

## The Three-Dimensional Structure of Fish Schools\*

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**Summary.** 1. Methods for producing and analyzing long-term three-dimensional records of the positions of individuals within fish schools are described. Detailed analysis of internal structure and overall shapes of schools of three species which school to varying degrees are reported: Data from cod (*Gadus morhua*), a weak facultative schooler, saithe (*Pollachius virens*), a strong facultative schooler, and herring (*Clupea harengus*), an obligate schooler, are presented.

2. Fish do not position themselves at random within schools (Figs. 1 and 2). This is shown to result from the maintenance of minimum approach distances between fish (Fig. 3). Comparison of the frequency of neighbors at different distances with that expected at random (Fig. 3), however, demonstrates that fish space themselves more regularly than one would expect if the structure resulted wholly from minimum approach distances.

3. Herring and saithe are shown to swim at nearly but not exactly the same depth as their neighbors (Fig. 5). Neighbors are more-or-less equally common in all directions (bearings) around fish, although herring show some tendency toward taking up positions at 45° and 135°, the positions expected if school structure were a cubic lattice. School structure is present in a statistical sense only.

4. Herring are shown to maintain proportionately larger interfish distances than do saithe or cod (Fig. 7). These results are discussed in terms of the body structure of the three species and the antipredator function of schooling. Shape of cod schools and, to a lesser degree, saithe schools, is shown to be highly

variable. Herring schools, however, appear fairly constant in their external shape (Fig. 10).

5. Factors affecting the structure of schools of saithe are studied. Increasing the number of fish in the school or the speed at which it is swimming results in smaller interfish distances (Figs. 8 and 9).

### Introduction

Over 10,000 species of fish are thought to school at some time in their lives (Shaw, 1978), so understanding how fish school and the way in which they do so is of considerable general interest as well as having economic implications for fisheries sciences.

Williams (1964) argued convincingly that one should not assume fish schools have an internal structure and that, at that time, no one had actually demonstrated that they did. It might be, for instance, that schools were just tight clusters of fish, and that within schools fish took up positions randomly. Nonetheless, and although there has been no convincing evidence for the notion, a number of theoretical treatments of how fish school have started with the assumption that fish take up positions within a rigid crystal lattice (e.g., Breder, 1965, 1976; Weihs, 1973, 1975; Serebrov, 1974; Cushing, 1977).

Attempts to characterize the internal structure of schools have been limited to qualitative observations (e.g., Breder, 1954, 1959; Keenleyside, 1955; Shaw, 1970) or have been based on a small number of photographs of fish schools (e.g., Cullen et al., 1965: 200 photos; Symons, 1971a: 50 photos; Pitcher, 1973: 200 photos; Partridge, 1979: 4,900 photos). We have compiled extensive data on the three-dimensional (3-D) structure of schools of three commercially important species: saithe (*Pollachius virens*, Gadidae), cod

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(*Cadus morhua*, Gadidae), and herring (*Clupea harengus*, Clupeidae).

We chose these species because they school in varying degrees and were readily available. Herring are obligate schoolers (Breder, 1967); they are always found in polarized schools (Blaxter, 1965; Shaw, 1970) and become extremely agitated if isolated (Bateson, 1889; Parr, 1927). Saithe are strong facultative schoolers (using the definition of Breder, 1967); they form schools most of the time, but casual observation suggests that the schools are less well organized than those of herring (Blaxter, 1965; Saetersdahl, 1967; Radakov, 1958). Cod are generally thought not to school, although they may aggregate at feeding grounds (Saetersdahl, 1967; C.S. Wardle, personal communication). With the cod, we hoped to study the positions individuals took up relative to one another when fish which did not normally school found themselves in a group. In the event, it turned out that cod did school weakly, although not as well as either herring or saithe, so we compare here the 3-D structure of schools of an obligate schooler (herring), a strongly facultative schooler (saithe), and a weakly facultative schooler (cod).

## Materials and Methods

The work reported here forms part of a series of experiments on schooling carried out between 1975 and 1978. On two occasions (for 3<sup>1</sup>/<sub>2</sub> weeks in September 1975, and for 6 weeks in August–September 1976), we visited the Department of Agriculture and Fisheries for Scotland (DAFS) Marine Laboratory in Aberdeen to film schools of saithe, cod, and herring in the 10-m annular gantry tank there.

*1. Capture and Care of Fish.* The experiments reported here were carried out on 187 saithe (mean length 31.7 cm, SD 5.1), 32 cod (mean length 48.8 cm, SD 7.3), and 38 herring (mean length 12.2 cm, SD 1.1). The cod were caught by local fishermen on long lines and kept in 3–5 m diameter fiberglass tanks at 8° C. The herring had been caught a year previously in a beach seine and kept in a display tank in the Marine Laboratory's public aquarium.

We caught the saithe on barbless hooks at 10–15 m depth in the Bay of Nigg, near Aberdeen harbor. Observations of DAFS divers suggest that all the saithe were from the same school. Fish survive better if transported in the dark (Wardle and Anthony, 1973), so the saithe were transported to the marine laboratory in lighttight containers. There, fish were anesthetized (MS 222, 1:15,000), weighed, measured, and then individually marked by cold-branding. Brass brands were dipped in a dry ice – alcohol mixture (Wardle and Anthony, 1973), dried, and held for 1.5–2.0 s against the fishes' left flanks, above and avoiding the lateral lines. Longer exposure sometimes led to tissue injury and shorter periods did not always produce a clear brand. Brands, easily visible at from 5 to 8 m, remained clear for 4–6 weeks. After branding, the fish were placed in the 10-m gantry tank, described below, for recovery. Extreme care was taken during handling and fish were bathed in Acroflavine to prevent infection whenever they were moved. As far as was possible, all handling was done in the dark or with only dim red light. Fish were fed on trout pellets or frozen

squid, always at the end of the day, since feeding affects schooling behavior for several hours (Pitcher, 1979).

*2. Methods for 3-D Recording of Fish Positions.* All experiments were carried out in a 10-m-diameter annular gantry tank 1.2 m deep. Water was cooled, aerated, and filtered, keeping oxygen tension fairly constant and temperature between 7° and 8° C. Above the tank was a steel gantry whose outer end rotated around the circumference of the tank. Gantry speed was controlled from an observation cabin. Two sets of slip rings carried power and sound-video signals between the control cabin and the gantry.

Detailed analysis of the structure and dynamics of fish schools requires extensive 3-D records of the positions of fish in schools, and several recording methods have been described (Cullen et al., 1965; Symons, 1971 b; Pitcher, 1973, 1975). Of these, the shadow method of Cullen et al. has the dual advantages that (a) photographs are taken from above the school, so fewer fish are obscured by the images of others compared with photographs taken from the side; and (b) the filming apparatus need not be stationary, so extended records can be made by moving the camera as the school swims. Rationale of the method is simple: a bright light is shone at an angle to the tank so that each fish casts a distinct shadow. The higher a fish swims in the water, the further it appears from its shadow. Knowledge of the position of the light and the depth of the water enables calculation of the 3-D coordinates of fish. A large red-filtered spotlight (Phillips 500-W Quartz halogen) was used to cast the fishes' shadows. Additionally, six smaller red spotlights were used to evenly illuminate the filming area. Silicon diode video cameras are sensitive to red light, but marine fish are not (Lythgoe, 1962; Hemmings, 1966), so filming was possible in light which did not appear very bright to the fish. Intensity of each spotlight was carefully matched to the rest so that only the shadow spotlight cast shadows. Since the spotlights were mounted on the moving gantry, geometry for reconstructing the fishes' 3-D positions remained constant as the schools swam around the tank. The camera frame of reference and hence the coordinate system was moving around the circumference of the tank, but this was easily converted into the real positions of the fish over time (Partridge, 1978).

Schools consisting of between 20 and 30 fish were trained to stay in view of the video camera by conditioning them to the red spotlit area. This was accomplished as follows: Individual fish follow a random speckled pattern projected from the gantry onto the tank floor in an optomotor response (see Wardle and Anthony, 1973; Pitcher et al., 1976). Also, in a dimly lit room, the fish would stay in front of a bright white spotlight projected from the trailing edge of the gantry and so could be herded along. The tendency to stay ahead of the trailing spotlight was reinforced by splashing the water near a fish if it entered the bright area. If fish swam too far forward, another bright spotlight was shone in front of them. After several days of training, the patterned spotlight and training spotlights could be turned off and the room lights turned on. The spotlights enclosed an area 5 m × 1.75 m, of which the school occupied a space rarely exceeding 1 m × 0.5 m. Schools would stay more or less in the brightly lit filming area as the gantry revolved around the tank. We could thus dictate a school's average speed by changing the gantry speed, but position of the school within the filming area and position of fish within the school were not controlled.

Schools were filmed at a number of speeds ranging from 1.0 to 2.5 body lengths/s. Because fishes' speeds depended upon their position relative to the center of the tank, we usually refer to school speed as the angular speed of the gantry. Actual velocities ranged between 20.4 and 29.2 cm/s at 3.5 rad/min and 49.6 and 70.8 cm/s at 8.5 rad/min.

During experiments, an observer on the gantry gave a continuous 'racetrack' commentary of the positions of each fish with

respect to the rest. This was recorded on the videotapes, and at a later stage individual fish were identified in each film sequence.

**3. Analysis Procedures.** After the experiments were carried out, suitable sequences were chosen for analysis. These were played on a high-resolution high-linearity video monitor and copied onto 35-mm film with a motor-driven Nikon camera running at 3 Hz (f 11, 1/30 s). In all, nearly 12,000 frames of film were made for the experiments in 1975 and 18,000 were made for those in 1976. This corresponds to 184 and 214 separate film sequences, respectively.

Once the films were made, the position of each fish's snout and its shadow in each frame of each sequence (total > 1.2 million points) was determined using an inexpensive online interactive coordinate plotter developed for the purpose (Partridge and Cullen, 1977; Partridge et al., 1978). In the infrequent cases where a fish's image was partially obscured by other fish, the position of the snout could be estimated in two ways: First, the position of a fish and its shadow lay on a straight line back to the position of the shadow-casting spotlight so that the position of the snout could be determined by the intersection between this line and the line of the body axis. Second, a cutout model the same size as the fish (determined from earlier film frames) could be placed on the partial image and the position of the snout estimated.

The plotting program was programmed to calculate the fishes' 3-D positions and to correct for parallax resulting from the shadow spotlight and the camera position. An iterative multiple regression comparing positions of points on a calibration object with their true positions further corrected for systematic errors due to lens aberration, nonlinearity of the video system, and so on (Pitcher, 1975). Final coordinates were accurate to  $\pm 0.25$  cm.

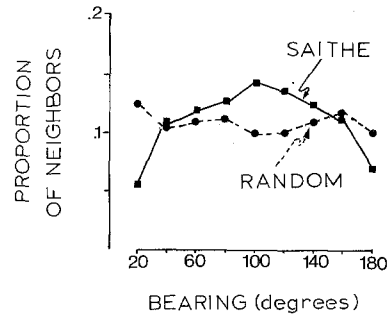
## Results

### 1. General Remarks on Cod Schools

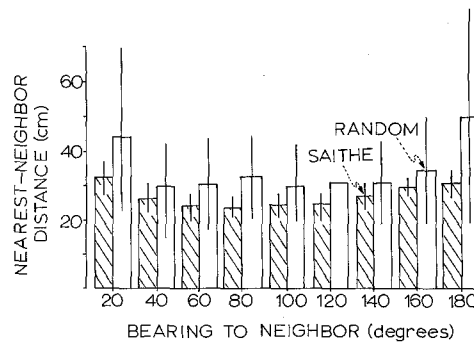
As mentioned in the introduction, and contrary to our expectations, cod did appear to school in the gantry tank. This could have been due to each fish following the spotlight pattern individually, but even with the pattern turned off, the school continued around the tank at a remarkably constant rate; 65 consecutive circuits of the tank took between 54 and 72 s each ( $\bar{x}=63.5$  s,  $SD=1.02$ ), corresponding to a speed of 6 rad/min, close to that at which we filmed the school. In 16 h that we left them free-running in the tank, the cod school swam close to 30 km! To check whether the training procedure had conditioned the fish to stay in a group, we added four cod, one at a time, to the gantry tank. Each joined the school the first time it came by and never left it, so there can be no doubt that cod do school at least some of the time.

*a) Demonstration that School Structure Is Not Random.* Although regular spacing among fish in schools has been assumed by many authors, it has never actually been demonstrated. With the coordinate data we do so in two ways.

**Method 1:** Points were generated at random in a space the same shape as a saithe school (see below) and at the same density. Relative positions of 'neighbors' in the generated schools were compared with



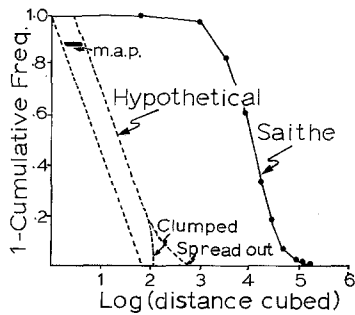
**Fig. 1.** Proportion of neighbors found in various directions (bearings) around reference fish for real saithe and computer-simulated schools. Bearings of  $0^\circ$  and  $180^\circ$  refer to directly in front and behind reference fish, respectively



**Fig. 2.** Mean distance to nearest neighbors (NND) in different directions (bearings) for real (*striped*) and randomly generated (*white*) schools. Fish in real schools show more consistent NNDs: NND is less affected by direction to the neighbor ( $P < 0.01$ , G-test) and variance within cells is less ( $P < 0.01$ , Wilcoxon 2-tailed test, Siegel, 1956). Error bars show standard deviations;  $n > 25,000$

those in real schools (Fig. 1). In the model schools, neighbors are equally common in all directions, but in real schools neighbors are most common in positions alongside a fish (bearing =  $80^\circ$ – $120^\circ$ ) ( $P < 0.001$ , G-test, Sokal and Rohlf, 1969). Saithe also show smaller and less variable nearest-neighbor distances than do randomly generated schools (Fig. 2). Similar results to those shown in Figs. 1 and 2 are obtained for herring and cod schools.

**Method 2:** Measuring the distance from points in space to their nearest neighbors, one often encounters reciprocal pairs (i.e., if point A is point B's nearest neighbor, the reverse is likely to be the case). One can calculate the expected frequency of reciprocal pairs (Pielou, 1969). If observed frequency is less than that expected by chance, the points making up the data must be more evenly distributed than random. Pielou provided no statistical test for this, but since expected variance is small (R.F. Green, personal communication), any consistent departure is probably significant. We calculated frequency of nearest-neighbor pairs in 48 film sequences of saithe schools, and compared this with the expected frequency (EF) ( $EF =$



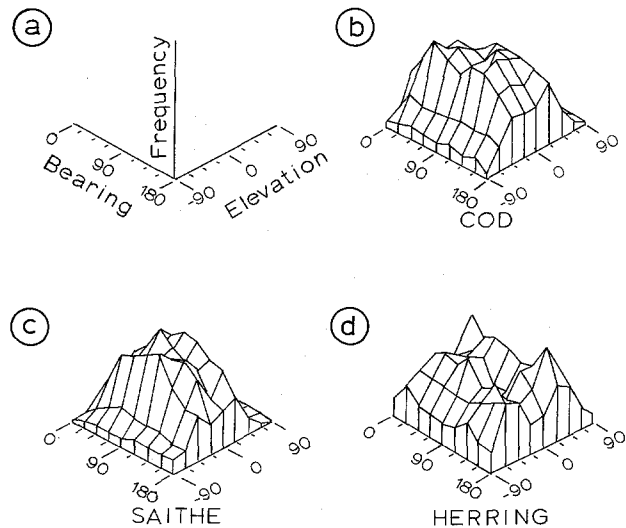
**Fig. 3.** Hypothetical log-survivorship curve for the distribution of nearest-neighbor distances. In the graph, 1.0 minus the cumulative frequency of neighbors at any particular distance is plotted against the log of the distance cubed. If the probability of finding a neighbor within distance  $r$  from a fish is simply a function of the volume of water contained in a sphere of the same radius, then the log survivorship curve should be a straight line. Hypothetical curves (dashed lines) for 'clumped' or 'spread out' distributions are also shown. Imposition of a minimum approach distance (*m.a.p.*) (see text) shifts the curve to the right. Actual results for saithe are shown in the *solid curve* ( $n > 16,000$ ). The curve resembles that for points which are more evenly spaced than random. The minimum approach distance can also be seen

0.293, calculated by an extension of Pielou's 2-D method, Partridge, 1978). In all 48 sequences, the observed value was less than half that expected, indicating that the saithe were spaced out more regularly than by chance.

*b) Minimum Approach Distances (m.a.p.).* Interpretation of results from the two methods detailed in 1a) above is complicated by the demonstration that fish do not approach closer than a certain distance from one another (see, e.g., Pitcher and Partridge, 1979). Even with the constraint of minimum approach distance, however, neighbors do not occur randomly around a fish. This is demonstrated in Fig. 3, in which a log survivorship curve of cumulative frequency of neighbors at different distances is plotted against distance cubed. (Expected likelihood of neighbors within various distances goes up as the cube of distance.) The figure shows hypothetical survivorship curves for distributions which are random, clumped, or dispersed (dashed lines). If fish show a minimum approach distance, the curve is displaced to the right, as shown. Also shown in the figure are results for saithe schools ( $n > 16,000$ ). Saithe are clearly more spread out than one would expect if they were taking up positions at random. (The model schools discussed above do not differ from random expectations.)

## 2. Description of the Internal Structure of Schools of Cod, Saithe, and Herring

In most of the discussion which follows, schools of the three species can be neatly ranked in terms of the

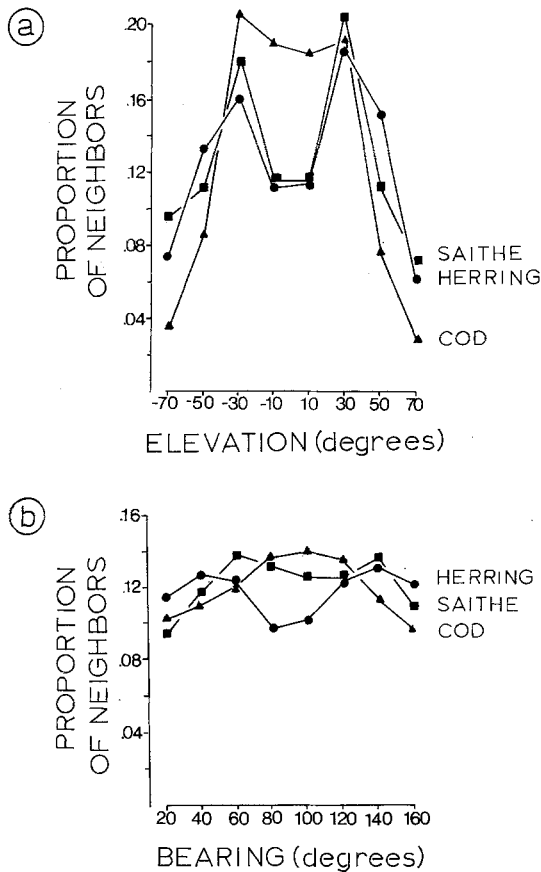


**Fig. 4a-d.** Bearing/elevation plots for (b) cod, (c) saithe, and (d) herring. Shown are distributions for nearest neighbors (NN1) as a function of bearing and elevation to them. As shown in (a), frequency of neighbors in different  $20^\circ \times 20^\circ$  sectors of bearing by elevation is represented by the *height* of the 3-D surface. In (c), for example, it can be seen that for saithe most neighbors lie at approximately but not exactly the same depth. That is, most neighbors occur at elevations between  $\pm 40^\circ$ , but not exactly at  $0^\circ$ , as can be seen by the *furrow* running along the figure

degree of structure present. Saithe schools are better organized than cod schools and herring schools are better organized than saithe schools.

*a) Position of Nearest Neighbors (NN1).* Figure 4 shows the frequency of nearest neighbors in various directions around reference fish for cod, saithe, and herring. Frequencies of neighbors (height) are plotted against bearing (angle in the horizontal plane) and elevation (angle above or below the horizontal). In this and figures which follow, left and right sides have been superimposed since, even for fish swimming in the annular tank, statistics for position and distance to neighbors as well as correlations between individual's headings and velocities are not significantly different for the two sides (Partridge, 1980).

The 3-D distributions for the three species, shown in Fig. 4, are significantly different in bearing and elevation to NN1 and in the interaction between bearing and elevation (G-test, Sokal and Rohlf, 1969), and a number of differences is apparent. For instance, saithe (4c) and herring (4d) tend to swim at a slightly different level in the water from their nearest neighbors, as has been shown previously for minnows (*Phoxinus phoxinus*) (Partridge, 1980). Cod, on the other hand, are just as likely to have neighbors at exactly the same level (elevation =  $0^\circ$ ) as above or



**Fig. 5a and b.** Proportion of nearest neighbors occurring at different elevations (a) and bearings (b) for saithe (squares), herring (circles), and cod (triangles). In (a), reluctance of fish to swim on the same level as near neighbors is especially clear for herring and saithe. See text for full explanation

below them. Fish of all three species are likely to have neighbors at close to the same depth (elevation between +40° and -40°), but this effect is least pronounced in herring.

Because frequency of nearest neighbors depends upon both the bearing and elevation to them, any statistical analysis must consider both dimensions simultaneously. The three-dimensional figures resulting from such analyses, such as those shown in Fig. 4, are difficult to interpret, however, so 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 3-D. Unless otherwise stated, each case in which a significant result is described refers to a three-dimensional G-test [Sokal and Rohlf, 1969],  $P > 0.001$ ,  $n > 15,000$ .)

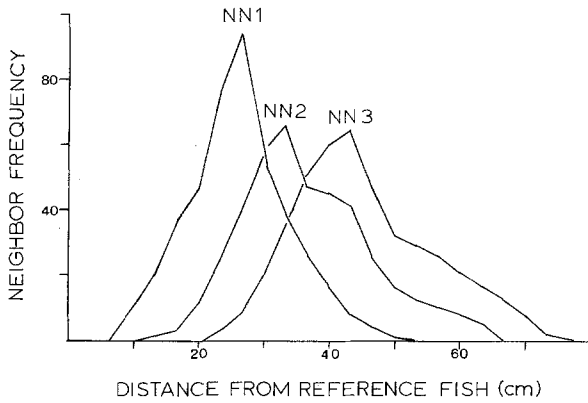
In Fig. 5a, the low number of neighbors on exactly the same level as reference fish is especially clear. Distributions for saithe and herring are similar in this regard, but cod frequently swim at the same level as their neighbors. In terms of bearing to neigh-

bors (Fig. 5b), saithe and cod are most alike; herring take up a somewhat different structure. Saithe and cod are most likely to have their nearest neighbors at around 90° (range 60°–140°). Herring, on the other hand, most frequently have nearest neighbors at 45° or 135°. These are the positions one would expect if herring schools were cubic lattices.

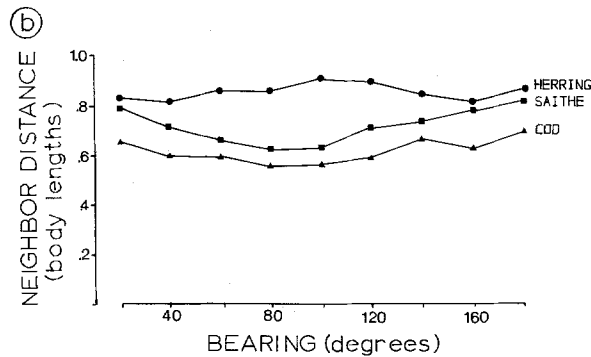
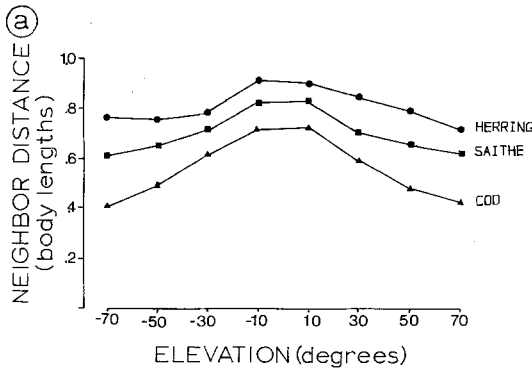
*b) Nearest-Neighbor Distance (NND).* Not surprisingly, the distance a pair of fish maintain between them depends upon their relative positions. Plots of neighbor frequency as a function of distance (e.g., Fig. 6) therefore show considerable overlap between NN1, NN2, and NN3. With the exception of one study (Partridge, 1980), however, previous investigations have only considered mean nearest-neighbor distance. NND may be a useful measure for comparing species, but it is unlikely to be very informative about the actual 3-D structure of schools. Normal variation in NND is such that subtle changes in school structure would go unnoticed, so NND must be considered as a function of fishes' relative positions. Because of the differences in absolute size of fish in our cod, saithe, and herring schools, we compare NNDs in terms of proportion of body length (BL), as have Breder (1965), Hunter (1966), and van Olst and Hunter (1970).

Figure 7 shows NND as a function of elevation (a) and bearing (b) between fish. The three species again fall into the order cod, then saithe, and then herring (weakly facultative, facultative, and obligate schoolers). Surprisingly, herring, the smallest of the three, take up positions farthest from one another. Distributions for the three species are significantly different from one another in NND as well as in variability ( $P < 0.001$ , G-test) with cod school NND the most variable, followed by saithe. (Standard deviations 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 about mean NND within individual cells of bearing by elevation ranged from 8 to 12 cm for cod, 2 to 5 cm for saithe, and 1 to 4 cm for herring.)

*c) Comparison of Distance to NN1, NN2, and NN3.* If the structure of a school were a perfect lattice of any sort, then the distance to a fish's second-nearest neighbor (NN2) or third-nearest neighbor (NN3) would not be markedly different from that to its NN1. The degree to which schools resemble a repeating lattice can thus be measured by comparing distances to NN1, NN2 and NN3. Table 1 shows that herring schools are the most structured, followed by saithe. Ratio of  $NND_1$  to  $NND_2$  to  $NND_3$  for cod schools



**Fig. 6.** Frequency of neighbors at various distances from reference fish. (Data are for saithe.) Distributions of NN1, NN2 and NN3 overlap considerably, showing that NND is a rough measure if the relative positions of fish are not taken into account. Similar results were presented by Major and Dill (1978)



**Fig. 7a and b.** Nearest-neighbor distance (mean distance to NN1, in body lengths) as a function of (a) elevation and (b) bearing for saithe (squares), herring (circles), and cod (triangles). NND depends upon both bearing and elevation, but ranking of the three species remains constant in all directions. Herring show largest NNDs (in terms of body size), saithe show the next largest, and cod show the smallest NNDs;  $n > 25,000$ . Since intrasequence variation in NND for individuals is as great as interindividual differences (Partridge, 1978, 1980), data from different individuals are lumped. (Data from individuals were sampled every four frames, the interval at which autocorrelations of NND, velocity, and swimming directions were nonsignificant.)

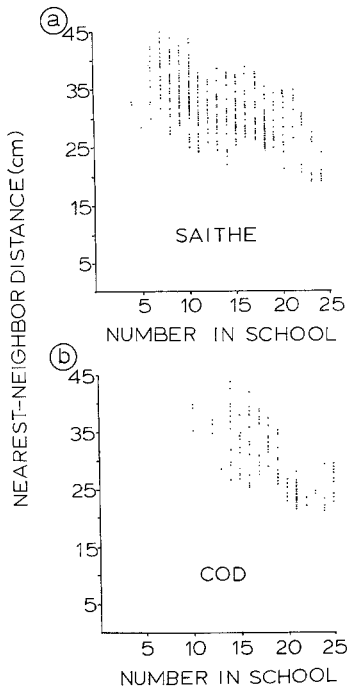
is not different from that for points generated at random.

d) *Distance to a Neighbor Depends upon Its Position in Space.* Much of the variability in NND shown in Fig. 6 stems from positional effects on the distance fish maintain between them. Saithe, cod, and herring all have greatest NNDs for fish on the same level (elevation = 0°, Fig. 7a) and directly alongside (bearing = 90°, Fig. 7b). The observation that NND depends upon fishes' positions, however, slightly complicates the picture of what positions they actually take up, since the greater the expected NND in a particular direction, the lower the probability that a fish's NN1 will lie in that direction. (Probability of NN1 occurring in a particular direction is 1-probability of fish occurring in any other direction at a lesser distance.) For instance, Fig. 5 showed that herring are not often nearest to fish directly alongside them (at bearing = 90°). This would be expected on the basis of probabilities, however, if fish maintained a larger distance to those fish beside them than to those in front or behind. The question then is whether the distributions of nearest-neighbor frequencies shown in Fig. 5 simply reflect a bias of preferred NNDs in various directions. Dividing the observed frequencies in each 20° by 20° cell of bearing by elevation by the mean NND in that cell corrects for the frequency bias. Doing this does not affect the significance of any of the conclusions drawn above. That is, for example, the number of neighbors which herring have at 90° bearing (Fig. 5b) is significantly less than expected *even* if the greater observed NND in that direction (Fig. 7b) is taken into account.

e) *Positions and Distance of Neighbors Depend upon School Size and Swimming Speed.* A number of authors have found that nearest-neighbor distance decreases as a function of the number of fish in a school (Breder, 1954; Keenleyside, 1955; Nursall, 1973; Partridge, 1980). This relationship also holds for saithe and cod schools (Fig. 8). (There was insufficient variability in herring school size to carry out a similar analysis.) Additionally, Fig. 9 shows that for four speeds over the range 5.5–8.5 rad/min, NND in any direction tends to fall off as speed increases ( $P < 0.001$ , G-test).

### 3. External Structure of Fish Schools

The external structure of fish schools can be characterized in terms of schools' shapes or volumes. In this paper, we will consider only the former. Methods for estimating school volumes and densities have been described elsewhere (Pitcher and Partridge, 1979).

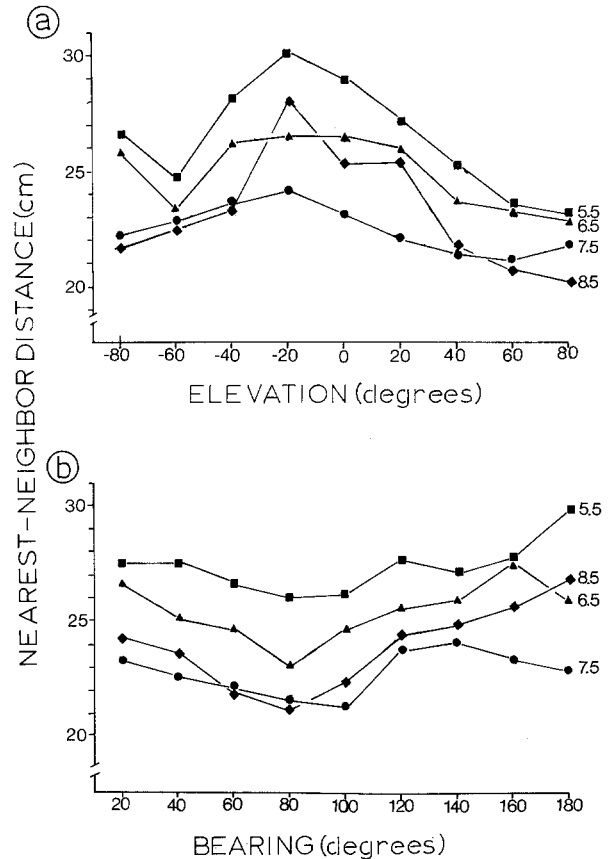


**Fig. 8 a and b.** Nearest-neighbor distance (NND) decreases as the number of fish in a school increases. Shown are data for schools of (a) saithe and (b) cod. Points drawn are independent estimates of mean NND for schools of various sizes. Schools of herring which we filmed were all of the same size, so no similar graph can be drawn

a) *School Shape.* Cullen et al. (1965) calculated dimensions of pilchard (*Harengula* spp.) schools and found that they were generally 2.1:1.7:1.0 (length: width:depth), and Pitcher (1973) estimates values of 3:2:1 for minnows (*Phoxinus phoxinus*). Measurements of saithe schools give values of roughly 6:3:1 (1975 data). Since fish are longer than they are wide, the schools have roughly the same number of fish in each direction. On average, the schools were seven fish long by five fish wide.

Measurements such as these, however, give the misleading impression that the shape of schools is constant, and this is far from the case. School shape is quite variable within each species. For herring, the least variable of the three species in terms of shape, dimensions ranged from 4:3:1 to 1.5:3.8:1 (length: width:depth). It is far more informative to look at the variety of shapes schools of a particular species take up than to measure mean dimensions of schools. When this is done, clear differences become apparent among the three species which we studied, and these differences correspond to the degree to which herring, saithe, and cod school.

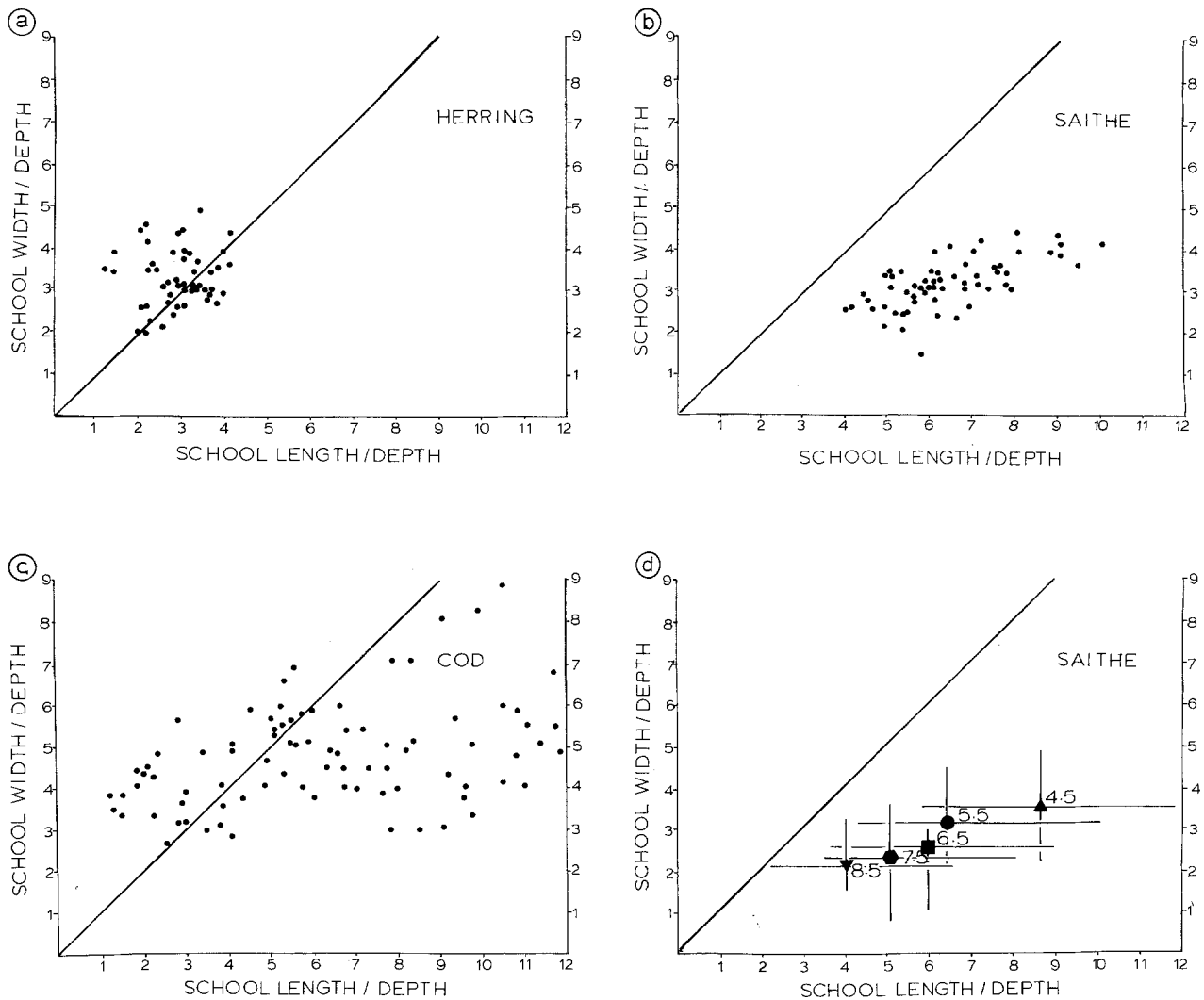
Scattergrams showing independent estimates of school dimensions for the three species are shown in Fig. 10. (Within graphs, all points are for schools



**Fig. 9 a and b.** Nearest-neighbor distance (NND) as a function of (a) elevation and (b) bearing at four school speeds. For normal cruising speeds (5.5–8.5 rad/min in the 10-m-diameter tank), NND decreases as school speed increases

swimming at the same speed.) The graphs show the length and width of schools, each divided by the depth of the school. Although variable, the herring schools we photographed were roughly circular, and, on average, about three times as long or wide as they were deep. Saithe schools (Fig. 10b) tend to be about twice as long as they are wide, and no generalization can be drawn for cod (Fig. 10c). Points for herring fall roughly on the diagonal, whereas a line drawn through the points for saithe has a slope considerably less than 1. That is, when the herring school became shallower (flatter) or deeper, the outline of the school when looked at from above did not change, but when the saithe school became deeper, it became progressively narrower. Fluctuations of school shape of this sort occur even while the number of fish in a school remains constant.

Herring schools are much less variable in shape than saithe schools and saithe schools are less variable than cod schools (*F*-tests carried out independently on length and width of schools,  $P < 0.01$ , Sokal and Rohlf, 1969). This result, too, is consistent with the



**Fig. 10.** a–c Shape of schools (a) herring, (b) saithe, and (c) cod. Each point represents an independent observation of a school. Points within one graph are all for schools filmed at the same speed (approximately 1.0 BL/s). The shape of the school is plotted as the width/depth (ordinate) against the length/depth (abscissa). Perfectly spherical schools would be plotted along the diagonal lines. Points below the line correspond to schools which are longer than they are wide, and points above the line correspond to schools which are wider than they are long. d Shape of schools is affected by the school's speed. The graph should be read in the same way as a–c: There is a reasonably smooth change in shape as speed is changed. Schools traveling at 4.5 rad/min were much longer than they were wide, but at higher speeds the schools became increasingly circular (length:width). Mean dimensions are shown. Bars indicate range of observations

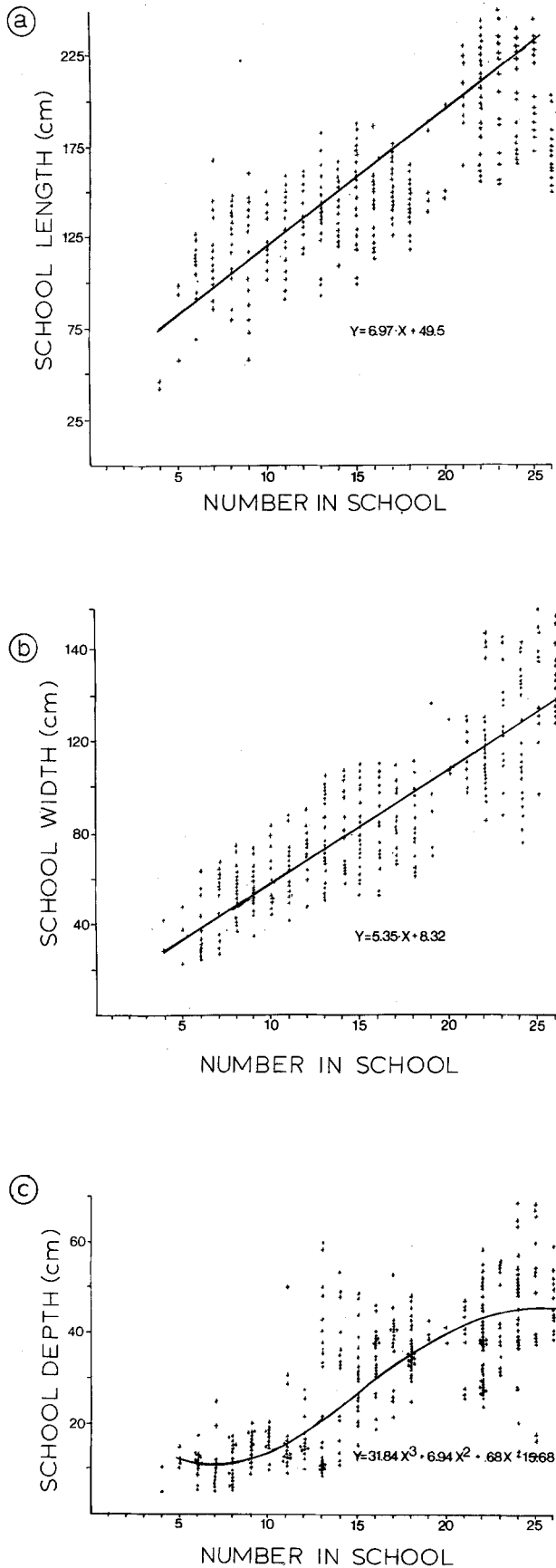
qualitative rankings of the three species as obligate, strong facultative, and weak facultative schoolers.

*b) Factors Affecting School Shape.* Breder (1959) and Radakov (1973) have both suggested that the faster a school swims, the more elongate will be its shape. This is definitely not the case for saithe. Figure 10d shows the effect of school speed on the shape of saithe schools. The faster a school swims, the more nearly spherical it becomes. Points fall on a line whose slope is less than 1, indicating that the ratio of length to width of the school does not remain constant as

depth changes. At low speeds, the school is much longer than it is wide, but at higher speeds it becomes nearly spherical.

Also affecting school shape, for saithe at least, is the number of fish in the school. The dimensions of the school increase smoothly if one plots length or width of a school as a function of the number of fish in it (Fig. 11a and b), but this is not the case for the depth of the school (Fig. 11c). Depth of the school remains fairly constant as the number of fish in a school increases from five to about 15, and then suddenly nearly triples as the school be-





comes multilayered. Data plotted in Fig. 10 were for schools of the same size (22–25 fish), so the effect of number of fish on school shape is not responsible for the variability observed.

**Discussion**

Results from this study are summarized in Table 1, which shows that in all eight characteristics schools of the three species fall into the same order. Cod schools are the least organized, saithe schools show somewhat more organization, and herring schools are the most organized. In most measures, saithe schools resemble herring schools more than they do cod schools. For example, saithe and herring tend to swim at nearly but not exactly the same depth as their neighbors. Herring, however, are more likely than saithe to have as their nearest neighbor fish which are above or below them. This is what one would expect if herring were taking up positions of any repeating lattice. Similarity between distances to NN1 and NN2 exhibited by herring, and to a lesser degree, saithe also suggests a repeating structure. By contrast, cod appeared randomly spaced.

Our finding that herring, the smallest of the three species which we studied, had the largest interfish distances is in direct contrast to that suggested by Breder (1965), who concluded that nearest-neighbor distance (in BL) increased linearly with fish size. He ranked the species which he studied by size, however, and if one considers NND in terms of absolute size there is no significant relationship (Partridge, 1978). Nonetheless, herring, the best schoolers of the three species, might be expected to swim closer together than cod or saithe. That they do not do so might be due to two causes. First, there is some indication that within species NND decreases as the fish become older (and larger). Van Olst and Hunter (1970) found that for four species NND decreased as fish size increased, but this effect was strongest for very small fish (3–5 cm). NND soon leveled off so that there was no apparent difference between NNDs for fish 5 cm and 13 cm long. It might be that larger herring would

**Fig. 11 a–c.** Dimensions of saithe schools as a function of the number of fish in them. Length (a) and width (b) go up fairly smoothly as the number of fish in the school increases, but the depth (c) of the school remains fairly constant until school size reaches around 15, at which point the school suddenly becomes multilayered. Increase in depth at about 15 fish was not due in any large part to the confines of the channel in which they were swimming. Although individual fish often swam within a few centimeters of one side or the other of the channel, the schools never took up more than about half the width of the channel

**Table 1.** Summary of school structure for three species

Comparison	Cod	Saithe	Herring
Neighbors at approximately the same depth (ranked, 1=most)	1	2	3
Neighbors at <i>exactly</i> the same depth	Yes	No	No
NN2 and NN3 at exactly the same depth	Yes	Yes	No
Most frequent bearing to NN1	60° But nearly uniform	90°	45°, 135°
Distribution of bearings to NN2 and NN3 different from that for NN1	Yes	Yes	No
NND <sub>1</sub> :NND <sub>2</sub> :NND <sub>3</sub>	1:1.5:1.9	1:1.3:1.5	1:1.2:1.4
Shape length:width:depth	10:4:1 to 2:4:1	6:3:1	3:3:1
Variability of shape (ranked, 1=most)	1	2	3

form denser schools, but those we studied were 12 cm long – within the level region of Van Olst and Hunter's curves.

An alternative and more likely explanation for the surprisingly large NNDs which herring show compared with saithe or cod is that characteristic NNDs for a particular species simply reflect the body structure of the fish rather than how well the species in question school. If individuals in a school are to respond to predators with complicated defensive tactics (e.g., Potts, 1970; Radakov, 1973; Nursall, 1973; Partridge, 1978, 1980), then fish must be able to turn in every direction. We suggest that NND depends primarily upon the maneuverability of the fish, with the stiff-bodied herring maintaining larger interfish distances than the more maneuverable saithe and still more maneuverable cod.

That herring most frequently had neighbors at 45° and 135° bearing suggests that they were taking up the positions of a cubic lattice. The majority of neighbors, however, were not in these positions. Further, the positions of neighbors as a function of elevation do not support the hypothesis that herring schools are cubic lattices. On the other hand, plots of neighbor positions for both saithe and herring may be compatible with predictions of a more complicated type of packing suggested by Pitcher (1973) and Breder (1976). The authors pointed out that a cubic lattice was not optimal packing to reduce visibility of a school by minimizing its volume and that packing based upon hexagons or tetrahedra would take up less space. Both the model based upon tetrahedra suggested by Pitcher and Breder and the simple cubic lattice model predict that nearest neighbors should lie at elevations of about +45° or -45°, whereas for both saithe and herring, the most common elevations to neighbors are about +25° and -25°. Positions in the horizontal dimension (bearing), however,

superficially resemble those for the tetrahedral model, and simulations examining how closely schools of saithe and herring resemble the optimal packing suggested by Breder and Pitcher are now under way.

Structure of cod schools is considerably less well defined than that for schools of saithe and herring. Close examination of the structure of cod schools shows that the currently accepted division of schools into 'polarized' or 'nonpolarized' (Shaw, 1970) may not be very helpful after all, since it fails to distinguish between cod and the saithe or herring schools. That is, although cod schools were less well organized than the other two species in all the measures above, they were nonetheless highly polarized. Breder's (1967) classification of species in terms of the amount of time they spent schooling (facultative vs obligate) seems to describe much better the differences among these species. Nearest-neighbor distance has also not proved a good indicator of structure in a school in contrast to previous suggestions (Breder, 1954, 1965; Cullen et al., 1965; Hunter, 1966; van Olst and Hunter, 1970). As a simple measure of structure, the ratio of the distances to the nearest and second-nearest neighbors is a more useful tool. The closer the ratio is to 1.0, the greater the degree of structure in the school.

We have demonstrated that there is organization in schools of saithe, cod, and herring, and that the structure mirrors the amount of time the fish spend in schools (i.e., their classification as facultative or obligate). School structure further mirrors the sensory capabilities of the fish. Fish normally take up those positions at which they can best monitor the velocity and headings of their neighbors. For example, response latencies for saithe are smallest (Partridge and Pitcher, 1980) and the degree of correlation is greatest with neighbors at 90° bearing (Partridge 1978, 1980) and, as we showed above, this is the direction in

which neighbors are most frequently found. That fish swim at different levels in the water is further evidence that the immediate function of school structure is to make it easier for fish to respond to one another. In contrast, for instance, Weihs' (1973, 1975) models for a hydrodynamic function of schooling predict that fish should lie at the same depth as neighbors. (A recent test of Weihs' models failed to confirm any of the predictions for saithe, cod, or herring [Partridge, 1978; Partridge and Pitcher, 1979].) We conclude that, in the immediate sense, the function of school structure is to position fish so that they can most quickly respond to their neighbors.

Considering school structure as reflecting sensory capabilities of the fish and the need to behave as a cohesive unit explains why a school's shape is affected by its speed. In order to explain why schools they observed were not perfect spheres, Breder and Radakov suggested independently that schools would be 'stretched out' along their axis of movement. There is no reason, however, why all fish might not accelerate at once so that the school could keep a constant shape at any speed. Although the saithe schools were longer than they were wide, the effect of increasing speed was to reduce this difference, the opposite to the effect predicted by Breder and Radakov. So the shape of schools is not an inevitable consequence of their movement.

Two other explanations seem plausible to us. First, hydrodynamics of swimming will be affected by speed and, if the structure of a school is dictated by, for instance, fish trying to keep out of the turbulence produced by other fish, then one might expect it to be affected by swimming speed. The second explanation is simply that at different speeds, the positions at which fish can best monitor their neighbors' velocities and headings may be different. Further evidence for this notion is that altering a fish's sensory capabilities by lateral line section or temporary blindfolding results in the fish taking up different positions with respect to its neighbors (Partridge, 1978; Partridge and Pitcher, 1980b). The implicit conclusion is that school structure has a function per se and does not simply result from fish packing into as small a space as possible (as suggested by Pitcher [1973] and Breder [1976]).

Understanding how fish school sheds light on why they do so. That the immediate function of structure seems to facilitate interactions between individuals suggests that the speed at which fish can respond to one another and the degree to which they can monitor one another's positions and velocities are important. We believe that this is due to the function of schooling as an active antipredator device. Antipredator value of schooling cannot lie simply in reducing

the chance of discovery, but, rather, must lie in the behavior of the school after it has been found.

It has been argued (e.g., Breder, 1959; Williams, 1964; Hamilton, 1971; Treisman, 1975) that schooling offers passive protection even after discovery of the school by predators, giving individuals the opportunity to hide behind one another. Only if the predator cannot eat the entire group, however, do any of its members gain more than a temporary advantage. And antipredator tactics such as the fountain effect (Potts, 1970) may result in individuals previously at the center finding themselves at the edge of the school. That the survival of individuals in natural schools is not simply due to predator satiation has been well demonstrated (Radakov, 1958; Neil and Cullen, 1974; Seghers, 1974; Major, 1976). A predator attacking a school does not only catch a smaller proportion of the total number than when confronted with solitary individuals; it may catch fewer fish overall, even though more are available.

The degree of protection which a school offers must be due to the tactics which the fish employ after discovery, and these, in turn, depend upon (a) the fishes' abilities to gauge one another's positions, and (b) their ability to decide upon a common tactic. Both (a) and (b) depend upon the fishes' sensory capabilities and the characteristic structure of the school.

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