

## THE SWIMMING SPEEDS OF PLAICE LARVAE

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### INTRODUCTION

Although there have been a number of studies on the swimming speeds of adult fish (e.g. Bainbridge, 1958; Blaxter & Dickson, 1959), there has been no work on their pelagic larvae apart from that of Bishai (1960). This clearly reflects the magnitude of the problems involved, for such larvae are difficult to obtain and so delicate that they are easily fatally damaged. Moreover, their transparency and small size add considerably to practical experimental difficulties.

However, hatchery technique developed in this laboratory facilitated the steady supply of suitable numbers of plaice (*Pleuronectes platessa* L.) larvae in excellent condition and at all stages of development. The plaice was a particularly desirable choice, because the larval biology of this species in the southern North Sea is receiving intensive study at the present time. One of the problems connected with such a survey of pelagic larvae is the development of an adequate sampling method, for it has been established that the larger fish larvae avoid capture by the commonly used Hensen and Heligoland nets (Ahlstrom, 1954; Bridger, 1956). Information regarding the swimming speed of larvae at different stages of development was therefore badly needed and was the object of the present investigation.

### MATERIAL

All fish used in these experiments were hatchery-reared. Eggs were collected from the Southern Bight of the North Sea on 30 January 1962, and those of the group III stages of development (Simpson, 1959; 7-10 days old at the prevailing sea surface temperature of 7.5° C.) were sorted into three glass tanks 60 × 30 × 30 cm. (2 × 1 × 1 ft.) in size. A depth of 20 cm. of circulating sea water was maintained in these by the position of the overflows through which water returned to a reservoir. It was then oxygenated and raised to a header tank by an airlift, returning to the aquaria by gravity feed.

After hatching and absorption of the yolk the plaice larvae were fed with *Artemia* nauplii. 140 l. of water were withdrawn from circulation daily and replaced by fresh off-shore water, thus avoiding the accumulation of metabolites in the system. All fish used were feeding and in good condition. The water temperature was maintained between 6.5 and 7.5° C.

Shelbourne (1957) defined five developmental stages through which the larvae pass after hatching. These stages, used extensively for convenience and because allometric growth makes length a rather poor criterion of age, are also adopted in the present paper. However, stage III as originally defined lasts too long for convenience and is

here further subdivided. These stages are characterized in Table 1 and the important diagnostic points are shown in Fig. 1. Their use to express the degree of development renders the rather misleading term 'post-larva' superfluous, and all fish prior to metamorphosis can be called larvae whether they are still feeding on yolk or not.

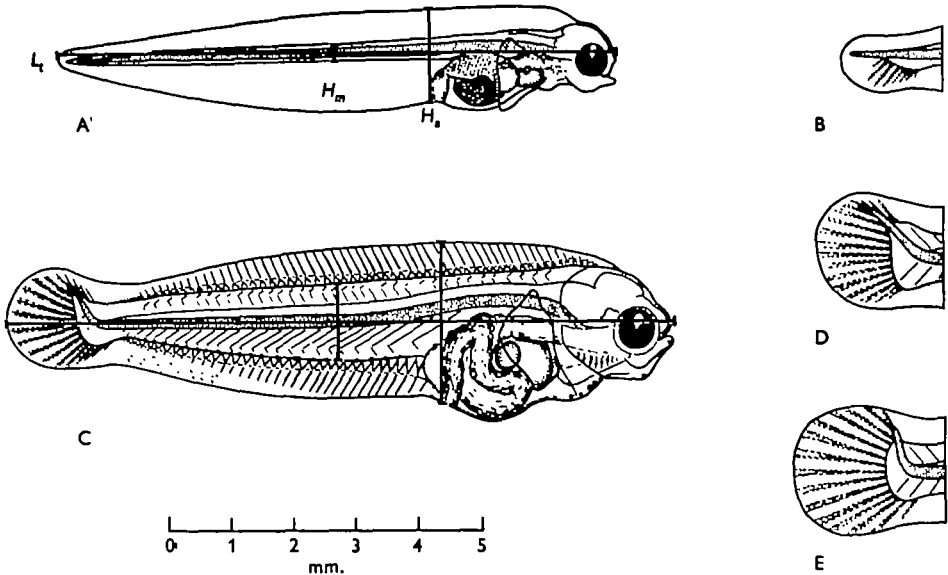


Fig. 1. Methods of staging and measuring plaice larvae (see also Table 1 and the text). A, Stage Ib, yolk still present, no hypural fin rays; B, stage II, tail showing development of fin rays, about late IIa or early IIb; C, stage IIIb; D, stage III, tail showing notochord in position transitional between IIIa and IIIb; E, stage III, tail showing notochord in position almost transitional between IIIb and IIIc. Measurements employed are indicated on A and C.  $L_t$ , Total length;  $H_a$ , total height at the anus;  $H_m$ , height of musculature halfway along fish's length.

Table 1. System of staging plaice larvae based on development of morphological features

Stage	Definitive character	Sub-stage	Definitive character	Subsidiary characters	
I	Yolk present (Fig. 1A)	a	Amount of yolk in sac	Gut straight	
		b		Gut looped	
		c		Hypural rudiment absent	} Intergrading occurs
		d			
II	Yolk resorbed; notochord straight (Fig. 1B)	a	Hypural rudiment present	Marginal fin rays absent	
		b	Hypural fin rays reach and extend fin margin		
III	Notochord bent; eyes symmetrical	a	Notochord upsloped ( $< 45^\circ$ ) (Fig. 1D)	Longest marginal fin rays not more than half way to fin margin	
		b	Notochord upturned ( $> 45^\circ$ ) (Fig. 1C)	Marginal fin rays more than half way to margin	
		c	Notochord turned straight up (Fig. 1E)	Marginal fin rays fully developed	
IV	Eyes asymmetrical	—	—	—	
V	Left eye on or over the edge of head	—	—	—	

The experiments extended from mid-February to the end of April, during which time the larvae progressed from hatching to metamorphosis. Fish were removed throughout this period, so that the experiments were conducted on larvae of all stages from I to IV. After consistent results had been obtained with a larva it was narcotized with 7.5%  $\text{MgSO}_4$  solution and fixed in Bouin. It was then staged and standard measurements (see Fig. 1) were made using a binocular microscope and calibrated micrometer eyepiece.

Larvae used in the 1961 experiments, also hatchery-reared, were supplied by my colleague Mr J. D. Riley.

#### METHODS

##### *Direct measurements in still water*

Work was started in 1961 using a moulded glass aquarium tank,  $34 \times 20 \times 20$  cm., standing in a water bath cooled to  $6.5^\circ \text{C}$ . It was hoped to be able to stimulate the larvae into activity and to measure the speed of swimming. The tank stood over a black background marked with a centimetre grid to assist measurement of distance, and the time was taken with a stopwatch calibrated to tenths of a second. The greatest difficulty, however, was to induce the larvae to swim (other than very slow cruising), though various methods were tried. Most successful was the simplest, touching or prodding with a glass rod or tube, the jagged broken edge of the latter being more effective. Some more elaborate methods, outlined below, were failures.

The knowledge that larvae can avoid vertically hauled nets suggested that they might respond to the movements and vibration of the hauling rope (though it is more likely that the response is visual). Plucking a length of taut elastic,  $6 \times 6$  mm. section, supported in the tank, produced no visible response from the larvae. The use of a transducer giving frequencies ranging from 5 to 100 c.p.s. was no more successful. According to Jones (1960) it is likely that the lateral line is used to detect low frequencies of this order, and a fully developed lateral line appears to be absent from the early larval stages. Larvae were also subjected to electric pulses of about 200 V. at 1 sec. intervals from a  $100 \mu\text{F}$ . condenser. The discharges caused the larvae to twitch and stunned them if the electrodes were positioned too near them, but there was no escape reaction or any apparent orientated movement such as swimming towards the anode (positive galvanotaxis).

This method, then, suffers from distinct limitations. Nevertheless, data on swimming speeds so obtained accord quite closely with those obtained by the use of a water current, and the difference that was found appears explicable (see below). Some darting speeds also were recorded, and these could not have been otherwise obtained.

##### *Use of the 'fish wheel'*

In 1962 it was possible to instal experimental apparatus in the temperature-controlled plaice hatchery and to employ other methods in addition to the tank. Among these was the 'fish wheel' (Bainbridge, 1958), in which the fish's environment is moved in a direction opposite to, and at the speed of, any sustained movement that the animal makes. Once again it was extremely difficult to make plaice larvae swim and, though larvae at different stages of development were tried, it was never found possible to induce them to swim steadily against the direction of rotation of the wheel.

The use of a striped background made no difference, and it appears that these pelagic larvae do not respond to displacement of the visual field. Metamorphosed plaice and other flatfish do not respond to a moving background of stripes but this may be because they are firmly in contact with the bottom, which of course is stationary (Jones, 1962).

### *Rheotaxis*

The third and most successful method was that employed by Bishai (1960) in which the fish is allowed to swim against a water current of known velocity passing through a long glass tube. The apparatus (Fig. 2) was essentially similar to Bishai's except that a wider experimental tube was used. Water was supplied from the hatchery header tank and passed through a T-piece to either end of the experimental tube. The latter, which

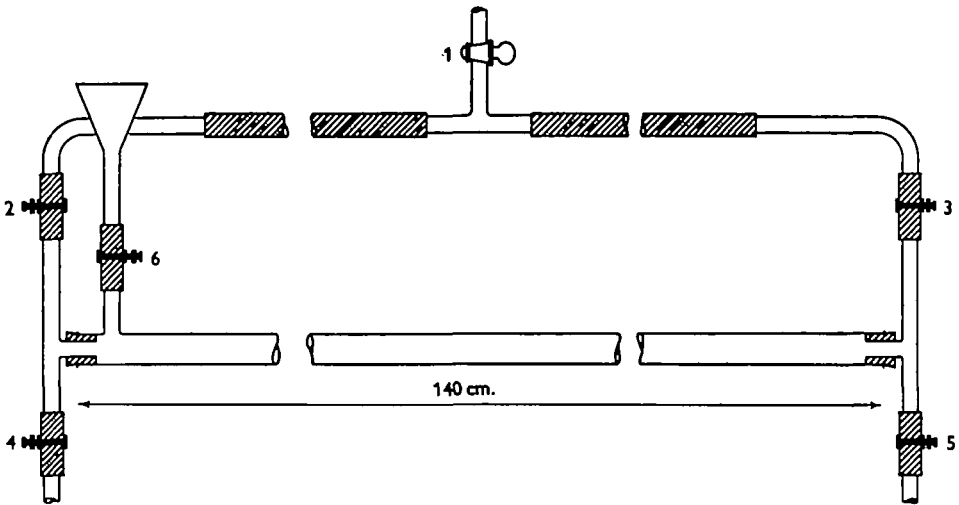


Fig. 2. Apparatus used to determine swimming speeds of larvae against a water current. For mode of operation see text.

was clamped horizontally in front of a plain white background, was 140 cm. long and 1.75 cm. internal diameter (area 2.42 cm.<sup>2</sup>). A funnel fitted near one end of the tube allowed for the introduction of larvae. The rate of flow was controlled by the adjustment of screw clips 2 or 3 and by the extent of the drop between the header tank and the tube. Water running out of the apparatus returned to the hatchery reservoir.

In use, the method was as follows. The entire apparatus was filled from the header and all air removed. A larva was selected from one of the aquaria and gently transferred with a wide bore pipette to the funnel, and clip 6 opened. Clip 5 was then slowly opened and the fish was carried gently down into the tube where it was allowed to rest for some minutes. The clips were closed. The desired direction of flow was obtained by the appropriate use of clips 2-5, and its rate was measured by collecting in a calibrated cylinder, for a period timed with a stopwatch, the water running to waste. The mean flow was the volume per second divided by the cross-sectional area of the tube. Several experiments were performed, allowing rest periods after five or six tries, reversing the direction of water flow between each. In this way the highest

mean flow which the larva would stem was ascertained. It may be noted here that, once the region of entry is passed, there is no change in velocity along the tube.

Bishai (1960) expressed his results solely in terms of mean flow through the tube: but this is quite unsatisfactory. Water flowing through a tube follows a definite pattern, and an understanding of this is essential for the interpretation of any results obtained with this apparatus. Crisp (1955) has discussed precisely these conditions, giving details and references.

In a long tube of circular section the conditions of non-turbulent flow are easily defined. There is a regular velocity gradient from tube surface to the centre, and the velocity  $v$  at any point  $r'$  measured from the centre will be

$$v = \frac{2q}{\pi} \left\{ \frac{1}{r^2} - \left( \frac{r'}{r} \right)^2 \right\}, \tag{1}$$

where  $q$  is the quantity flowing through the tube in unit time and  $r$  is the radius. This equation also shows that the velocity at the centre of the tube,  $v_c$ , is twice the mean velocity,  $v_m$ :

$$v_c = \frac{2q}{\pi r^2} = 2v_m. \tag{2}$$

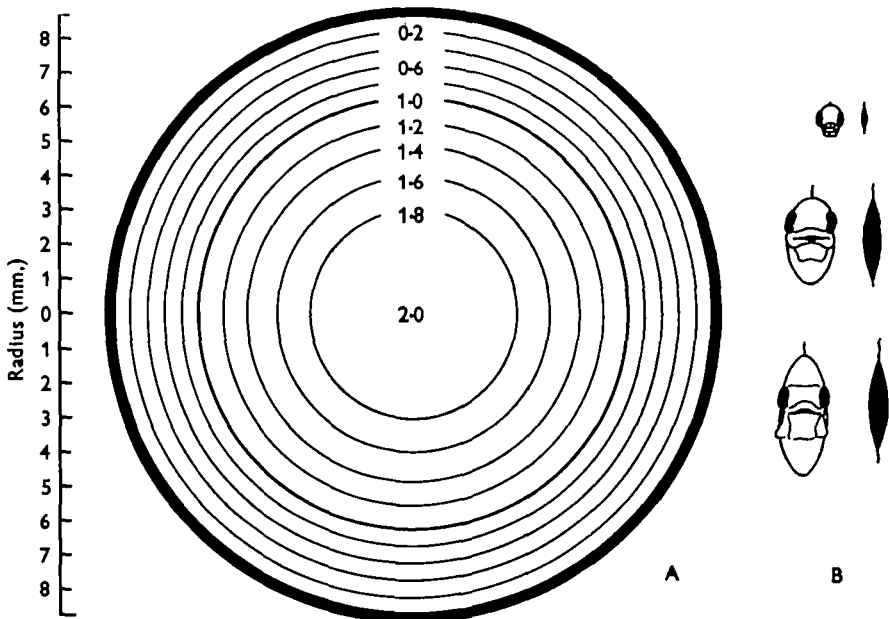


Fig. 3. A, Section of experimental tube 8.75 mm. radius showing the flow contours of the velocity gradient expressed in terms of the mean flow (1.0). B, Head views and transverse body sections at the anus of stage Ib, IIIa and IIIb larvae to the scale of the tube section, A.

These flow characteristics have been represented graphically in Fig. 3. The spacing of the contours shows that the velocity gradient near the tube wall is almost linear, and that it falls away as the centre is approached. It will be appreciated that a fish at the centre will experience a velocity of practically  $2v_m$  while one near the wall will find only about one-sixth of this. Some head-on views of plaice larvae are also shown to

scale in Fig. 3, and it can be seen that the velocity experienced by a fish stemming the flow depends not only on its distance,  $r'$ , from the centre, but also on whether its dorso-ventral axis lies parallel to or across the contours. This information was recorded during the experiments.

## RESULTS

### *Response to water currents*

Larvae introduced into the experimental glass tube tended either to orientate and swim against the flow or to drift passively with it, partly according to the current velocity. While this is broadly what Bishai (1960) found with herring (*Clupea harengus*) larvae, the actual details differ in so many ways that the following résumé of his results will first be given.

Bishai used herring larvae in which the yolk-sac was not absorbed, together with some older larvae which were not, however, feeding. On this account probably only the former should be considered, and these correspond to plaice of stage I. Many of his larvae died on transfer from the rearing tanks to the experimental tube; with careful handling no trouble was experienced with plaice larvae. Once in the tube: 'In every case the fish orientated itself...to face into the current whether drifting or actively swimming... In most cases... their bodies were inclined downwards at  $45^\circ$  to the horizontal... The larvae remained in the middle of the tube where the current was strongest... The larvae maintained themselves against the current [mean velocity 0.58 cm./sec.] for at least 45 minutes without drifting from their position' (Bishai, 1960, pp. 139-40).

With Bishai's results in mind, it was intended to ascertain the maximum current velocity against which a fish could maintain station for a period of some minutes. In practice it became apparent that plaice larvae just would not produce this type of behaviour, and the longest sustained period ever recorded was only 40 sec. After the first experiments, therefore, the objective was somewhat altered to determining the maximum velocity that the fish could just stem, for however brief a period. This means that some of the earliest results were somewhat lower than they should be in comparison with the rest, though it has become apparent that this difference was quite small.

The larvae in general were reluctant to swim, and frequently drifted the entire length of the tube quite passively. Sometimes they would swim against the current, occasionally briefly with it or across it. Larvae orientated head to current generally maintained this posture for several seconds, either holding their position or slowly being carried downstream. In both cases they would frequently give up and be rolled passively down the tube for some distance before reorientating head to stream. Sometimes, also, while swimming steadily they would surge forwards; but this vigorous swimming was never more than momentarily maintained. This behaviour is in striking contrast to that reported for herring larvae.

When swimming against the current the plaice larvae were always near the periphery of the tube; never in the centre. It is difficult to appreciate by what mechanism a herring larva maintaining position in the centre of a tube could detect the direction and strength of the current; for there would be virtually no velocity gradient immediately around the larva (see Fig. 3). Since: 'It must be emphasized that fish have

Table 2. Results of experiments in which plaice larvae were allowed to swim against a current of water flowing through a horizontally supported glass tube

(For explanation of measurements and stages see Table 1 and Fig. 1. The estimated current velocity is one-half that of the distance  $H_a$  from the side of the tube (see Fig. 3).)

Experiment	Fish					Results				
	Stage	Length $L_t$ (mm.)	Height $H_a$ (mm.)	Muscle band $H_m$ (mm.)	$L_t \times H_m$	Flow (cm./sec.)	Mean flow (cm./sec.)	Swimming velocity (cm./sec.)	Remarks	
1	I	7.05	1.36	0.50	3.5	4.9	2.03	0.61	Fish mainly passive; stemming for a few seconds at a time	
2	I	7.50	1.13	0.40	3.0	5.0	2.08	0.52	Stemmed briefly	
3	I	7.60	1.28	0.45	3.8	3.4	1.41	0.42	Stemmed for 15 seconds	
		—	—	—	—	4.6	1.91	0.57	Stemmed for 20 seconds	
4	I	7.75	1.13	0.40	3.1	4.0	1.66	0.42	Steady for 40 seconds	
5	IIa	7.35	1.28	0.45	3.3	10.0	4.15	1.25	Mainly passive; stemming for short spells and once surging 1 cm. forward	
6	IIa	8.50	1.36	0.50	4.25	5.1	2.12	0.64	Stemmed	
7	IIa	9.30	1.68	0.65	6.05	7.4	3.07	1.10	Stemmed for periods of about 5 seconds	
		—	—	—	—	7.5	3.10	1.10	Stemmed for 8 seconds	
		—	—	—	—	7.9	3.28	1.15	Stemmed momentarily	
8	IIIa	8.20	1.90	1.00	8.2	9.4	3.75	1.50	Just stemmed at times	
		—	—	—	—	12.8	5.30	2.10	Just stemmed with short spurts	
		—	—	—	—	12.6	5.25	2.10	Just stemmed	
9	IIIa	9.60	2.08	1.20	11.6	9.0	3.6	1.45	Stemmed for periods of 1-2 seconds	
10	IIIa	10.00	1.76	1.00	10.0	6.6	2.74	1.10	Briefly stemmed	
		—	—	—	—	9.6	3.99	1.60	Not stemmed; once darted forward	
		—	—	—	—	6.0	2.49	1.00	Stemmed for 6 seconds	
11	IIIb	9.70	2.05	1.10	10.7	13.6	5.65	2.25	Very slowly drifting back while swimming hard; just able to advance by spurting	
		—	—	—	—	12.8	5.30	2.10	Twice stemmed for periods of 4 seconds	
		—	—	—	—	13.0	5.40	2.15	Just stemmed	
12	IIIb	10.40	2.55	1.40	14.5	19.0	7.90	3.95	—	
13	IIIc	10.75	2.80	1.35	14.5	15.4	6.40	3.85	Briefly stemmed	
		—	—	—	—	17.2	7.05	4.20	Briefly stemmed	
		—	—	—	—	15.6	6.50	3.90	Stemmed for several seconds	
14	IIIc	10.90	3.50	1.6	17.45	20.6	8.5	5.95	Briefly just stemmed	
		—	—	—	—	20.0	8.3	5.80	Briefly just stemmed	
		—	—	—	—	19.6	8.15	5.90	Several times briefly stemmed; once spurted forward	
15	IIIc	11.85	3.20	1.55	18.4	19.6	8.15	5.30	Briefly advanced against flow	
16	IIIc	12.00	3.60	1.65	19.8	19.6	8.15	5.70	Very briefly held in centre at top of tube; held more easily a little to side	
		—	—	—	—	20.8	8.6	6.00	Just stemmed when spurted	
17	IIIc	12.10	3.50	1.75	21.2	20.4	8.5	5.95	—	
		—	—	—	—	20.8	8.6	6.00	—	
		—	—	—	—	21.0	8.7	6.10	—	
18	IIIc	13.2	4.3	2.1	27.7	19.6	8.15	6.90	Briefly stemmed	
		—	—	—	—	20.0	8.3	7.05	Briefly stemmed	
		—	—	—	—	19.6	8.15	6.90	Briefly stemmed	
19	IV	14.0	4.85	2.5	35.0	20.8	8.6	8.6	Stemmed for 1 second	
		—	—	—	—	22.0	9.1	9.1	Stemmed for several short spells	

never been shown to be orientated with or against the flow of a body of water moving with a constant linear velocity unless they are close to or in sight of the bottom' (Jones, 1960), such a response might be thought to be a visual one. But though adult herring respond to a moving background by swimming against the direction of movement (Jones, 1962), Bishai (1960) asserted that this was not the case for the larvae. Neither do plaice larvae appear to respond to a background of moving stripes, but there is no problem in explaining their means of orientation: the larvae were either in contact with the wall of the tube, in which case they could respond to tactile stimuli;

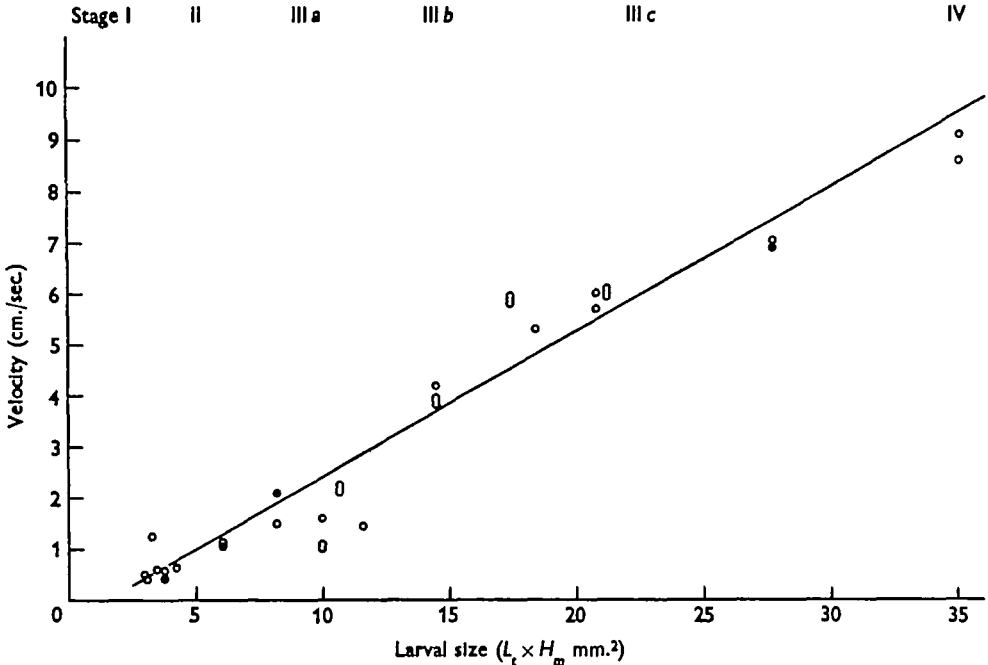


Fig. 4. Regression of the relative velocity achieved by plaice larvae in stemming a water current against larval size (see Table 2). Points shown black represent two identical values.

or across the tube, in which case they would experience a considerable velocity gradient down their length; or orientated head to stream, near and parallel to the periphery of the tube and therefore lying in the region of maximum gradient. It seems uncertain whether fish can detect velocity gradients of the order occurring in this tube (Jones, 1960) and, since it was virtually impossible to be certain whether or not part of a larva was in contact with the glass wall of the tube, it remains undecided whether the velocity gradient was itself detected.

Larvae always took up a position at or near the top of the tube. The posture of a larva swimming against the current was with the body sloping head up tail down at about 25–30° to the horizontal, the antero-dorsal region probably in contact with the wall of the tube most of the time. The fact that larvae always faced the current at the top of the tube may have the following explanation. Being denser than sea water they would have to swim with a slight upward component which, against the current and in the restricted space of the tube, would quickly bring them into contact with the top



Wall. The tilt of the body would then have to be maintained or increased to give the tail freedom of movement, and the larvae would inevitably remain at the top of the tube so long as they continued to swim.

Table 3. Steady swimming speeds attained by plaice larvae in a tank of water

Experiment	Fish					Results			
	Stage	Length $L_t$ (mm.)	Height $H_a$ (mm.)	Muscle band $H_m$ (mm.)	$L_t \times H_m$	Distance (cm.)	Time (sec.)	Velocity (cm./sec.)	Remarks
1	I	7.5	1.23	0.32	2.4	11	8.5	1.3	Swimming. Average measurements of 5 newly hatched larvae under observation together
		—	—	—	—	8	7.5	1.1	
2	Id	8.6	1.45	0.4	3.4	8.5	5	1.7	Fast swimming
3	IIb	7.6	1.3	0.6	4.4	21	8.3	2.53	Rapid swimming
		—	—	—	—	11.5	4.5	2.56	
		—	—	—	—	17	6.7	2.54	
		—	—	—	—	14	5	2.80	
4	IIIa	7.9	1.5	0.8	6.3	10	3.5	2.86	Climbing at 45° } Observations on 2 fish of similar size
		—	—	—	—	17	4.9	3.47	
		—	—	—	—	11.5	3.2	3.60	
		—	—	—	—	16	5.4	2.96	
		—	—	—	—	19.5	6.4	2.97	
5	IIIa	8.25	1.4	0.75	6.2	10	4.4	2.3	Swimming—not full speed
		—	—	—	—	10	4.2	2.44	Swimming—not full speed
6	IIIa	8.25	2.0	1.2	9.9	8.5	2.9	2.9	Swimming
7	IIIa	9.6	2.08	1.2	11.5	24	9.8	2.45	Steady swimming
		—	—	—	—	13	5.2	2.5	Swimming, fast at times
8	IIIb	7.9	1.65	0.8	6.3	16	6.7	2.4	—
		—	—	—	—	17	7.0	2.43	—
		—	—	—	—	22	9.2	2.4	—
		—	—	—	—	27	11.6	2.33	—
		—	—	—	—	19	7.5	2.34	—
9	IIIb	9.1	1.9	1.0	9.1	11.5	4.6	2.5	Swimming, not flat out
10	IIIc	8.95	2.15	1.2	10.8	11	2.6	4.2	Swimming, climbing at 45°
11	IIIc	9.4	3.1	1.8	16.9	13	2.7	4.8	—
		—	—	—	—	19	5.0	4.0	—
12	IIIc	9.8	3.1	1.5	14.7	10	2.6	3.85	Fast swimming
		—	—	—	—	19	5.0	3.81	Fast swimming
13	IIIc	9.85	2.6	1.2	11.8	14	4.3	3.25	Swimming along tank wall
14	IIIc	9.85	2.05	1.0	9.85	10	3.4	2.94	Did not appear flat out
15	IIIc	12.0	4.1	1.75	21	10	2.25	4.45	Fast swimming
16	IV	9.3	2.8	1.3	12.1	19.5	5.8	3.36	Swimming, climbing at 25°
		—	—	—	—	10	2.9	3.45	—
17	IV	9.4	3.4	1.9	18.0	17	4.4	3.86	Swimming

The results obtained with this apparatus, based on nineteen successful experiments, are given in Table 2. As explained above, it is insufficient to express results merely in terms of the mean flow, and a more precise answer is needed. Obtaining this was simplified by the constancy of the position taken up by the fish, such that its dorso-ventral axis was always at right angles to the flow contours. The height of the fish

at the anus,  $H_a$ , was measured (Fig. 1) and the actual fraction of the mean flow experienced at a point one-half of this distance from the periphery of the tube obtained from Fig. 3. This gave a reasonable estimate of the actual velocity felt by the fish. In each experiment the quoted mean flow (Table 2) was the highest the fish could stem, and was always based on a large number of trials. These estimated velocities of the fish relative to the water have been plotted against their size in Fig. 4.

It is of course quite impracticable in the case of flatfish larvae, which change shape so greatly during development, to try to relate swimming speed simply to length. The abscissa employed in Fig. 4 is length multiplied by the height of the musculature halfway along the animal's length,  $L_t \times H_m$ , the use of which will later be discussed in more detail, as will further consideration of these results.

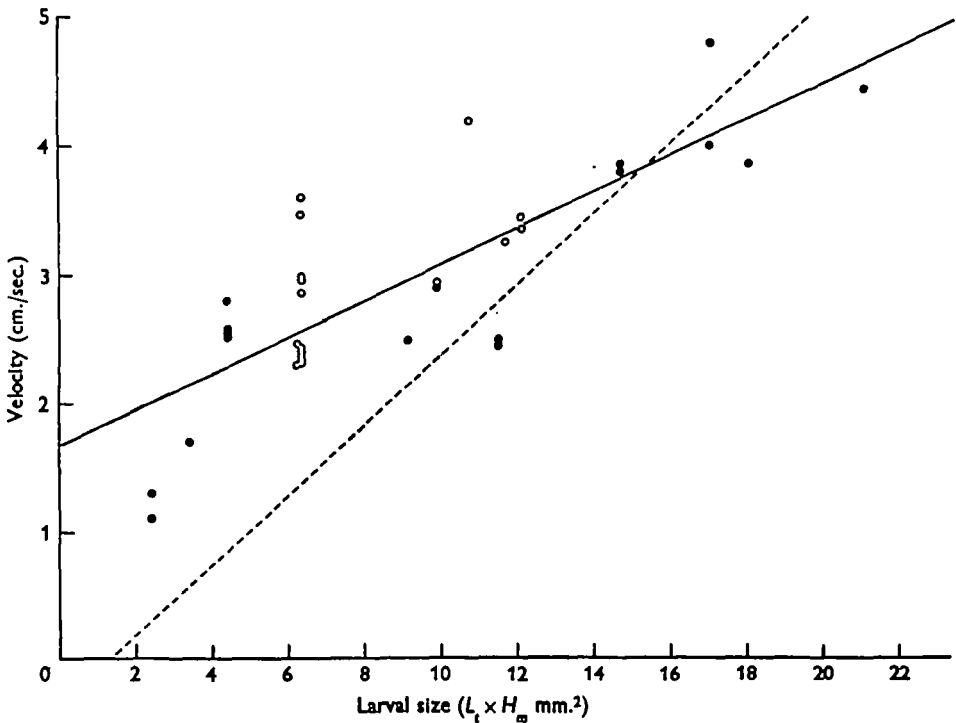


Fig. 5. Steady swimming speeds achieved by plaice larvae in a tank of water (see Table 3). Open circles indicate values obtained with larvae later found to be stunted. Broken line is the regression from Fig. 4.

#### *Swimming in still water*

The swimming speeds attained by larvae in a tank of water, together with distances covered, are given in Table 3. Results were only recorded when the distance exceeded 10 cm., or 10 fish-lengths in the case of small larvae. With experience it became possible to decide whether a fish was swimming at or near its fastest speed, and it is these that have been entered in Table 3.

The results have been graphed in Fig. 5, using the same co-ordinates as in Fig. 4. A comparison of the two regressions indicates that, while the general order of velocity observed is similar, the slopes are significantly different ( $P < 0.001$ ). The present

method is considered to have given the less accurate picture, for which there were two contributing factors: first, the rather high degree of scatter inherent in the method and, second and more important, the unavoidable use in the late spring of 1961 of small larvae which turned out to be stunted (a result of hatchery overcrowding). While the question of size and swimming performance will be considered later, it should be noted that speeds higher than might have been expected in the light of subsequent experience were obtained from these stunted larvae. Though small, they were of stage III and not of stage II; they would therefore be more muscular for their size. When this is understood it can be seen that the results confirm quite well those obtained by the previous method.

Table 4. Maximum (darting) speeds achieved by plaice larvae in a tank of water

Experi- ment	Fish					Results				Remarks
	Stage	Length $L_t$ (mm.)	Height $H_a$ (mm.)	Muscle band $H_m$ (mm.)	$L_t \times H_m$	Distance (cm.)	Time (sec.)	Velocity (cm./sec.)		
1	I	7.4	1.04	0.5	3.7	12	1.5	8.0	—	
		—	—	—	—	10	1.6	6.3	—	
		—	—	—	—	15	1.6	9.4	—	
2	I	7.5	1.23	0.32	2.4	12	3.2	3.7	—	
3	I	8.6	1.45	0.4	3.4	9	2.0	4.5	—	
4	IIIb	10.25	2.5	1.6	15.6	12	1.0	12.0	—	
5	IIIc	8.95	2.15	1.2	10.8	12.5	1.1	11.4	—	
6	IIIc	9.4	3.1	1.8	16.9	36	2.4	15.0	—	
7	IIIc	9.8	3.1	1.5	14.7	18	1.5	12.0	—	
8	IIIc	9.85	2.6	1.2	11.8	16	1.7	9.4	—	
		—	—	—	—	36	3.9	9.2	—	
		—	—	—	—	22	2.2	11.0	Climbing at 45°	
9	IV	9.3	2.8	1.3	12.1	19	2.1	9.0	—	
		—	—	—	—	20	2.0	10.0	Almost vertical climb	

Another important observation resulted from this method. Larvae had not only a maximum steady swimming speed, but could produce quite vigorous darts at about three times this velocity (Table 4, Fig. 5). Within the confines of a small tank the darts become erratic in direction, and the distance covered can be considered only approximate, but the order of velocity is quite clear. The two types of locomotion could be distinguished easily by eye, quite apart from the difference in velocity.

DISCUSSION

While it is to be expected that the swimming speed of a fish would bear some relation to its size, it is less clear precisely how it is related to length. Bainbridge (1958) found a direct dependence of speed upon length for a given frequency of tail beat. There is no information on how frequency of beat varies during development of plaice larvae; but in any case, the marked allometry during growth makes direct relation of speed to length of doubtful value. An additional subsidiary point is that young larvae swim with their pectoral fins as well as with their tails, though the relative importance of the two mechanisms is not known.

In view of the change in shape of young plaice during growth, it seemed likely that speed would not show a linear relationship to length, and velocity was first plotted against length multiplied by height at the anus,  $L_t \times H_a$  (Fig. 1) as an expression of body area. This measurement was not satisfactory for it became apparent that, while the overall dimensions of young larvae (stages I–III*a*) may change very little, their musculature develops considerably. Thus in a III*b* larva the musculature halfway along the body occupies about one-half of the total height, but in a stage I larva the fraction is only one-fifth (Fig. 1). When the measurement  $H_m$ , height of the musculature, was substituted for total height, a satisfactory graduation of points was obtained indicating a linear relationship of velocity to  $L \times H_m$  (Fig. 4), an index of the sagittal area of the body musculature.

The 1961 experiments, in which swimming-speed measurements were made in a tank of water, emphasize very strongly the dependence of speed upon the extent of the musculature. Work was commenced rather late in the spring and it subsequently became apparent that certain small larvae selected from the hatching tanks were stunted, not young, individuals. If the speeds obtained from these small stage III larvae are plotted against larval size  $L_t \times H_a$ , it is found that they form a series of points directly above those obtained from normal stage I larvae. Even when the values of  $L_t \times H_m$  constitute the abscissa (Fig. 5) these points still appear high; no doubt a measurement of volume or weight of muscle, thereby allowing for the greater thickness of the fish, would give a plot more consistent with the slope from Fig. 4. When, however, the remaining points in Fig. 5 are considered—those not based on stunted fish—they are seen to accord perfectly well with the regression line transferred from Fig. 4: they thus provide confirmation for the actual velocities obtained with the experimental tube and for the conclusion that speed is dependent on the amount of muscle, which is adequately expressed for a young flatfish as total length multiplied by height of the muscle band.

It is important to note that the highest speeds obtained in the experimental tube, as revealed by the tank results, correspond to cruising speeds and not to the maximum (darting) velocity attainable. That plaice larvae will not swim steadily against a current seems to be an idiosyncrasy in the behaviour of the species, or perhaps of flatfish in general, and is not true of all marine fish larvae (Bishai, 1960).

While the allometric growth of the plaice makes it difficult to compare with other species their performance in relation to size, a useful exception may be made in the case of larvae of early stage III. These (Figs. 1, 3 B) approximate to roundfish in body form, though the post-anal body section is rather slim. Bainbridge (1960) summarized published records of swimming speeds, expressing them in terms of fish-lengths,  $L$ , covered per second. There is considerable evidence that the cruising speed, or that which can be sustained for some time, lies in the region of 3–6  $L$ /sec. according to species, and Bainbridge himself found a maximum value of about 10  $L$ /sec. If the data for stage III*a* and III*b* larvae are combined, it is interesting to find that the mean length is 9.6 mm. and the average velocity (Fig. 4) is 2.7 cm./sec.: a value of 2.8  $L$ /sec. Again, for maximum velocity (Fig. 6) the average is 10.0 cm./sec. or 10.4  $L$ /sec. These figures indicate that, so far as can be judged from this short suitable phase of development, the performance of the larvae, expressed in terms of fish-lengths per second, accords well with that of larger fish.

The results for stage I larvae may also be compared with those obtained by Bishai (1960) for early herring larvae. He stated that his larvae swam in the centre of the tube, so that the true relative speed of the fish will be approximately double the mean flow velocity he quoted (see Fig. 3). It appears that the herring larvae could maintain station against a current of up to about 1.5 cm./sec. or even more, which is twice as fast as that stemmed by plaice larvae of the same size. However, it was stated earlier that the present values were too low, and there is close agreement with speeds measured in the tank (Fig. 5). It appears that herring larvae may be capable of more sustained swimming than plaice larvae of a comparable stage of development.

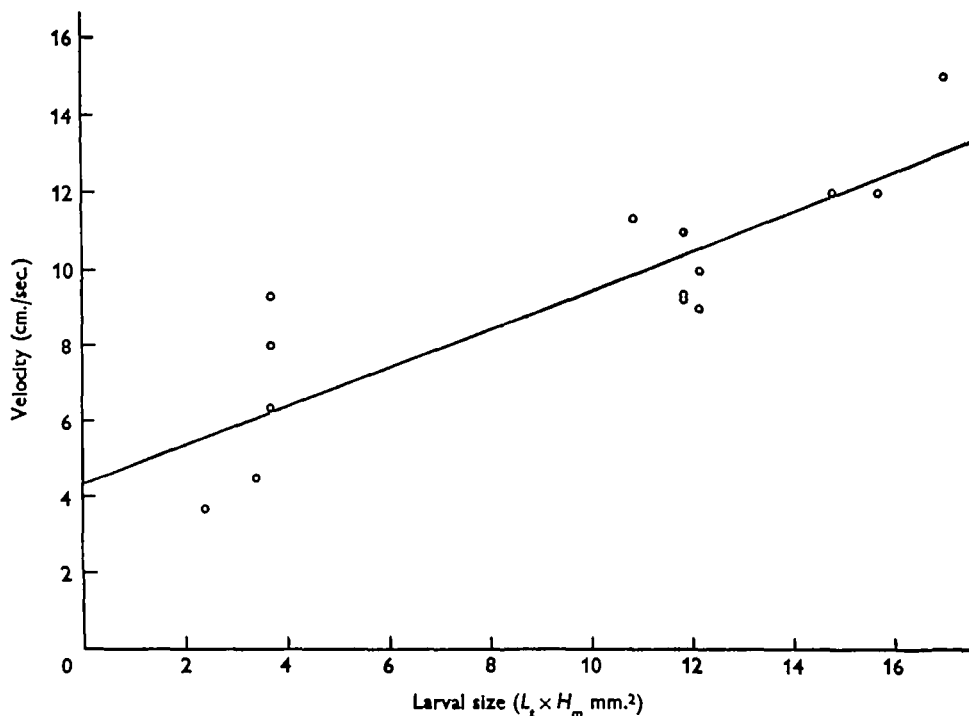


Fig. 6. Maximum (darting) speeds achieved by plaice larvae in a tank of water (see Table 4).

Brett, Hollands & Alderdice (1958) found that peak sustained speeds of sockeye salmon (*Oncorhynchus nerka*) and coho salmon (*O. kisutch*) under-yearlings were greatly influenced by temperature. No information was obtained in the present work as to the effect of temperature, but it should be noted in the discussion that follows that the temperature at which the experiments were conducted, 6.5–7.5° C., corresponds closely with average late winter temperatures in the southern North Sea.

It remains to be considered how the information on swimming speed could affect the design of collecting gear used at sea. Fish larvae in the past have been collected by vertically hauled bolting-silk nets raised at a speed of 30–40 cm./sec. As quantitative sampling gear such nets have a number of defects: they are hauled by a rope or warp secured in the centre of the mouth of the net by three bridles; thus, as the net is raised it passes through water already disturbed by the rope. Hauling, in typical depths of the Southern Bight, lasts some 1–1½ min., and the disturbing effect of the

rope on the more active creatures of the plankton could be considerable. Moreover, since the nets are white and therefore conspicuous to organisms with well-developed eyesight, the rather slow rate of hauling must allow many swimming animals to avoid the net.

Since all the evidence available suggests that fish larvae are very responsive to visual stimuli, and since, as stated earlier, no other stimuli have been found to induce locomotion or escape reactions, it seems hardly surprising that catches of fish larvae in vertically hauled nets are much higher by night than by day, and higher still in total darkness (with ship's lights extinguished; Bridger, 1956). A dark net rising by the buoyancy of floats would seem to be the best design for a net of this sort; but it might still be queried whether a net rising at 30–40 cm./sec. can be considered adequate for sampling organisms capable of moving at velocities of about half this figure.

Though data for the plaice are not available, Ahlstrom (1954) found in the Pacific sardine (*Sardinops caerulea*) that the ratio of catch by night to catch by day rose steadily from unity for fish about 5 mm. long to ten for fish 16–18 mm. long. If these larvae are considered capable of steady swimming at 3*L*/sec. and darting at 10*L*/sec., then a 5 mm. fish could swim at about 1.5 cm./sec. with a maximum of 5 cm./sec., while for a 20 mm. long fish the corresponding values would be 6 and 20 cm./sec. (values quite comparable with those for plaice of stages I and IV respectively). The increase of escaping power with size seems quite sufficient to explain Ahlstrom's catch data.

If apparatus designed to collect larvae at sea is to fish as well by day as by night and sample all stages equally, it must (a) give no warning of its approach, and (b) travel at a velocity such as to catch organisms themselves able to swim away at up to 20 cm./sec. The Gulf III high-speed metal tow-net (Gehring, 1952; Bridger, 1958) and its subsequent modifications seems to fulfil these requirements. The attachment of the towing warp above the orifice, aided by bowing as a result of drag (Krause & Siedler, 1962), allows the net mouth to pass through undisturbed water; while the strength of the net permits its being towed at speeds of 5 knots (about 250 cm./sec.) or more. It is important that the design should aim at complete water flow through the net, and therefore cause the smallest possible pressure wave in front of the net. If the disturbance of the net extends approximately 1 m. in front of it (no precise information on this important point is available), advance warning of the net's approach would be only  $\frac{1}{2}$  sec. or so. It seems most unlikely that larvae in or near the path of the net could make orientated movements away from it on a scale sufficient to influence the catch seriously. The high-speed metal tow-net therefore seems to be the most reliable sampling gear so far devised.

#### SUMMARY

1. The swimming speeds attained by hatchery-reared plaice larvae have been determined by measurements made (a) in still water, and (b) against a current flowing through a long glass tube.

2. In still water contact stimuli were used to initiate swimming. No optomotor response was found, and it was not possible to use the 'fish-wheel' of Bainbridge (1958).

3. Larvae in the experimental tube stemmed the current for brief periods only, their position then being near the periphery of the upper quadrant. The speeds were

found to show a linear relationship to larval length multiplied by the height of the post-anal musculature. Observations in still water show that these values correspond to those of steady swimming: they are not maximum speeds.

4. Speeds ranged from about 1.5 cm./sec. when newly hatched to 9 cm./sec. in late larvae. Darting velocities of up to 15 cm./sec. were recorded with half-grown (stage III) larvae. In such larvae cruising speeds were about three fish-lengths (3L) per second, and the maxima about 10L/sec.

5. The design of gear for collecting fish larvae at sea is discussed. Only a high-speed tow-net, towed at about ten times the velocity attainable by the largest larvae and giving almost no warning of its approach, can be considered to collect a quantitatively balanced sample.

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