The Sensory Basis of Fish Schools:
Relative Roles of Lateral Line and Vision*

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Summary. Quantitative analyses of the effects of temporary blindfolding (BL) or lateralis section (LS) on the schooling performance of saithe (*Pollachius virens*) are reported. Comparison of effects of the sensory deprivations on school structure and dynamics allow determination of the relative roles of the lateral lines and vision in normal schooling. Extended 3-dimensional records were made of the positions of sensorily deprived individuals in normal schools as well as whole schools with sensory treatments.

1. Blinding had little effect on the position experimental fish took up with respect to their neighbors within the school (Fig. 2). In contrast, lateralis section resulted in a great increase in the frequency of neighbors at 90° bearing (directly alongside) (Fig. 2).

2. Both BL and LS fish exhibited different characteristic nearest neighbor distances (NNDs) than controls, with blinding increasing NND and lateralis section decreasing NND (Fig. 4).

3. Importance of the lateral line in transmission of a fright response and sudden velocity changes within a school is demonstrated by experiments in which schools were intentionally startled. In schools of LS fish there exist significant relationships between latency to startle and the distance and angle between a fish and the startling object. Such relationships are not seen in normal schools: with intact lateral lines, fish respond with similar latencies to objects in all directions (Fig. 5).

4. Fish which are blindfolded are able nonetheless to match short-term changes in velocity of their neighbors and actually show higher correlations than do controls (Fig. 8b). Lateralis section does not reduce correlations between fish and neighbors (Fig. 8d) probably because LS fish take up positions at which they can best determine neighbors' velocities by vision alone.

We conclude that the role of the lateral line in schooling is much greater than has been recognised previously. Our experiments suggest that characteristic NND in a travelling school is maintained by opposing forces of attraction and repulsion mediated by stimuli perceived by the visual and lateralis systems respectively. School structure and dynamics depend upon both senses, with vision primarily important for the maintenance of position and angle between fish and the lateral lines primarily important for monitoring the swimming speed and direction of travel of neighbors.

Abbreviations: LS, lateralis section; *BL,* temporary blindfolding; *NND,* nearest neighbor distance; *NN1, NN2, NN3,* nearest neighbor, second nearest neighbor and so on

Introduction

The most striking feature of fish schools is their remarkable synchrony. Not only do fish swim at a constant pace and maintain characteristic individual distances, but schools as a whole execute complicated defensive maneuvers requiring individuals to respond quickly to short-term changes in the velocity and direction of their neighbors. Mechanisms underlying such uniformity are poorly understood. Most authors have concluded that vision is required for fish to school and that other senses, if involved at all, are not very important (see for e.g. Bateson, 1889; Parr, 1927; Breder, 1951, 1959; Shaw, 1970). Our recent demonstration that blinded saithe (*Pollachius virens*) are ca-

pable of maintaining their position indefinitely within actively swimming schools (Pitcher et al., 1976) provided the first clear evidence that vision is not necessarily required and that fish can use their lateral lines to maintain positions within a school.

The qualitative results reported previously, however, do not explain how the lateral line is used or the relative roles of the acoustico-lateralis sense and vision in normal schooling. This paper describes the results from quantitative analyses of the roles of the two sensory modalities in conditions approximating normal schooling.

Methods

1. Experimental Procedures. Schools of 20–30 *Pollachius virens* were videotaped over extended periods while cruising in a circular channel 1.8 m wide and 31 m in circumference at the Department of Agriculture and Fisheries for Scotland Marine Laboratory, Aberdeen (Wardle and Anthony, 1973). Fish were individually identified by freeze-branding and three-dimensional information was obtained by a cast-shadow method (Cullen et al., 1965). Schools were filmed from a moving gantry which was kept above the actively swimming school. A red spotlight, mounted on the gantry, shone at an angle to the tank floor and thus cast a shadow for each fish. Measurements of the distance between each fish's image and its shadow allowed calculation of the fishes' 3-D positions in the water. Full details of filming and handling techniques are given in Partridge et al. (1980).

In order to investigate relative roles of lateral line and vision in schooling, individuals were sensorily deprived by lateralis-section or temporary blindfolding and then placed back in normal schools. Posterior lateral lines in saithe run just under the external canal for the length of the animal. Fish were anaesthetized (MS222, 1:15,000) and the lateral lines were cut in two places, just behind each operculum. Temporary blindfolds (blinkers) were constructed from fully exposed 35 mm film which was sprayed with matt black enamel to ensure that it was opaque and held in conical shape with PVC cement. Blindfolds were trimmed to the appropriate size, gently crimped with a pair of forceps, filled with sea water and slid under the bony ridge surrounding the fish's eye. After every handling, fish were put in a bath of Acraflavine to reduce the chance of infection. One important difference between our methods and those of Parr (1927) or Keenleyside (1955), both of whom temporarily blinded fish, is that our experimental fish were given at least 24 h to recover from the operations before testing. Also, since lateral line activity is inhibited for several hours after treatment with MS222 (McNicholl and McKay, 1975) studies of schooling where fish were tested soon after anaesthesia must be viewed with caution.

We tested five fully blinded fish (BL), five whose lateral lines were cut on both sides (LS) and five fish with both blinkers and lateral line cuts. In each case, behavior of the experimental fish was compared with that of randomly selected control fish from the same school. In addition, we filmed schools in which every member was sensorily deprived by blinkers or lateralis section. Results of whole school experiments are the subject of analyses which will be reported elsewhere, but where applicable, results from schools of LS fish will be described here.

Schools were filmed during continuous cruising (sampled at 2.7 Hz) and during instances (sampled at 50 Hz) in which the fish were intentionally startled by the sudden appearance of a large black or white card overhead. Relative positions of individuals were recorded during experiments as a "race-track commentary" on the videotape soundtrack, and careful viewing of the videotapes later allowed individuals to be identified. Videotape sequences were chosen for analysis and these were copied onto 35 mm film with a Nikon motor-drive camera. The position of the snout of each fish and its shadow in each film frame (7400 in all) was then plotted using an interactive coordinate plotter developed for the purpose (Partridge and Cullen, 1977; Partridge et al., 1978). Plotted data were corrected for errors due to parallax and lens distortion as described elsewhere (Partridge et al., 1980); final coordinates were accurate to ± 0.5 cm ($= \pm 0.015$ body lengths).

2. Analysis Methods. Statistical analyses of 3-dimensional structure of animal groups have for the most part followed the conventions of Cullen et al. (1965), calculating mean nearest neighbor distances (NNDs) or frequencies of neighbors in various directions (e.g. Pitcher, 1973; Major and Dill, 1978; Partridge, 1980). There are, however, problems of independence if one tries to measure average NND or frequency since the closer two fish are together the more likely it is that they form a reciprocal pair (i.e. if fish A is fish B's nearest neighbor, then it is likely that the reverse is the case). Most studies have ignored the problem of independence, but this biases estimates of NND downwards. Another technique, adopted by Hunter (1969) and Pitcher (1973) has been to include only one member of each reciprocal pair. This has the opposite effect, biasing estimates of NND upwards. In these analyses, we have used a method suggested by J.M. Cullen (pers. comm. and in prep.) to produce independent estimates of interfish distances. The idea is analogous to calculating distances between birds on a telephone wire by measuring the distance between each bird and, say, the bird on its right. For three dimensions, one simply measures the distance between each individual and the nearest individual in a particular hemisphere.

One difficulty with the hemisphere method is that schools of many species are longer than they are wide. Hence, fish near the edge of the school are more likely to have neighbors behind them and in front simply because there are no more fish further outside them. This effect is the same for experimental and control fish in the same schools, however, and the hemisphere provides independent measurements allowing comparison of the two.

We have shown elsewhere (Partridge et al., 1980) that NND as such is a highly variable measure since the distance between two fish depends strongly upon their relative positions. Variability resulting from positional differences is sufficiently great to mask effects of the sensory treatments. It is important, therefore, to look first at where neighbors lie in space and then to look for differences in the distances to them. To do this we divided space surrounding fish into 20° by 20° cells of bearing, the angle in the horizontal plane, and elevation, the angle in the vertical plane (see Fig. 1), and calculated the mean distance to neighbors in each section (as per Pitcher, 1973).

Because frequency of nearest neighbors and distance to them depend upon both bearing and elevation (Partridge, 1980) in any statistical analysis one must consider both dimensions simultaneously. Three dimensional figures resulting from such analyses are difficult to interpret, so for simplicity in the results which follow we show frequency and distances to neighbors as a function of bearing and elevation separately. (Statistics were carried out in three dimensions. Throughout the text unless otherwise stated, each case where a significant result is described refers to a 3-dimensional G-test, a non-parametric n-dimensional analysis of variance (Sokal and Rohlf, 1969), $P < 0.001$, $n > 15,000$).

In order to investigate the degree to which sensory deprivation affected a fish's ability to respond to short-term movements and

accelerations within a school, we calculated serial correlations of the velocities of fish with those of their neighbors for various time lags. Such an analysis investigates whether when one fish accelerates/decelerates its neighbors do as well, and, if so, how long (=lag) it takes the neighbors to respond (see Partridge, 1980). In all the correlograms presented here, positive lags refer to the responses of a particular fish to changes in its neighbor's velocity: the lag of +n frames corresponds to the correlation to the neighbor's velocity n frames earlier. There is no problem of independence such as for calculation of NNDs, because in any one film sequence only two fish (experimental and control) were compared with their three nearest neighbors. Routines for randomly choosing control fish were constrained to exclude fish too near the experimental fish so the problem of neighbor pairs does not arise. All correlations discussed below are between fish and their arithmetically nearest neighbors and not the neighbors in one hemisphere.

For each film sequence (BL: 13 at 45 cm/s, 10 at 60 cm/s, and LS: 13 at 45 cm/s, 6 at 60 cm/s) Spearman rank correlations were calculated for velocities of control and experimental fish with those of their first three nearest neighbors and a fish chosen at random from the school. Average angular speed of the school in the filmed sequences was either 5.5 or 8.1 radians/min, corresponding to velocities of 44.5 and 60.2 cm/s in the center of the channel. All fish in the school must have had the same average velocity or they would not have remained within it. Correlations, therefore, are of the short-term changes in velocities of school members.

Results

1. School Structure

a) Position of Neighbors

Sensory deprivation affects both the positions fish take up with respect to neighbors and the distance at which they swim. If one looks first at the positions of neighbors, differences between LS and BL fish and between each and their controls are apparent (Fig. 2). Blind fish and controls take up more-or-less similar bearings with respect to their neighbors, but this is not the case for fish with cut lateral lines. LS fish show a marked increase in the frequencies of neighbors directly alongside at around 90° bearing (Fig. 2b). These results are consistent with those of Cahn (1972) who found that a pair of tuna (*Euthynnus affinis*) swam side-by-side when separated by a transparent partition and Pitcher (1979) who reported similar results for bream (*Abramis brama*). In Cahn's and Pitcher's experiments, the partitions presumably prevented fish receiving mechanical stimuli from their neighbors. Shifts in the positions of nearest neighbors may be part of the cause of another change in school structure exhibited by LS fish. Cutting lateral lines of a whole school greatly reduces the degree to which members all headed in the same direction. Swimming directions (headings) of fish were calculated based upon positions in successive frames. As shown in Fig. 1b, this is a less variable measure than instanta-
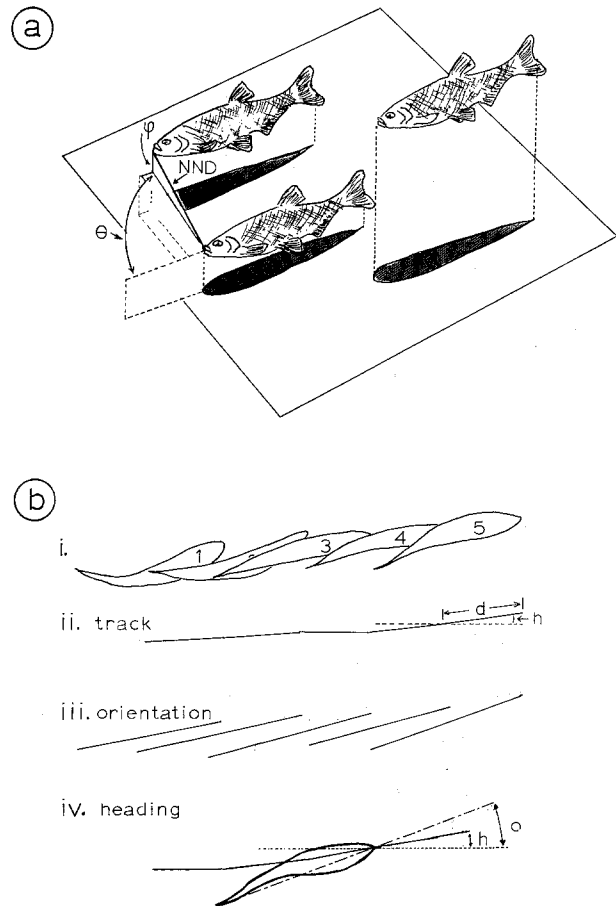

Fig. 1. a Representation of three fish in a 'school', showing measurements made of school structure. Distance between each fish and all other fish in the school was calculated from their 3-dimensional coordinates and the three nearest neighbors (NN1, NN2, NN3) were identified. Shown in the figure are nearest neighbor distance (NND), bearing ($=\Theta$, or angle in the horizontal plane) and elevation ($=\varphi$, or angle above or below the horizontal) between two fish. For a pair of fish with coordinates (x_1, y_1, z_1) and (x_2, y_2, z_2) respectively, the bearing from fish 1 to fish 2 is arctan $((y_2-y_1)/(x_2-x_1))$ and the elevation is arctan $((z_2-z_1)/((x_2-x_1)^2+(y_2-y_1)^2)^{1/2})$. b Calculation of a fish's swimming direction or heading. i) shows tracings of a single saithe in 5 consecutive frames of 35 mm film (copied from the videotapes at 2.7 Hz). ii) swimming track of the fish as determined by successive positions of the snout. d, distance swum per frame; h, heading with respect to the x-axis of the arbitrary coordinate system. iii) fish's body axis, drawn as a line between nose and tail in five successive frames. iv) difference between body orientation (o) as in iii and heading (h) calculated from the swimming track as in ii. Although fish headings have generally been calculated from individual's body orientations (e.g. Cullen et al., 1965; Hunter, 1966), swimming movements by the fish make this a more variable measure than calculating headings from the actual paths of the fish

neous body orientation since it is not affected by swimming movements (Partridge, 1978, 1980). Mean angular deviations of headings from the heading of the school increased from about 2.5° to more than 10.4°. This may be because it is more difficult for
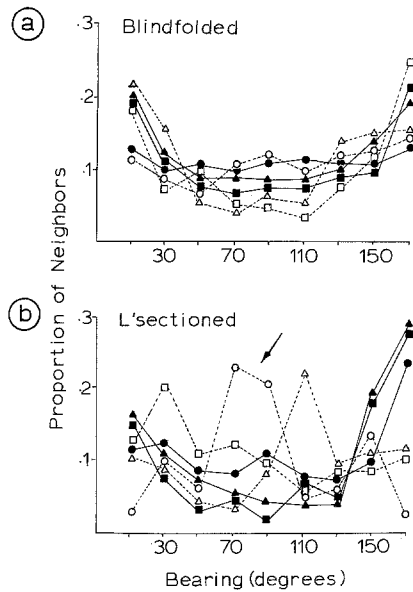
Fig. 2a and b. Proportion (=frequency/total) of neighbors at different bearings (summed across all elevations) for control (solid) and experimental fish (dashed) for blindfolded (a) and lateralis sectioned (b) fish. Relationships between bearing and frequency of neighbors for the first three nearest neighbors (NN1-circles, NN2-triangles, NN3-squares). Blinding has little systematic effect on bearing to neighbors, but lateralis section results in a great increase in frequency of neighbors alongside a fish, at 90° (arrow)

a fish to determine the heading of a fish beside it than in front as van Olst and Hunter (1970) have suggested. It is also probable that the lateral line is normally important in monitoring neighbors' swimming directions and that without it saithe are less able to respond to small changes.

Figure 3 shows that blindfolding or lateralis section also affects the elevation fish take up with respect to their neighbors. Both types of experimental fish tended to swim above nearest neighbors ($P < 0.01$, G-Test). They did not, however, actually swim above the entire school. Viewing the original videotapes confirms this notion as does plotting tracks of individual fish within a typical school (Partridge, 1978).

b) Nearest Neighbor Distance

Sensory deprivation also affects the distance fish maintain from their neighbors, although the difference is, of course, masked by the responses of their neighbors to them. The important result to note from Fig. 4a and b is that compared to control fish in the same film sequences, blinkered fish have greater NNDs (for NN1, NN2 and NN3; $P < 0.001$, $n > 18,000$) while lateralis sectioned fish show smaller NNDs ($P < 0.001$, $n > 10,000$). As described above,
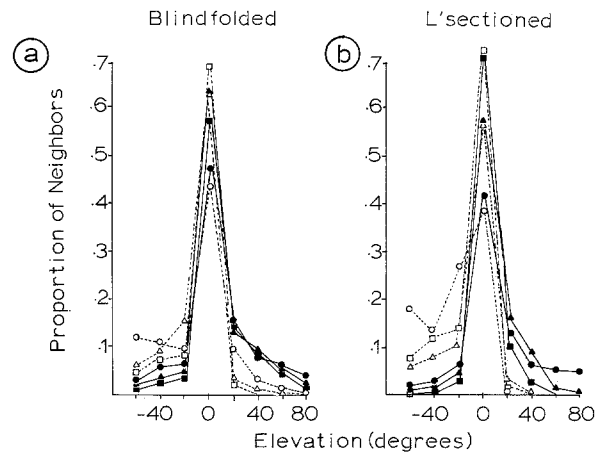

Fig. 3a and b. Proportion of neighbors at different elevations (summed across all bearings) for BL (a) and LS (b) fish. Plotting conventions are the same as in Fig. 2. Both sensory treatments result in fish swimming above their neighbors more than do controls
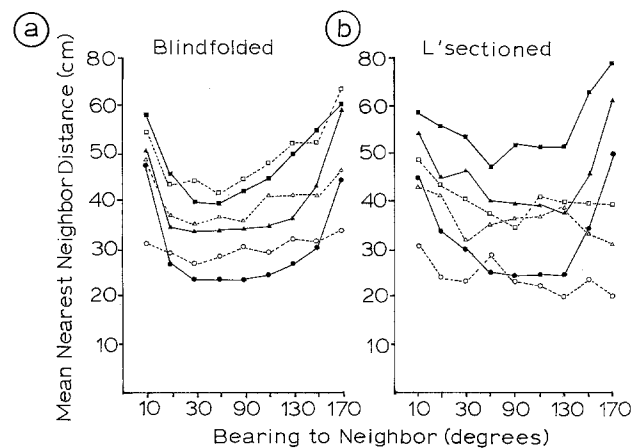

Fig. 4a and b. Distance to nearest neighbors (NND) as a function of bearing. As in Figs. 2 and 3, solid lines refer to controls and dashed lines refer to experimental fish (NN1 – circles, NN2 – triangles, NN3 – squares). Mean NNDs for BL (a) and LS (b) fish and their controls from the same film sequences. Standard deviations of NND at the various bearings shown are in the range of 9–11 cm. They are not plotted in the figure since means at each bearing are summed over all elevations and the variation simply reflects the interaction between bearing and elevation. Standard deviations of NND within individual 20° by 20° cells of bearing by elevation were 2–5 cm

statistics were carried out in three dimensions although results are presented as a function of bearing only for clarity. In the graph for LS fish (Fig. 4b) the apparent increase in NND at bearing $=60°$ is due to the interaction between bearing and elevation. In all 20° by 20° cells of elevation by bearing where neighbors were recorded, LS fish exhibited smaller NNDs than did controls. Results were the same for the LS schools: NND is significantly less than for
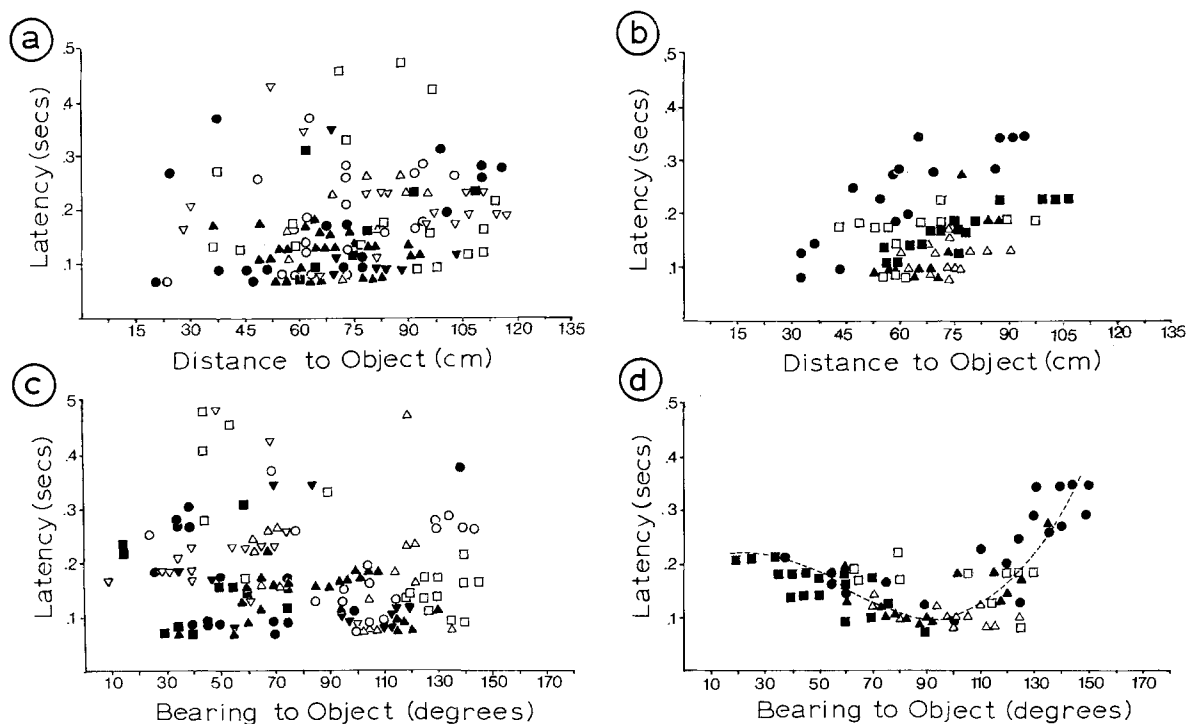
Fig. 5a–d. Latency to startle as a function of distance (**a, b**) and bearing (**c, d**) to the startling object. Figures **a** and **c** show responses of normal schools; **b** and **d** show results from lateralis sectioned schools. In each graph, different symbols refer to different film sequences. Figures **a** and **c**, referring to control schools, have been divided into two groups: solid symbols refer to startles which took place early on in experiments whereas open symbols refer to those startles taking place later. The saithe clearly habituated to the stimulus. Minimum latencies are not affected, but average latency is higher for the later startles. There is considerable scatter in the graph showing latency as a function of distance for LS schools (**b**), but for individual sequences latency increases smoothly with distance. In neither control nor LS schools did fish show a significant relationship between latency and either direction or angle to other fish which had already startled

control schools (0.3–0.5 body lengths rather than 0.6–1.1 body lengths, $P < 0.001$, G-test).

If depriving fish of either vision or lateral line information greatly affected their ability to determine distances then one would have expected variation of NND to be greater for experimental fish than for controls. Neither LS nor BL fish showed greater variance in NND (Wilcoxon one-tailed test, Siegel, 1956) than before sensory treatment.

2. Startle Responses

Both sensory treatments affected fishes' responses to sudden startling of the school. As we reported previously (Pitcher et al., 1976) blind fish only responded if their neighbors were less than a body length away and even then exhibited greatly increased lags. Role of the lateral line in this response is demonstrated by results of experiments in which LS schools were deliberately startled.

The time taken from appearance of the startle object to a fish's response was taken as the latency of response, and this was plotted against the distance (Fig. 5a,b) and angle (Fig. 5c,d) between individual fish and the startle object. For normal schools there is no obvious relationship between startle latency and either measure. For LS schools however, there is a significant linear relationship between latency and distance to the object (Fig. 5b, $P < 0.01$) as well as a significant second order relationship between latency and angle to the startle object (Fig. 5d, $P < 0.001$). In Fig. 5b, there is considerable scatter in latencies. Individual sequences, shown by different symbols, however, show latency increasing smoothly as a function of distance to the startle object. In neither control nor LS schools did fish show a significant relationship between latency and direction or distance to other fish which had already startled.

The conclusion one must draw from these experiments is that fish normally respond to sudden accelerations by fish anywhere in the school, and that this

masks the relationships exhibited by LS schools. Minimum latencies are for objects at 90° bearing (i.e. alongside) (Fig. 5d). Latencies rise considerably for objects in front (angles much less than 90°) or behind (angles much greater than 90°). The graph is not symmetrical about the minimum: latencies for angles of 10–20° are much less than those for angles greater than 160°. This result agrees with that reported by Hunter (1969) who pointed out that stimuli at 10° from directly ahead were within a fish's binocular field. Our results suggest stereopsis, although this remains to be proven.

.The relationship between distance and latency could have been spurious because distance was not independent of angle to the startle object. The startle object was introduced perpendicularly to the direction of movement of the school, so those fish whose angle to it was 90° must have been closer to it than those whose angle was 0° or 180°. Hunter's (1969) results suffer from the same difficulty: he also found latency increasing as a function of distance, but because his jack mackeral schools were longer than they were wide, his distance measurements were not independent of angular measurements either.

Differences between response latencies of LS and control schools demonstrate the role of the lateral line in fishes' responses to major school disruptions. Its importance in these situation is not limited to transmission of the fright response, however. In five filmed startles of the LS school, pairs of fish actually collided on four different occasions, once with sufficient force to stun the fish. In contrast, normal fish never collided in any of the more than fifty startles which we filmed. Clearly, saithe normally use their lateral lines to monitor the directions in which other members of the school are swimming when the school is disrupted.

3. Interactions Between Fish

a) Velocity Correlations

Spearman rank correlations were calculated for the velocities of control and experimental fish with those of their first three neighbors and a fish chosen at random from the remainder of the school (as described in Methods, and in Partridge, 1980).

Figure 6 shows a typical series of correlograms for a BL and control fish swimming at approximately 45 cm/s. The uppermost graphs show autocorrelations of the velocities of each fish. There were marked differences between sequences in how long (in terms of lag) the autocorrelation was significant, but re-
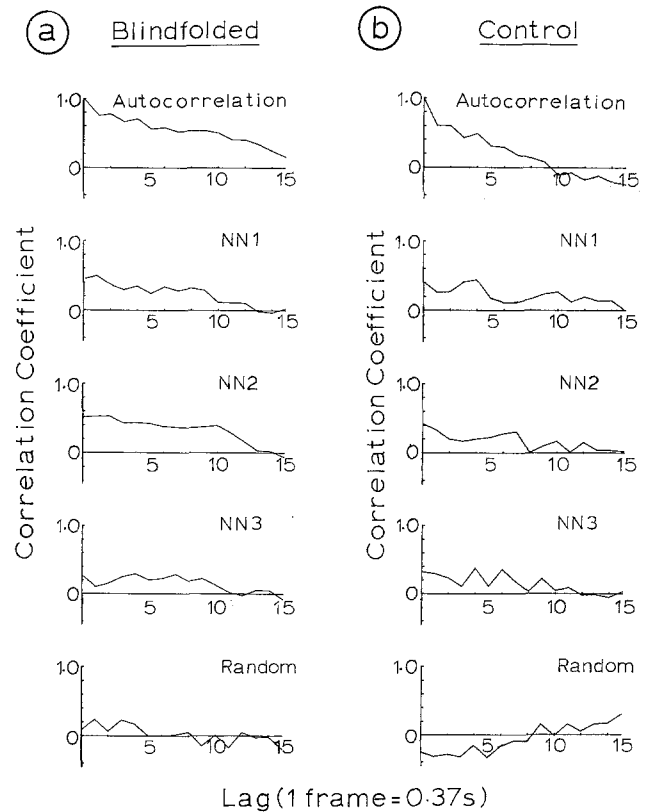

Fig. 6a and b. A typical series of correlograms for a BL fish (a) and a control fish chosen at random from the same school (b). Shown are velocity autocorrelations as well as cross-correlations to NN1, 2 and 3 and a randomly chosen fish, at a school speed of approximately 45 cm/s

markably little difference between graphs for fish within the same sequence. This is not surprising: in a film sequence where the school kept a relatively constant velocity, all fish would show high autocorrelations for long lags. Similarly, if the school was maneuvering a great deal all fish would probably be affected. This is shown in Fig. 7 where average autocorrelations are plotted for each of the treatments at two school speeds. (The method used for averaging correlation coefficients follows Kendall, 1973.) Average velocity autocorrelations of BL, LS and control fish are not significantly different from one another at either 45 cm/s or 60 cm/s, but all three show a marked drop at the higher speed ($P < 0.01$). In other words, at the higher speed much more is going on within the school. That is, individuals are accelerating, decelerating and changing relative positions more often. Also, at 60 cm/s the saithe were swimming near their maximum sustained swimming speed (Wardle, 1975) and this may have altered the normal pattern of schooling.
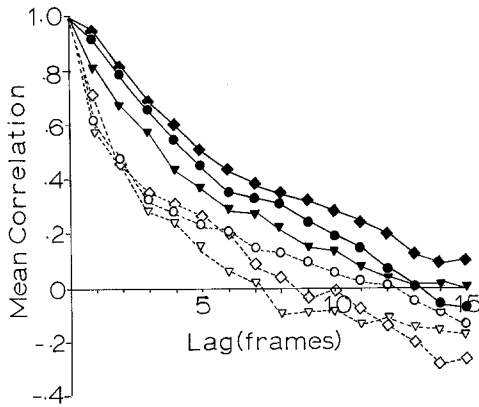
Fig. 7. Average velocity autocorrelations (i.e. correlation between a fish's velocity at some instant and its own velocity some time in the past). Magnitude of the autocorrelation gives an indication of the degree to which fish accelerate and decelerate over time. A value of 1.0 would indicate that the fish were swimming at a constant acceleration, either maintaining a steady velocity or increasing/decreasing speed monotonically. Mean autocorrelations are shown for BL (diamonds), LS (triangles) and control (hexagons) fish swimming at either 45 cm/s (solid lines) or 60 cm/s (dashed lines). There are no significant differences between control and experimental fish at either school speed, but autocorrelations for all three drop off significantly at the higher speed

b) Velocity Cross-Correlations: Blind Fish

An important finding is that the rest of the school responds to blindfolded (and LS) fish as though they were normal. For negative lags, correlograms for experimental (BL or LS) fish are not different from those for controls (Fig. 8a). Since negative lags refer to the response of neighbors to changes in the experimental fish's velocity, this means that they were neither ignoring the oddly behaving experimental fish, nor were they paying more attention to it than normal.

There was considerable variation between film sequences in the degree to which fish were correlated with their neighbors. Nonetheless, within sequences, differences between control and BL fish were consistent – and surprising. From Fig. 8b it can be seen that while control fish are, on average, significantly correlated with only their NN1, BL fish are significantly correlated with both their first and their second nearest neighbors. Neither is significantly correlated with its NN3 or with a randomly chosen fish (not shown). And not only did blind fish show significant
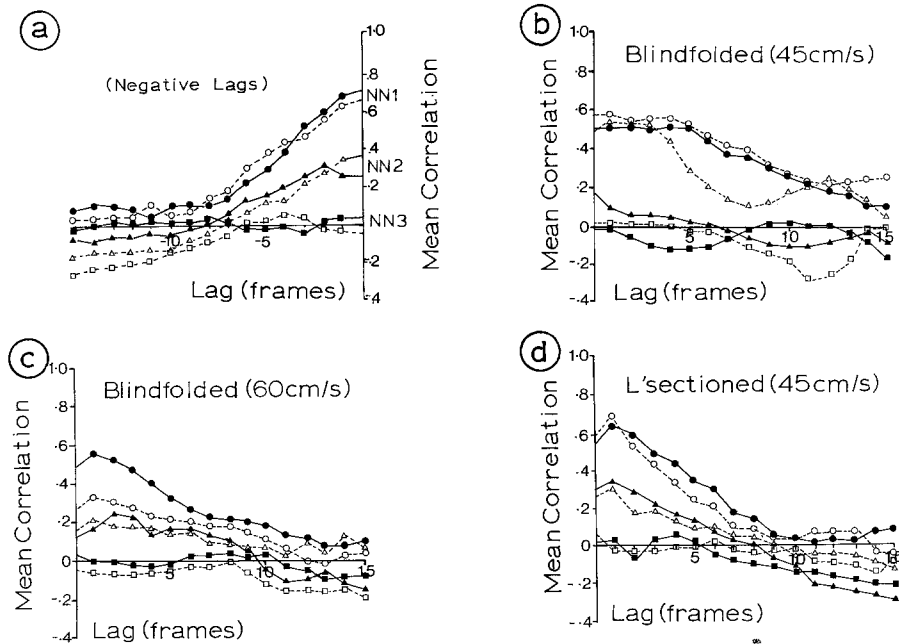

Fig. 8. a Correlation of instantaneous velocities for "negative" lags. The graph shows average correlation coefficients for lags of −1 to −15 frames, corresponding to latencies of up to 5.5 s. Negative lags correspond to the degree to which a neighbor responds to changes in the velocity of the experimental fish. Shown are mean correlations to NN1 (circles), NN2 (triangles) and NN3 (squares) for control (solid) and BL (dashed) fish. Neighbors of BL fish match their velocities to those of the experimental fish as well as they do to other control fish. Similar results are seen for LS fish. b Average correlation with a neighbor's velocity for BL (dashed) and control (solid) saithe in a school travelling at approximately 45 cm/s. Blind fish show high correlations to NN1 (circles) and NN2 (triangles), whereas control fish only show significant correlations to NN1. Neither shows significant correlations to NN3 (squares). c Average correlations for BL fish and controls in schools travelling at 60 cm/s. BL fish are no longer significantly correlated to NN2 and are less correlated to NN1 than are controls in the same film sequences. d Average correlation coefficients with neighbors' velocities for LS fish (dashed) and controls (solid). Experimental fish are not significantly different from controls at either 45 cm/s or 60 cm/s (not shown)

correlations with both their two nearest neighbors, but in every single sequence, blinkered fish showed higher correlations than control fish to both their first two nearest neighbors ($P < 0.01$, Wilcoxon two-tailed test, Siegel, 1956). Neither control nor BL fish showed significant correlation with their third nearest neighbor and neither was consistently more correlated than the other.

At higher speeds (Fig. 8c) blind fish appear much more like controls: they are significantly correlated with only their NN1 and not with the NN2. Whereas they showed significantly higher correlations with NN1 than did controls at 45 cm/s, they showed significantly lower correlations than controls at 60 cm/s ($P < 0.05$, Wilcoxon two-tailed test). Performance of control fish does not seem to suffer at higher speed, although there is some indication that maximum correlation occurs at a slightly larger lag.

c) Velocity Cross-Correlations: Lateralis Sectioned Fish

Demonstration that blind fish show higher correlations with neighbors than did controls suggests that the lateral line is important for measuring the velocities of neighboring fish. One would expect, therefore that cutting the lateral lines would result in a decrease in correlation. Figure 8d, however, shows that lateralis section does not have this effect. Experimental fish are not significantly different from controls at either 45 cm/s or 60 cm/s. So it must be possible for saithe to monitor their neighbors' velocities without using their posterior lateral lines.

4. Velocity Cross-Correlations: Apparent vs Actual Velocities

Our experiment provides evidence that fish normally make use of information from both vision and lateral line in determining their neighbors' velocities. We determined fishes' velocities from the distance that they actually swam in the tank: because the tank was circular, two fish swimming side-by-side must have been swimming slightly different speeds, with the one on the outside travelling a greater distance per unit time. Fish were thus presented with slightly conflicting information from their visual and acoustico-lateralis systems. The former would record the apparent speed of neighbors as they progressed around the circumference of the tank, the latter would record their true speed, based upon vibrations and pressure waves set up by their swimming. Fish in the wild would exper-

ience similar conflict whenever the school turned. Those fish on the outside of the turn would appear to be moving slower than they really were.

In order to measure what effect the slight curvature of the channel had on the extent to which fish matched their neighbors' velocities, each fish's velocity was re-calculated as if it had been swimming in an endlessly long straight channel and all of the correlations were recomputed. Had the fish really been swimming in a straight channel, then information from the two sensory systems would have been identical. Even in the real curved channel, the difference between information given by the two systems was very small.

The absolute difference between speeds of two fish swimming side-by-side depends, of course, on school velocity, but since neighboring fish were rarely more than 20 cm apart, a maximum likely figure for the difference is about 1.5 cm/s or 3% of the fishes' velocities, and the mean difference was less than 0.3 cm/s. Nonetheless, calculating fish speed as for a straight channel decreases blind fishes' correlations in 9 of 12 cases ($P < 0.05$, Wilcoxon two-tailed test). In contrast, correlations for control fish are increased in 8 of 12 cases ($P < 0.05$, Wilcoxon two-tailed test) and those for LS fish are increased even more (11 of 13 cases, $P < 0.01$, Wilcoxon two-tailed test). The significance of these results will be discussed below.

Conclusions

In the apparatus used for these experiments, both temporarily blinded and lateralis sectioned fish can school. Only if both senses are impaired are they unable to do so (Pitcher et al., 1976). These results do not mean that blind fish in the wild would necessarily be able to school, but one can conclude that the role of the lateral line is much greater than has been previously recognized. Although several authors have suggested a role for the lateral lines (Backus, 1958; Disler, 1963; Shaw 1962, 1968, 1970; Cahn et al., 1972) it has never been conclusively demonstrated before. Moulton (1960) concluded that turning movements which his blinded *Anchoviella choerostoma* made toward a passing school were due to sounds which the school produced, but it is certainly possible that his fish were responding to information from the lateral line as well (or instead).

Demonstration that blind fish match their neighbors' velocities more closely than do control fish refutes Shaw's (1978) suggestion that the blind saithe in our experiments were not really schooling with their companions but that they only appeared to be

since the rest of the fish were responding to them. These results suggest that fish monitor their neighbors' velocities by lateral line. LS fish, however, maintain normal velocity correlations with their neighbors, so it must be that vision also plays a part.

LS fish took up positions at 90° bearing to their neighbors, that is, side-by-side. In those positions fish deprived of their lateral lines would be best able to monitor small changes in their neighbors' velocities since the change in visual angle would be maximum (Hunter, 1969).

Our results shed some light on mechanisms by which school cohesiveness is maintained. Parr (1927) and Breder (1954, 1959) suggested that this was mediated entirely by vision, with the sight of a conspecific generally attractive but somehow becoming repulsive if fish moved too close to one another Characteristic NNDs would result from balance of the two opposing forces. The difficulties of monocular depth perception coupled with the fact that fish within a school may vary in size by up to 50% (Oshima, 1950; Breder, 1951; Partridge, 1978) make this seem unlikely. Results presented here suggest that the repulsive force (in the causal sense) which keeps fish from swimming closer together than they do is the pressure currents or low frequency sounds set up by swimming fish and monitored by the lateral lines. Temporary blinding results in an increase in NND (Fig. 4a) since, 1) these saithe no longer had the visual stimulus of the rest of the school, and, 2) they may have been paying more "attention" to displacement waves impinging on the lateral line, thus perceiving them as having been stronger than they really were. There was probably a limit to how far the BL fish could "see" with their lateral lines, and therefore their estimate of the number of fish in the school (and hence its attractiveness) was too small. In normal schools, NND decreases as a function of the number of fish in a school (Nursall, 1973; Partridge, 1980; Partridge et al., 1980).

Lateralis section has the opposite effect from blinding on NND, as would be predicted from the hypothesis above. If a fish only had the attractive visual stimuli of its neighbors and not the usual pressure displacement information tending to make it move away then it should swim closer than normal to them. We were recently pleased to learn that J.W. Burgess and E. Shaw have repeated part of our experimental paradigm for golden shiners (*Notemigonus crysoleucus*) with comparable results (pers. com.). From 2-dimensional evidence, they suggest that, as for saithe, lateralis section causes individual shiners to swim closer than control fish to their neighbors. (Burgess and Shaw's results are consistent with an-

other result we have noted for saithe, namely that LS fish tend to swim above their neighbors (Fig. 2b). Two-dimensional projections (ie. photographs from above a school) would make fish swimming above one another appear closer together than they really were, thereby magnifying the observed change in NND.) It should be kept in mind that both the increase in NND exhibited by BL fish and the decrease shown by LS fish were to some degree masked by the responses of control fish to them. This explains why, for instance, LS fish did not swim so close to their neighbors as to bump them.

The lateral lines do not provide the only source of information regulating spacing, however. If lateral lines of every fish in the school are cut, the school does not collapse. Vision could be used here, or it is possible that pressure could still be detected, since even with the posterior lateral lines cut at the opercula, fish still had their anterior lateral lines as well as cutaneous pressure receptors (Parker, 1904; Parker and van Heusen, 1917).

Our results indicate that roles of vision and lateral line overlap. Both are used to judge distance to neighbors and both affect fishes' preferred NND. Vision seems to be of primary importance for maintaining a particular position (and angle) with respect to other fish, and the lateral line is probably important for monitoring swimming speeds and directions of other fish in the school.

If fish use their lateral lines to monitor their neighbors' velocities, as indicated by the blind fish experiments (Fig. 8b) one would expect LS fish to fare considerably worse than normal. Observation that they show as high correlations as controls (Fig. 8d) suggests that the fish can compensate for the sensory loss. LS fish took up positions where they could best measure small changes in neighbors' velocities by vision alone. So instead of a change in velocity correlation, one observes a change in school structure. Conversely, BL fish compensated for the loss of visual cues by increasing their velocity correlations and thus maintaining more-or-less normal positions with respect to their neighbors.

Fish swimming in an endless circular channel are presented with conflicting information about the velocity of their neighbors from lateral line and vision. The way in which they resolve this conflict provides convincing evidence that both sensory modalities are used in normal schooling and that their roles are complementary. Results from comparisons of correlations for "straight" and "curved" channels can be explained as follows: BL fish could not have been relying upon visual cues to position themselves with respect to their neighbors, so they

did not receive conflicting information from two sensory systems. Instead, they matched their velocities to the actual velocities of their neighbors, as monitored by the lateral lines. This resulted in a decrease in velocity correlation calculated for a "straight channel". LS fish, on the other hand, relied upon vision to gauge their neighbors' velocities so calculating fishes' apparent speeds should have increased their mutual correlation, as indeed it did. That control fish also showed a significant increase in correlation for straight channels suggests that when information from vision and lateral line conflicts, fish pay more attention to visual cues. This effect would tend to keep the school from disintegrating whenever it turned.

These results may explain some of the other differences observed between the behavior of BL and control fish. The increased correlations between BL fish and their neighbors (Fig. 8b) may result partly from their not receiving conflicting information about their neighbors' velocities. This in turn could have produced the effect we mentioned in Pitcher et al. (1976) that blind fish made fewer course corrections but of greater magnitude than controls and that they showed more fore-and-aft and side-to-side movement within the school. If BL fish matched the true velocities of lateral neighbors, then they would have tended to move forward relative to those on the outside and backward relative to those on the inside. Also, matching their neighbors' velocities, they would have tended to swim in a series of straight lines rather than in a smooth curve around the circular track as was indeed observed.

In the wild, it is possible that comparisons of information from vision and lateral lines allows fish to swim in a straight course in the absence of visual landmarks (Partridge, 1978). Fish could turn toward any individual which appeared (on the basis of visual information) to be travelling slower than pressure cues indicated that it actually was (i.e. a fish on the outside of a turn) and away from fish which appeared to be travelling faster than pressure cues indicated. If all fish in a school balanced turning errors of fish on either side of them, then the school should be able to swim in a straight line with accuracy depending on the number of fish in the school. Such a navigational system could not correct for the effects of cross currents, but since many fish migrate along major currents (Harden-Jones, 1968) this might not be a problem.

References

Backus, R.H.: Sound production in marine animals. U.S. Navy J. Underwater Acoust. 8(2), 1–32 (1958)
Bateson, W.: The sense-organs and perceptions of fish: with remarks on the supply of bait. J. Mar. Biol. Assoc. U.K. 1, 225–256 (1889)
Breder, C.M., Jr.: Studies on the structure of the Fish School. Bull. Am. Mus. Nat. Hist. 98, 7–28 (1951)
Breder, C.M., Jr.: Equations descriptive of fish schools and other animal aggregations. Ecology 35, 361–370 (1954)
Breder, C.M., Jr.: Studies on the social groupings of fish. Bull. Am. Mus. Nat. Hist. 117, 397–481 (1959)
Cahn, P.H.: Sensory factors in the side-to-side spacing and positional orientation of Tuna, Euthynnus affinis. U.S. Fish. Bull. 70, 197–204 (1972)
Cahn, P.H., Shaw, E., Evans, F.C.: Lateral line nerve maturation related to development of schooling in the atherinid fish Menidia. Bull. Mar. Sci. 18, 660–670 (1972)
Cullen, J.M., Shaw, E., Baldwin, H.: Methods for measuring the 3-D structure of fish schools. Anim. Behav. 13, 534–543 (1965)
Disler, N.N.: Lateral line sense organs and their importance in fish behavior. Transl. from Russian, National Technical Information Service, Springfield, Va. (1963)
Harden-Jones, F.R.H.: Further observations on the movements of herring schools in relation to the tidal current. J. Con. Int. Explor. Mer. 27, 52–76 (1968)
Hunter, J.R.: Communication of velocity changes in jack mackerel Trachurus symmetricus schools. Anim. Behav. 17, 507–514 (1969)
Keenleyside, M.: Aspects of schooling behavior in fish. Behaviour 8, 183–248 (1955)
Kendall, M.G.: Time-series. London: Griffen 1973
McNicholl, R.G., McKay, W.C.: Effect of DDT and MS222 on learning a simple response in rainbow trout. J. Fish. Res. Bd. Can. 32, 661–665 (1975)
Major, P.F., Dill, L.M.: The three dimensional structure of airborne bird flocks. Behav. Ecol. Sociobiol. 4, 111–122 (1978)
Moulton, J.M.: Swimming sounds and the schooling of fish. Biol. Bull. 119, 210–223 (1960)
Nursall, J.M.: Some behavioral interactions of spottail shiners (Notropis hudsonius), yellow perch (Perca flavescens) and Northern pike (Esox lucius). J. Fish. Res. Bd. Can. 30, 1161–1178 (1973)
Olst, J.C. van, Hunter, J.R.: Some aspects of the organisation of fish schools. J. Fish. Res. Bd. Can. 27, 1225–1238 (1970)
Oshima, Y.: An experiment on the shoaling behavior of fish: the case when two homotypic shoals consisting of large and small individuals met with each other. J. Jap. Soc. Sci. Fish. 16, 195–200 (1950)
Parker, G.H.: The function of the lateral line organ in fishes. Bull. U.S. Bur. Fish. 24, 183–207 (1904)

Parker, G.H., Heusen, J. van: The reception of mechanical stimuli by the skin, lateral line organs and ears in fishes, especially in *Ameiurus*. Am. J. Physiol. **44**, 463–489 (1917)

Parr, E.A.: A contribution to the theoretical analysis of the behavior of fishes. Occas. Pap. Bingham Ocean. Coll. **1**, 1–32 (1927)

Partridge, B.L.: Sensory aspects of schooling. D. Phil. thesis. University of Oxford. 520 pp. (1978)

Partridge, B.L.: The effect of school size on the structure and dynamics of minnow schools. Anim. Behav. **28** (1980)

Partridge, B.L., Cullen, J.M.: A low-cost interactive coordinate plotter. Behav. Res. Methods. Instrum. **9**, 473–479 (1977)

Partridge, B.L., Dawkins, R., Amlaner, C.: Voltage controlled oscillators: inexpensive alternative to analog-digital converters. Behav. Res. Methods Instrum. **10**, 712–714 (1978)

Partridge, B.L., Pitcher, T.J., Cullen, J.M., Wilson, J.: The 3-dimensional structure of fish schools. Behav. Ecol. Sociobiol. (in press) (1980)

Pitcher, T.J.: The 3-dimensional structure of schools of the minnow *Phoxinus phoxinus*. Anim. Behav. **21**, 673–686 (1973)

Pitcher, T.J.: Sensory information and the organisation of behaviour in a shoaling cyprinid fish. Anim. Behav. **27**, 126–149 (1979)

Pitcher, T.J., Partridge, B.L., Wardle, C.S.: A blind fish can school. Science **194**, 963–965 (1976)

Shaw, E.: The schooling of fishes. Sci. Am. **206**, 128–138 (1962)

Shaw, E.: Some new thoughts on the schooling of fishes. FAO Fish. Rep. **62**, 217–233 (1968)

Shaw, E.: Schooling in fishes: critique and review. In: Development and evolution of behavior. Aronson L.R., Tobach, E., Lehrman, D.S., Rosenblatt, J.S. (eds.), pp. 452–480. San Francisco: Freeman 1970

Shaw, E.: Schooling fishes. Am. Sci. **66**, 166–175 (1978)

Siegel, S.: Nonparametric statistics for the behavioral sciences. London: McGraw Hill 1956

Sokal, R.R., Rohlf, F.J.: Biometry. San Francisco: W.H. Freeman 1969

Wardle, C.S.: Limits of fish swimming speed. Nature **255**, 725–727 (1975)

Wardle, C.S., Anthony, P.D.: Experimental methods used for the study of fish behavior in large tanks. I.C.E.S. CM **1973**, b:22 (1973)