.D. thesis, University of British Columbia 1986

Webb, P. W.: Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivore, *Amphiprion percula*. Fish. Bull. U.S. *79*, 727–735 (1981)

Webb, P. W. and R T. Corolla: Burst swimming performance of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull. U.S. *79*, 143–150 (1981)

Weihs, D.: The mechanism of rapid starting of a slender fish. Biorheology. *10*, 343–350 (1973)

Wyatt, T.: Some effects of food density on the growth and behaviour of plaice larvae. Mar. Biol. *14*, 210–216 (1972)

Yin, M. C. and J. H. S. Blaxter: Morphological changes during growth and starvation of larval cod (*Gadus morhua* L.) and flounder (*Platichthys flesus* L.). J. exp. mar. Biol. Ecol. *104*, 215–228 (1986)

Yin, M. C. and J. H. S. Blaxter: Feeding ability and survival during starvation of marine fish larvae reared in the laboratory. J. exp. mar. Biol. Ecol. *105*, 73–83 (1987a)

Yin, M. C. and J. H. S. Blaxter: Temperature, salinity tolerance and buoyancy during early development and starvation of Clyde and North Sea herring, cod and flounder larvae. J. exp. mar. Biol. Ecol. *107*, 279–290 (1987b)

Date of final manuscript acceptance: August 7, 1987.
Communicated by J. Mauchline, Oban