

## A new stereophotographic technique for analyzing the three-dimensional structure of fish schools

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### Synopsis

A technique using two downward-directed 35 mm cameras has been modified to measure the three-dimensional structure of fish schools. The resulting stereo pairs of photographs are analyzed, producing the 3-coordinate location of each fish's nose, after correction for lens distortion and refraction. Separation angles (bearing and elevation) and distance can then be determined for any pair of fish in the school. The technique's high level of accuracy is demonstrated for an underwater calibration field. It is then applied to the measurement of the 3-D structure of schools of coho salmon (*Oncorhynchus kisutch*) swimming in a hatchery trough. Although the fish were not organized in a rigid crystal lattice, the analysis provided some evidence of structure.

### Introduction

Precise, quantitative data on the structure of fish schools allow the testing of hypotheses concerning the school's adaptive significance or sensory integration. For example, Partridge & Pitcher (1980) have provided convincing evidence that schooling saithe (*Pollachius virens*) use information provided by the lateral line, by examining changes in school structure that followed lateral line section. Partridge & Pitcher (1979) have also effectively refuted Weihs' (1973) model of the hydrodynamic advantages of schooling by comparing its predictions on

spacing with actual measurements in the laboratory.

Many workers have attempted to measure the internal structure of fish schools. Studies by Breder (1954, 1959), Hunter (1966) and Van Olst & Hunter (1970) examined the spacing between neighbours in two-dimensional projections (dorsal photographs). However, most schools are three-dimensional entities; two-dimensional measurements will provide interfish distances which are considerably underestimated, and the nearest-neighbour may even be incorrectly identified. Symons (1971b) discusses these difficulties.

Several techniques for three-dimensional mensuration of school structure have also been developed. Apart from the method of Graves (1977), which assumes invariant fish size and uses the size of each

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individual's image on the photograph as a measure of its distance from the camera (i.e. the third dimension), these techniques have been of two major types: stereo and shadow. The stereo method requires obtaining two simultaneous photographs from different angular positions, using either a stereo prism lens (Cullen et al. 1965) or an arrangement of mirrors (Symons 1971a, b, Healey & Prieston 1973, Pitcher 1973, 1975). The shadow method uses the shadows of the fish projected onto the substrate as the second view of the school and has been applied by Dambach (1963), Cullen et al. (1965), Partridge (1980), Partridge & Pitcher (1980), and Partridge et al. (1980).

The above techniques are for the most part highly sophisticated, requiring apparatus which effectively restricts their use to a laboratory situation. There is a great need for a technique which can be used in the field to obtain measurements rapidly of the structures of schools of a variety of species in a range of environmental circumstances. Our group had previously developed a stereo method for measurements of the three-dimensional structure of airborne bird flocks (Major & Dill 1978). This technique, which obtains pairs of photographs simultaneously with two cameras, is here modified and applied to fish schools. Following a description of the technique and a check on its degree of accuracy, we provide some preliminary data on the three-dimensional structure of schools of juvenile coho salmon (*Oncorhynchus kisutch*) swimming in a hatchery raceway.

## Methods

### Apparatus

Stereo pairs of photographs were taken with two identical motor driven 35-mm cameras (Nikon Photomic F2) with 28 mm lenses. The cameras were mounted side-by-side (32 cm between lens centres) on an aluminum plate (Fig. 1). Each camera 'floated' on a spring-loaded three-point levelling device, and could be independently levelled to an accuracy of 20 s with a level bubble. Care was taken that the two film platens were in the same plane by levelling a plate placed across both of them after removal of the camera backs.

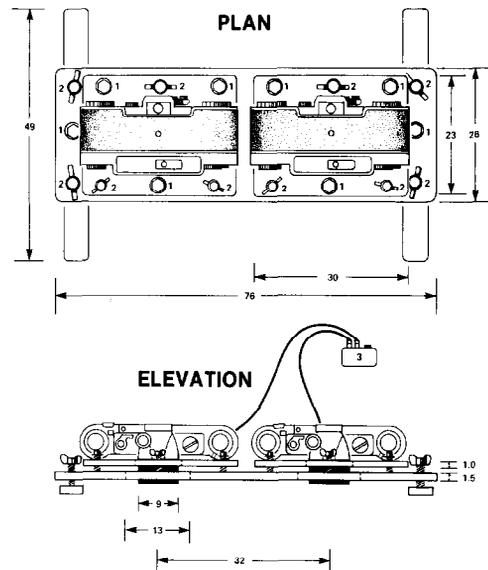


Fig. 1. The camera apparatus used in this study. Two motor-driven 35 mm cameras are mounted on separate levelling platforms, and fired simultaneously (see text for further details).

The entire apparatus was placed on a ladder spanning a hatchery trough, with the cameras pointed downward, their lenses projecting through holes in the aluminum plates. A plexiglass box (open at the top) was suspended below the ladder with its bottom plate a few cm below the water surface. This provided an air-plexiglass-water interface a known distance (462 mm) below the lens faces and eliminated any surface ripple. It was also levelled to an accuracy of 20 s. A black curtain draped over the cameras eliminated excessive surface glare. Water depth (below the plexiglass) was 725 mm.

The cameras were fired simultaneously from a common electronic shutter release box (single frame only; simultaneity checked with a photocell beam through the two camera apertures mounted in tandem). Kodak Plus-X (ASA 125) film was exposed for the minimum time possible given ambient light conditions, and developed according to manufacturer's instructions.

### Analysis

The resulting left and right stereo pairs of photographs were analyzed, using a Zeiss-Jena Topocart Analyzer, by Integrated Resources Photography Ltd., Vancouver, B.C. Standard photogrammetric

methods were used to determine the three-coordinate position of the tip of the snout of each fish in a school. The procedure incorporated corrections for radial lens distortion characteristics (based on photographs taken of a calibration field in air using the same focal distance and aperture settings as were used in the field) and for refraction (from physical principles and the known geometry of the situation). Numbering the fish on enlarged prints prior to analysis allowed subsequent identification of individuals.

From the three-coordinate data, the following spatial characteristics of each fish's three nearest neighbours were calculated on an IBM 370/148 computer:

$$\text{Distance} = [(\Delta X)^2 + (\Delta Y)^2 + (\Delta Z)^2]^{1/2} \dots(1)$$

$$\text{Bearing} = \text{TAN}^{-1} (\Delta Y/\Delta X) \dots(2)$$

$$\text{Elevation} = \text{TAN}^{-1} \left[ \frac{\Delta Z}{((\Delta X)^2 + (\Delta Y)^2)^{1/2}} \right] \dots(3)$$

Axis 'X' is the snout-to-tail axis of the fish, but a mean value, taken to be parallel to the walls of the trough, was used in this analysis. Axis 'Y' is perpendicular to the 'X' axis in the same plane, and 'Z' is vertical and perpendicular to the 'X-Y' plane. Mean angle vectors and angular deviations were determined using the methods of Batschelet (1965).

### Accuracy

A variety of possible sources of error (discussed in Major & Dill 1978) can reduce the accuracy of measurements obtained using the methods described here. We checked the reliability of our technique by photographing an object whose spatial structure could be independently determined; a lattice structure constructed of laboratory bench hardware. Sixteen black spots (8 mm diameter) were placed at various points on the structure, and the distances between the centres of all possible pairs of spots measured by hand. The lattice was then placed in the water beneath the cameras, photographed, and the three-coordinate position of each spot determined photogrammetrically. Thirteen spots were visible in both photographs, providing 78 'neighbour distances' to compare with those measured directly from the lattice. The average discrepancy in

these pairs of measurements was 2.74 mm or 0.67% of the true distance (Fig. 2), and there was no apparent tendency for percentage error to increase with distance (Fig. 3). This level of accuracy was deemed adequate for the present study.

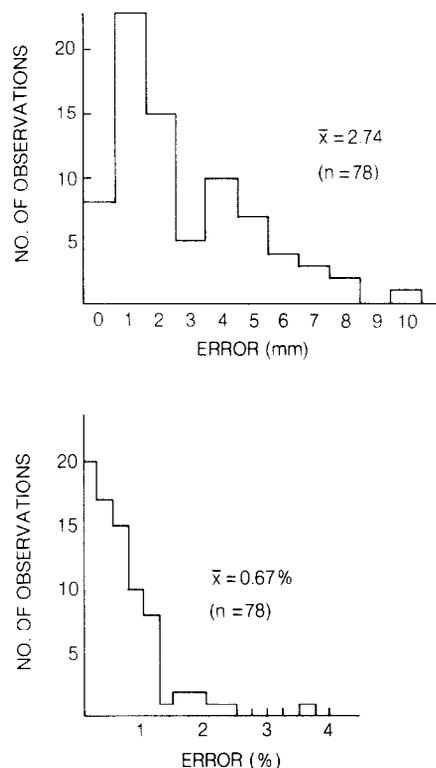


Fig. 2 Frequency distribution of absolute (above) and relative (below) errors in measurements between points on the test lattice.

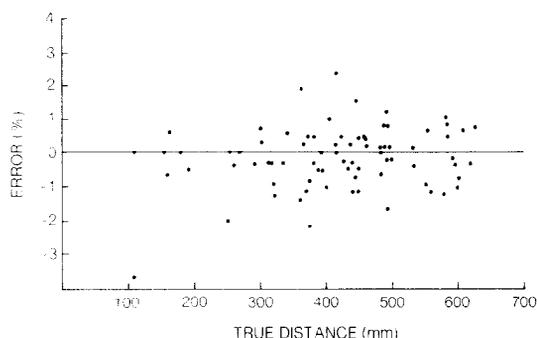


Fig. 3. Percentage measurement error as a function of the distance separating two points on the test lattice.

## Application

Stereo pairs of photographs were taken of schools comprising several hundred juvenile coho salmon (*Oncorhynchus kisutch*) swimming in an outdoor trough at the Capilano salmon hatchery, North Vancouver, B.C., on October 5, 1978. The fish averaged 9.6 cm total length (measured from the photographs). The procedures followed were as described above, except that a sheet of opaque white plexiglass (ruled out into 25 × 25 cm squares) was placed on the floor of the trough beneath the cameras in order to enhance contrast. Portions of three separate schools were photographed, and their internal structure analyzed. An example of a stereo pair is shown in Figure 4.

As the salmon reached the edge of the white sheet they appeared to increase their swimming speed, and the cohesiveness of the schools seemed to break down. Cohesiveness was probably not great to start with, since coho salmon are facultative schoolers only. These factors may explain why there is little evidence for any particular structure in the schools photographed. The data are presented more to illustrate the use of the technique than to enhance our understanding of fish school structure.

Frequently, two fish formed a nearest neighbour

pair, i.e. they were closer to one another than either was to any other member of the school. Retaining both values in the calculations of mean spacing characteristics can bias the results obtained, in that some values are duplicated in the data set. We have therefore calculated first nearest neighbour distances, bearings, and elevations in two ways: including all fish, and with one member of each nearest neighbour pair excluded. We adopted the convention of discarding data for lead members of all pairs. Mean nearest neighbour distance and mean elevation vector were affected only slightly by this procedure (bearing obviously changes, since only values greater than 90° are eliminated), so it was not repeated for 2nd and 3rd nearest neighbour pairs.

All data for the three schools measured are summarized in Table 1. Not surprisingly inter-fish distances (Fig. 5) increase from 1st through 3rd nearest neighbours. Considering the pooled data, these represent 0.7, 1.0, and 1.2 body lengths, values which correspond well to those determined in other three-dimensional studies (Cullen et al. 1965, Pitcher 1973, Partridge 1980, Partridge et al. 1980).

Mean bearing angles were always close to 90° (i.e. abeam). Note that data for neighbours to the left and right have been pooled in these analyses, as the two distributions did not differ by visual inspection.

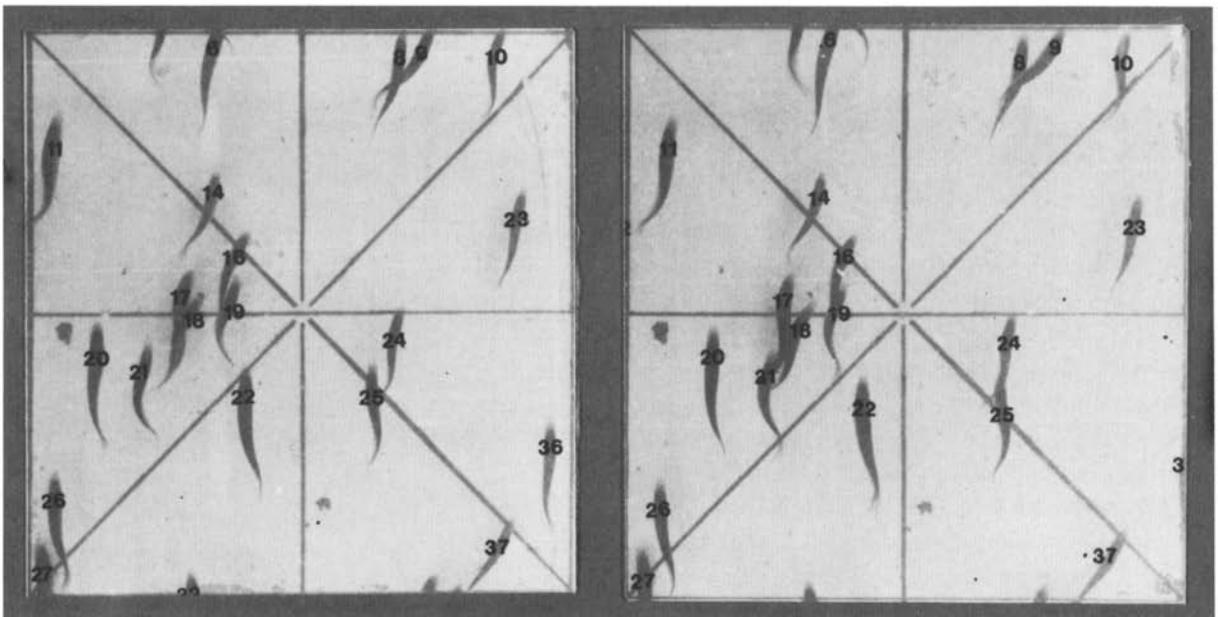


Fig. 4. Portions of a stereo pair of photographs of a school of juvenile coho salmon. The disparity in relative positions of the fish (e.g. fish 24 and 25) is an indication of their relative depths in the water.

Table 1. Distances and angles (means and standard or angular deviations) between nearest neighbours in coho salmon schools (9 = mean angle vector. S = angular deviation).

School	NN <sub>x</sub>	n	Distance (cm)			Bearing (°)			Elevation (°)		
			$\bar{x}$	$\pm$	$\sigma$	9	$\pm$	S	9	$\pm$	S
A	1	44	6.6		2.6	94		45	1		37
	1*	30	7.0		2.8	77		47	2		34
	2	44	9.4		3.5	96		42	-2		32
	3	44	11.4		4.1	90		55	-3		29
B	1	33	6.6		3.1	91		50	3		40
	1*	19	7.0		3.2	53		37	11		38
	2	33	12.1		3.8	85		39	-2		27
	3	33	14.7		4.0	89		33	1		14
C	1	60	6.0		2.1	97		44	-1		35
	1*	41	6.3		2.1	79		44	2		36
	2	60	8.3		2.6	83		42	-1		31
	3	60	10.2		2.7	87		41	-6		28
Pooled	1	137	6.3		2.5	95		46	1		37
	1*	90	6.7		2.6	72		45	3		36
	2	137	9.6		3.2	88		42	-1		31
	3	137	11.7		3.5	89		44	-3		26

\*Recalculated for 1st nearest neighbours but with leading members of all nearest neighbour pairs excluded from the analysis.

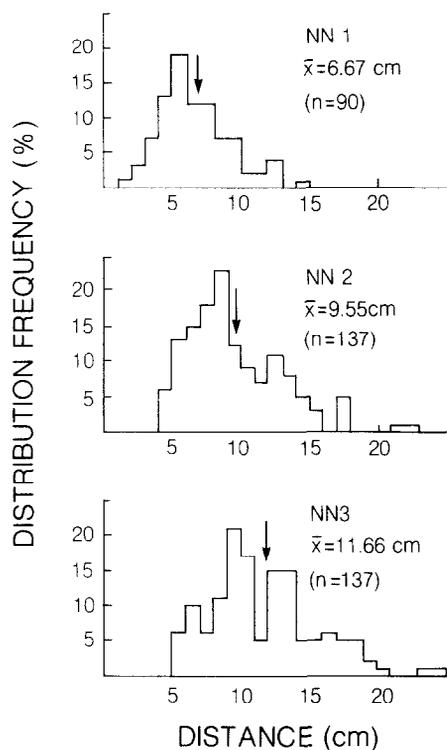


Fig. 5. Frequency distribution of coho first, second, and third nearest neighbour distances (cm). Data for first nearest neighbour exclude leading members of nearest neighbour pairs. Arrows denote mean values.

The frequency distribution of bearing angles was nearly uniform (Fig. 6), except that few nearest neighbours occurred directly in front of or directly behind the reference fish. Mean elevation vectors (Table 1) were always near 0°, i.e. at the same level. Once again this resulted from a nearly uniform frequency distribution (Fig. 7), except that few nearest neighbours occurred directly above or below the reference fish. Similar results have been found for other facultative schoolers (saithe and cod, Partridge et al. 1980), but preferred angular positions for nearest neighbours seem to exist in more obligate schooling species (pilchards, Shaw et al. 1965; minnows, Pitcher 1973, Partridge 1980; herring, Partridge et al. 1980).

If a particular preferred spatial location for nearest neighbours exists in salmon schools, it should reveal itself in a plot of elevation angle against bearing angle. Preferred locations would appear as clusters of data points; none seem to exist in coho salmon, or at least they are not revealed in our relatively small sample (Fig. 8). However, some evidence for a particular structure is provided by the plots of 1st nearest neighbour distance against bearing and elevation angles (Fig. 9). Neighbours are somewhat closer ( $p < 0.1$ ) when diagonally ahead of the reference fish, or when swimming on the same level ( $p < 0.05$ ). Partridge et al. (1980) report

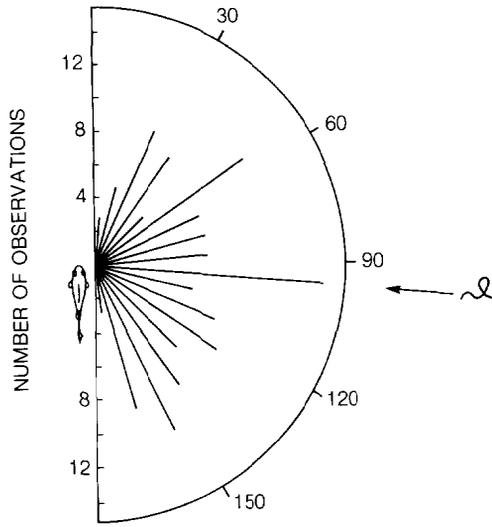


Fig. 6. Frequency distribution of bearing angles for first nearest neighbours in coho schools ( $n = 137$ ). Arrow denotes mean vector.

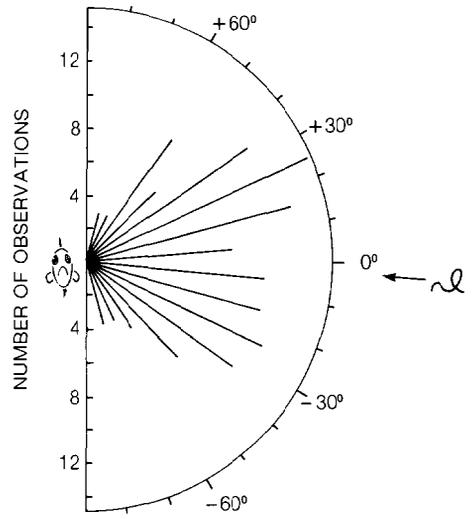


Fig. 7. Frequency distribution of elevation angles for first nearest neighbours in coho schools ( $n = 137$ ). Arrow denotes mean vector.

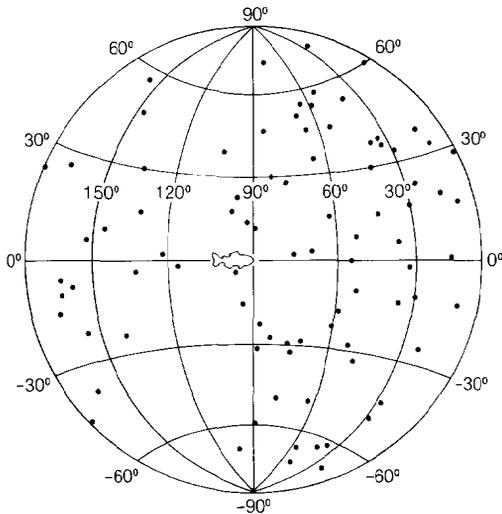


Fig. 8. First nearest neighbour bearing and elevation angles plotted against one another on a hemisphere, for all fish excluding leading members of nearest neighbour pairs ( $n=90$ ). Each fish is placed at the centre of the hemisphere and the angular location of its neighbour plotted. Each point therefore relates only to the reference fish's position, not to other points.

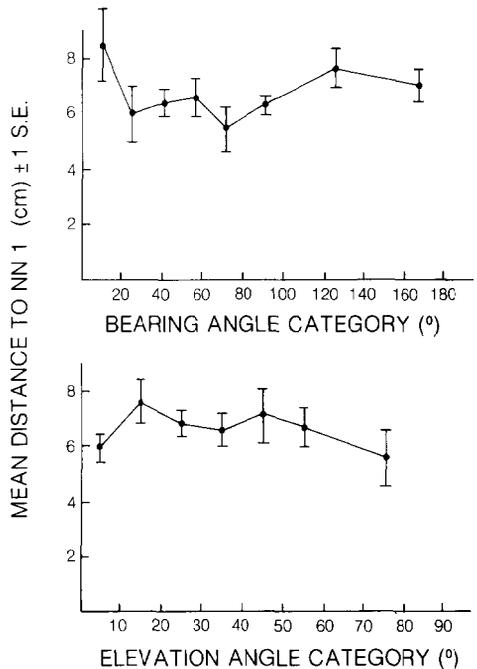


Fig. 9. Mean first nearest neighbour distance ( $n=90$ ) when neighbours occur in various bearing (above) or elevation (below) intervals. Interval size was varied to keep sample sizes roughly constant. In the elevation plot, similar intervals above and below the reference fish have been combined.

very similar patterns for saithe and cod.

Increasingly it appears that fish schools are not organized in a rigid lattice structure as some have believed (e.g. Breder 1976). Instead the internal structure is in a constant state of flux, as fish change position relative to one another. Any structure is present only in a statistical sense, and can be revealed only by accurate studies in three dimensions, preferably in situations as natural as possible. We believe that our technique, which could fairly readily be adapted for use underwater or in a glass-bottomed boat, provides investigators with a rapid and reliable tool for further studies of this kind.

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