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Aquatic Living Resources 16 (2003) 113–122
Aquatic Living Resources
www.elsevier.com/locate/aquliv

The three-dimensional morphology and internal structure of clupeid schools as observed using vertical scanning multibeam sonar

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Accepted 3 February 2003

Abstract

Fish schools are known to take a large number of different shapes and dimensions, in such a way that defining a school from its morphology is still an unanswered question. Nevertheless, some school typology and classification has been done successfully in different areas of the world using vertical echo sounding data. This implies that some morphological patterns may correspond to or reflect behavioural specificities. The objective of this paper is to take advantage of the 3D exhaustive observation capabilities of multibeam sonar to extract the morphological and internal characteristics of tropical clupeid schools. The main parameters measured are geometrical properties (overall dimensions, volume, surface, etc.) and relative distribution of densities inside the school (heterogeneity, existence of nuclei, etc.). The main results show that a school is usually formed of one or several nuclei of high density connected by less dense parts, including empty areas (vacuoles). The dimension of these sub-units is highly variable, but remains inside a diameter of 5-20 m. The reliability of these dimensions is evaluated, and some thoughts on the behavioural mechanisms constituting schools are presented.

Keywords: Fisheries acoustics; Fish school; Fish behaviour; 3D image; structure

1. Introduction

Pelagic fishes tend to gather into schools. These are innate structures for most of the Clupeidae, Engraulidae, Carangidae, and represent a major biological characteristic in the life of these species. Fishers take advantage of these aggregations of individuals to adapt their fishing effort, and several fishing gears have been designed specifically for exploiting fish schools. Nevertheless, even though the idea of a "school" is rather clearly understood, the knowledge of the structure of these features is weak, and attempts to provide a universal definition of a school, based on its morphology, have failed so far.

Fish schools are heterogeneous and variable structures. The heterogeneity was observed soon after the implementation of acoustic devices in fisheries research. One of the first images of the horizontal heterogeneity of a fish shoal has been drawn by Cushing (1977), using a scanning sonar with a 30° overall scanning angle. His results are descriptive and given in a single scale of presence/absence of fish, but the envelope of the fish distribution shows that the school morphology is complex and mostly amoeboid. Visual observations were more numerous, and gave some indications on the way individuals were behaving in a school. The inter-fish distance was often measured and the individual distribution within a school was modelled (Radakov, 1973). An "extreme" example was given by Breder (1976), who described a quasi-crystalline structure of the school, with each fish taking the position of an atom in a rhomboidal crystal. Such a regular distribution, noted through visual observation and at very short range (maximum 5 m) implies high densities within the school (Aoki and Inagaki, 1988) and is contradictory with the acoustic measures of fish school densities: Simmonds et al. (1992) have summarised the literature on the mean number of fish per cubic meter in schools for different species using different methods. The densities vary from 0.05 (20 cm herring) to 300 fish per m^3 (12 cm anchovy) for in situ studies, and up to 3000 fish per m^3 from modelling exercises. Although fish density has been found to depend on the species, the fish length, and the biological characteristics of the animals, a reasonable estimate would be in the 0.5-30 fish

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doi:10.1016/S0990-7440(03)00027-5

per m^3 range. A synthesis of these contradictory observations was given by Fréon et al. (1992), who described for the first time the global internal structure of a whole fish school in situ, observed by vertical echo sounding, visual observation (video camera) and aerial pictures. Their conclusions that at short distance fish remain almost always equidistant to one another were consistent with small scale visual and aquarium observations. However, on a global scale they observed that a fish school was a very heterogeneous 3D structure, with numerous empty sub-volumes that they named as vacuoles. Consequently, it was normal to obtain high fish densities per cubic meters when observing part of the school, or very weak densities when considering the whole structure.

Another characteristic was described by Misund (1993), as patchiness inside schools. The author observed "packing density structures" inside a school recorded by echo sounders, which were followed during several minutes. Inside these structures, the density was found similar to the densities measured with visual recording. He proposed the "moving mass hypothesis" for explaining the large variations in the packing density. This hypothesis is based on the individual fish dynamics and differences in speed and directions among individuals. It is worth noting that dense areas were recorded in the vertical (Fréon et al., 1992; Misund, 1993) as well as in the horizontal plan (Soria, 1994; Fréon et al., 1992; Axelsen et al., 2001), although only relative densities were given for the horizontal plan.

Another feature that has been studied is the external shape of the school. Since the beginning of fisheries acoustics, fishers were able to recognise species, with a rather acceptable precision, according to the shape of the school image on the echogram. Using this characteristic, two kinds of research were developed: one attempting to identify fish species (Rose and Leggett, 1988; Scalabrin, 1997); the other one focused on the variability of the school shapes (Petitgas and Lévenez, 1996; Gonzalez et al., 1998). Both approaches were successful, indicating that although the variability of the school shape is important, it is not completely random and depends on several characteristics, such as the species, the biology and behaviour conditions, and the global oceanographic conditions. A good synthesis on this "echo trace classification" is given by Reid (2000). All these studies were done using two kinds of acoustic devices: vertical echo sounder and horizontal omnidirectional multibeam sonar (MBS).

The vertical echo sounder presents a set of limitations for species classification/identification research, among which the most important are:

- Limited precision in image definition. A standard transducer typically has a 10° beam angle. This reduces dramatically the precision of the image with distance from the vessel. All the details of the internal structure and the external envelope are smoothed, and the external envelope is highly skewed by the location of the target inside the beam angle. Moreover, the horizontal dimensions of the school are biased and corrected (e.g. Johannesson and Losse, 1977; Diner, 2001).
- Limited biological value. The vertical echo sounder observes the most perturbed and noisy sector of the sea around the vessel. It only provides information on what has not avoided the vessel horizontally, and cannot discern whether the recorded structure corresponds to a natural behaviour of the fish or is strictly induced by its reactions to the vessel.

The horizontal MBS is much more accurate in observing and recording fish schools, as it is capable of observations at large horizontal distances from the vessel, and in two actual dimensions (independent of the vessel motion). This tool is particularly useful for observing the movements and dynamics of the schools (e.g. Diner and Massé, 1987). Nevertheless, the horizontal sonar is usually not applied for school shape analysis, because its definition is too low (i.e. beam angles are around 5-10°) and, as sound is emitted horizontally, school images at long distances can be biased or even hidden by the changes in sound direction due to the presence of a thermocline, for instance (e.g. Medwin and Clay, 1998). Some particularly narrow beam MBS was designed (Misund et al., 1995), which allowed for a very precise image of the fish distribution inside a school. Nevertheless, the third dimension was still lacking for an exhaustive view of a school structure.

This third (horizontal) dimension is obtained through the use of vertical MBS (Gerlotto et al., 1999; Mayer et al., 2002), which records a wide swath through successive pings along a vessel route. For the first time, questions regarding the dynamics of the school vs. the vessel were answered using this tool. Soria et al. (1996) showed that fish schools were avoiding horizontally, following a "double wave of avoidance". Bahri (2000) showed that the schools were presenting different lengths and widths depending on their location relative to the vessel, which she linked to the avoidance dynamics.

This paper explores the 3D structure and shape of fish schools using vertical MBS developed for fisheries acoustics.

2. Materials and methods

The acoustic device used in this study was developed in an European Project (AVITIS, FAIR CT96 1717) and presented by Gerlotto et al. (1999) and Fernandes et al. (1998). The system was a 455 kHz RESON model Seabat 6012 MBS with 60 beams of 1.5 × 15°, forming a 2D image on a 90° field, at a range setting up to a maximum of 100 m. The observation plan was vertical, normal to the vessel route, and observing from the surface to the vertical below the vessel (Fig. 1).

The digital data are recorded for each ping and stored. Once the complete school has been recorded, the data can be reconstructed into a 3D image of the structure using the software SBI Viewer (Lecornu et al., 1998). It calculates the morphological characteristics of the school, such as its over-

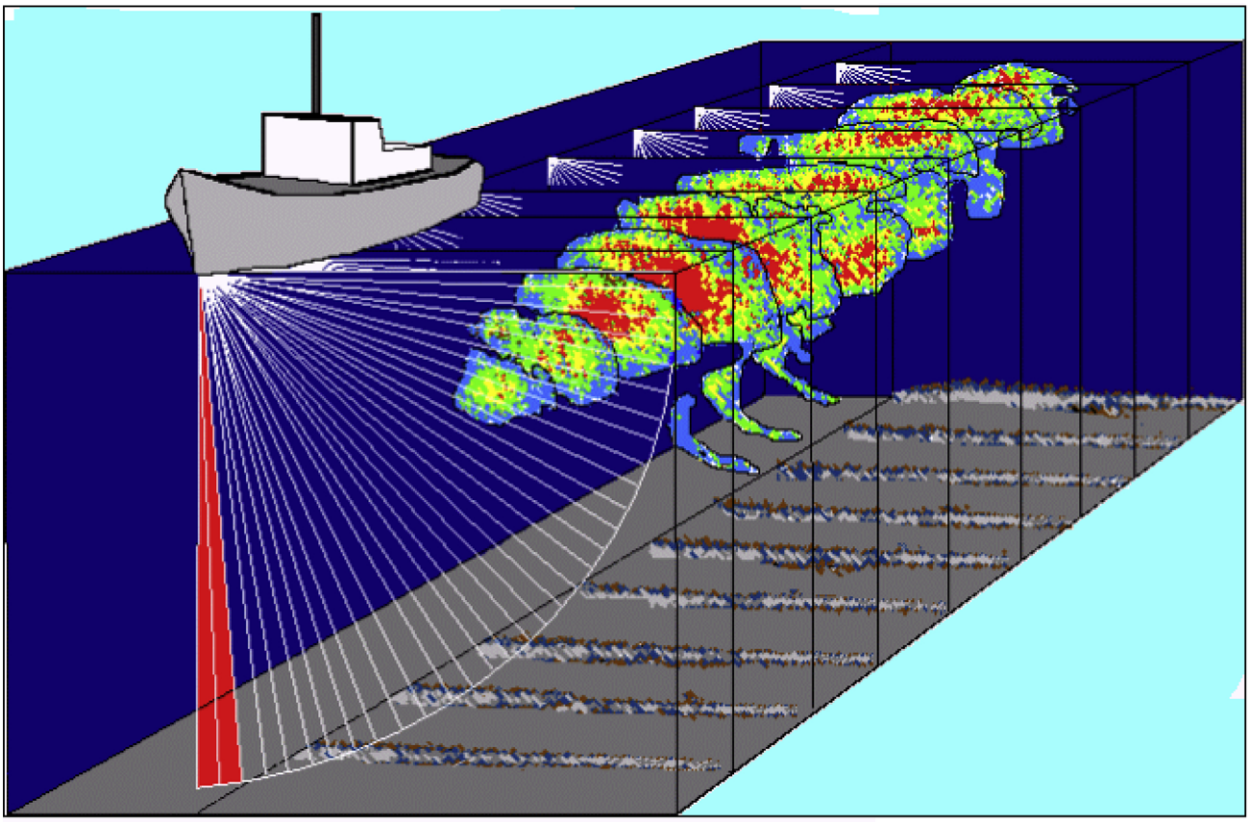

Fig. 1. Display of the MBS data in a vertical plan on the side of the vessel (from Fréon and Misund, 1999).

all dimension (length, width and height, which are the dimension of the rectangular box surrounding completely the school), its actual volume and surface, the number, surface and volume of holes inside the school, the school position in the water column with reference to the vessel and the relative density inside the school. The software also extracts all the voxels (defined as 3D volumetric pixels) inside the school and constructs a 4 column file, with the three spatial coordinates and the density value of each voxel. This allows for the calculation of 2D or 3D characteristics inside the school.

Some correction must be applied to the data, especially the length, using the classical correction related to the distance of the target (Johannesson and Losse, 1977). Simmonds et al. (1999) developed a calibration procedure for this MBS, which gives a beam angle of 22 × 1.5° for our sonar (instead of the nominal 15 × 1.5°), that we applied for correcting the length.

We must point out some potential sources of bias related to the data collection and processing methods. Data are collected during a survey, but the collection is not systematic, due to storage limitations. Therefore, the operator decides when a school has to be recorded. This may induce two biases: one on the location of schools, as it is easier to see and record a school in the centre of the screen than on the edges, and a bias in the actual dimensions of these schools, as small schools may be undersampled. When processing the data, some limitations due to the software may also affect the sampling, as the operator must have an implicit definition of a school, and applies particular thresholds. Finally, another point has to be taken into account when studying the linear dimensions: they represent the dimensions of a rectangular box surrounding the school. Therefore, when the school has a complex shape, these dimensions may not be completely realistic. For instance, in the case of a school with a shape in C: the length will be underestimated and the width largely overestimated.

The data were recorded during two acoustic surveys; Venezuela (survey VARGET 99/2) in March 1999, and Senegal (VARGET 99/1) in May 1999. These surveys were performed in order to measure the school behaviour. Data were collected during the day along transects aboard the R/V Antea, at a fixed speed of 8 knots. In tropical regions, the species assemblage is complex. For instance, in Venezuela we may observe up to 10 Clupeids, 15 Engraulids and 10 Carangids forming schools (less in Senegal: four Clupeids, one Engraulid, six Carangids), with no possibility to allocate with absolute precision each recorded school to a given species. Nevertheless, in the two areas the most abundant schooling fish is the Clupeid *Sardinella aurita*, which represents 60-80% of the total biomass in both countries (Gerlotto, 1993; Levenez, pers. comm.). Moreover, the recordings come from the part of the shelf where *S. aurita* is the most abundant, as proved by our own trawlings and the fisheries data. Hence, it is reasonable to assume that the majority of schools belong to *S. aurita*, and that the potential error in the species identification is probably less than 5% (which is the

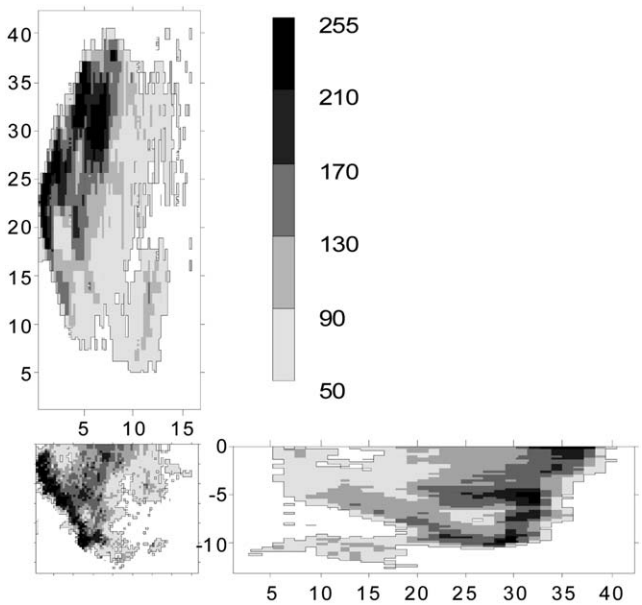

Fig. 2. The three images of the fish school structure in the three plans: above, horizontal plan; below left, vertical plan perpendicular to the vessel route; below right, vertical plan parallel to the vessel route. Densities represent a relative scale from 0 to 255, averaged on the dimension perpendicular to the plan. Same scale in m for the three dimensions (school # 770. Senegal).

proportion of the schooling biomass allocated to other pelagics).

Not all the schools can be processed by SBI Viewer. In some cases, the edges of the school were cut by the borders of the observed volume (e.g. for schools being observed vertically below the vessel), in other cases they are included in noisy volumes, and the discrimination between the school echoes and background noise is impossible. In a few cases, the structure of the school was extremely complex, the school belonging to a layer of schools with no clear borders, and no extraction of a single structure was possible. This reduced the field of our observations to well identified single schools.

The heterogeneity of fish distribution inside the schools was explored using geostatistics. For such measurements, we calculated a global horizontal section, by projecting each voxel on the horizontal plan to calculate the mean density for all the pixels of this horizontal image. The horizontal dimension was preferred to the vertical ones, as schools are usually more extended horizontally. An isotropic horizontal variogram was calculated for each school. In all the schools, dense patches are observed that allowed for extraction of information on the frequency and characteristics of these patches (that we called "nuclei"). The extraction of information was not always possible due to limitations of the software. We processed the information in two ways.

In the global analysis, the nucleus was defined as a single dense volume, with density superior to twice the "background density" of the school and linear dimensions greater than 1 m vertical and 3 m horizontal (these dimensions being decided after the results of geostatistical analysis). All the schools were mapped in 2D in the three plans (Fig. 2). Using these maps, we explored whether there were zero, one or several nuclei. No measurement of the nucleus dimension was performed.

In the second analysis, where additional processing was possible, we extracted the nucleus using the normal procedure for school extraction, but setting a higher threshold for the densities to be selected. For the extracted nucleus, we obtained the same morphological and density values as on the whole school.

3. Results

We extracted 427 schools, of which 359 were from Venezuela and 68 from Senegal. Among these 427 schools, 126 nuclei were extracted; a few of them belonging to the same school (Table 1).

Schools from Senegal and Venezuela are slightly different in shape. Curiously, even though the dimensions were different (i.e. the two groups differed in length, width, and surface, S_{sen} = 5326 m^2; S_{ven} = 3581 m^2; t = -2.07, P < 0.007), no significant difference was observed for height or volume (V_{sen} = 1576 m^3; V_{ven} = 1399 m^3; t = -0.62, P < 0.53).

It is also interesting to analyse the schools related to the distance from the vessel. Table 2 gives the mean values of the most important variables at intervals of 10 m from the vessel

Table 1
Mean values of the main morphological and density parameters of the schools and nuclei. Linear dimensions are given in m, surfaces in m^2, volumes in m^3. The density is the mean value of echo energy in a relative scale of 0-255. As the settings remained fixed, these relative values are comparable for all the schools. The fractal dimension is the ratio surface/volume. (*) The software SBI Viewer cannot count more than 1024 holes inside a single school (a hole is defined by an empty voxel). Only seven schools in our database have equal or more than 1024 holes

Parameter	School (n = 427)				Nucleus (n = 126)			
	All	Venezuela	Senegal	P-value	All	Venezuela	Senegal	P-value
Length	28.9	33.1	39.9	0.111	15.2	15.1	15.3	0.891
Width	17.4	16.9	20.1	0.026	8.4	8.3	8.6	0.661
Height	11.3	11.2	11.7	0.834	5.6	5.6	5.7	0.928
Volume	1427.0	1398.8	1576.0	0.239	203.8	203.4	205.8	0.911
Surface	3859.5	3581.8	5325.6	0.027	844.3	802.8	1029.1	0.720
Nb of holes (*)	125.4	120.1	153.4	0.051	23.0	20.9	32.4	0.821
Surface of holes	121.3	115.2	153.7	0.716	19.3	17.7	26.4	0.810
Volume of holes	13.8	13.0	17.6	0.035	2.1	1.9	2.8	0.947
Density	92.2	94.8	78.5	0.008	131.3	132.5	126.0	0.498

Table 2
Mean values of the morphological parameters of the schools depending on their distance to the vessel. Nb of schools = 427. All dimensions in m, surfaces in m^2, volumes in m^3. Holes in number of voxels. Density in relative units. Nuclei: number of nuclei per school

Parameter	Distance classes (m)								
	0/10	10/20	20/30	30/40	40/50	50/60	>60	*F*-value	*P*-value
Number of observations	92	101	60	48	58	43	25	–	–
Length	32.7	40.1	28.5	20.4	21.5	21.3	21	18.394	0.000
With	14.3	21.3	18.8	15.9	16.3	16.5	16.7	0.277	0.599
Height	9.8	13.1	11.3	10.1	11	12.1	11.8	1.119	0.291
Volume	690	1648.9	1610.2	1145.8	1501.5	2203.3	1980.6	30.314	0.000
Surface	2329.2	4750.1	4743.3	2863.5	4047.1	4648.3	4250.9	13.831	0.000
Holes	91.1	172.4	161.6	75.2	121.2	118.2	104.2	0.697	0.404
Density	107.61	98.73	87.95	73.93	77.03	88.47	91.91	29.719	0.000
Nuclei	0.96	1.16	0.77	0.67	0.66	0.53	0.41	12.650	0.000

(0-10, 10-20, etc.). We can see that the distance to the vessel may have an impact on the school shape.

3.1. General school morphology

We studied two points in this field: the main characteristics of the overall structure of the school and its anisotropy in length and width. *t*-Tests between length vs. width, length vs. height and width vs. height were calculated (Table 3).

As far as the overall structure is concerned, the question is whether a school can present a permanent regular shape. The first method was to compare the values of length, width, volume and surface. The linear dimensions cannot be compared easily with the volume and surface, as they are not calculated in the same way. Table 4 shows that most of the morphological parameters are correlated. The only parameter with no or weak correlation with the others is the density.

One important result is that there is a significant relationship between length and width (Tables 1 and 2). The width on an average represents 60.5% of the length (test $t = 12.3$, $P < 0.01$). If we consider the schools according to their distance from the vessel separately, we can calculate that the width varies from 47.3% (0-10 m) to 79.5% (>60 m) of the length. Although this is not the objective of the paper, we may note that this result is consistent with the avoidance scheme described by Soria et al. (this volume).

The second way to study the school shape is to consider the fractal dimension, which represents a "roughness factor". It is calculated by the ratio surface/volume (S/V). The mean roughness factor on the school studies has no real meaning, as the ratio S/V is inversely proportional to the radius R of the school. One other way to evaluate the roughness characteristics of the school is to compare the actual S/V values to a theoretical fractal dimension that would be obtained for regular shapes. We calculated two theoretical S/V ratios for two types of shapes: spherical and cylindrical. In the first case, we assumed that the volume of the school was the volume of a sphere and calculated the surface of this sphere, then we calculated the S/V on these values. We did the same with the cylinder, using the actual volume and height of the school to calculate the surface. Then we compared the three fractal

Table 3
Test *t* on relationships between length and width, length and height, width and height of the schools (d.f. = degrees of freedom). All the results below show a significant difference with $P < 0.005$

Variables	Mean	Standard error	*t*	d.f.
Length	28.97	24.12	12.3	426
Width	17.34	9.91		
Length	28.97	24.12	17.5	426
Height	11.30	6.67		
Width	17.34	9.91	20.5	426
Height	11.30	6.67		

Table 4
Correlation matrix of the morphological parameters of the 427 schools. Significant correlation at $P < 0.05$ are in italics

	Width	Height	Volume	Surface	Fractal	Hole	Density
Length	*0.633*	*0.596*	*0.669*	*0.706*	–0.0630	*0.594*	*0.135*
Width	1.000	*0.793*	*0.650*	*0.751*	*–0.1153*	*0.678*	0.016
Height		1.000	*0.628*	*0.664*	*–0.1209*	*0.616*	0.059
Volume			1.000	*0.878*	*–0.2779*	*0.740*	0.091
Surface				1.000	–0.0872	*0.861*	0.018
Fractal					1.0000	–0.010	*–0.219*
Hole						1.000	*0.128*

Table 5
Test *t* on roughness and fractal dimensions. *R*: roughness *S*/*V*; Fs = fractal dimension for a sphere; Fc = fractal dimension for a cylinder

	Mean	Standard deviation	*N*	Diff.	Diff. standard deviation	*t*	d.f.	P
R	3.15	1.057						
Fs	0.58	0.257	427	2.564	0.984	53.9	426	0.000000
R	3.15	1.057						
Fc	2.45	0.209	427	0.699	0.966	15.0	426	0.000000

dimensions, the actual roughness (*R*), and the ratios *S*/*V* for the cylinder (Fc) and the sphere (Fs). A *t*-test comparing the roughness and the fractal dimension of the sphere and cylinder, shows that they are significantly different at $P < 0.01$ (Table 5).

From these results, we can extract the following observation: a fish school has an irregular morphology, mostly amoeboid, which cannot be assimilated to any regular volume such as a cylinder or a sphere. Nevertheless, its morphology obeys some rules, and some constants in the shape can be recognised. The most important is the strong anisotropy between length, width, and height as already observed by several authors (Soria et al., 1996; Bahri, 2000).

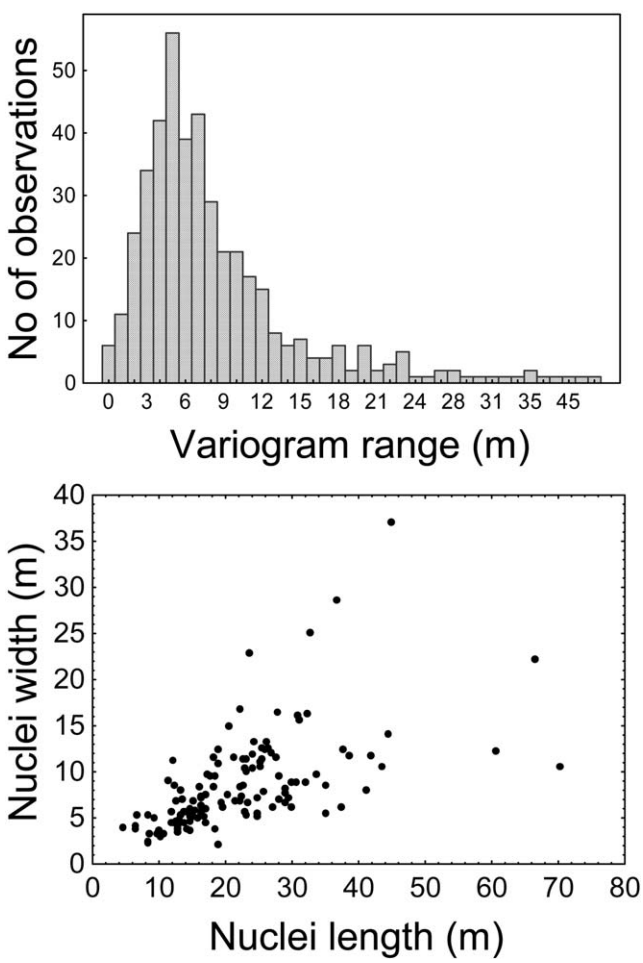

Fig. 3. Left: histogram of variogram ranges for the 427 schools; right: relations between length and width for the 126 extracted school nuclei.

3.2. Vacuole and nucleus morphology (Table 6)

3.2.1. Vacuoles

The vacuole information provided by SBI Viewer is limited to the number, global volume and global surface of empty voxels inside the extracted school. SBI Viewer cannot count more than 1024 "holes", which was the case for seven schools in our data base. It was also difficult to assimilate these holes to actual vacuoles as they did not have the same meaning. The holes were small empty spaces with no clear biological meaning, and more related to threshold and heterogeneity features. A single hole measures 0.1 m^3, which is much smaller than that observed by visual recordings (Fréon et al., 1992).

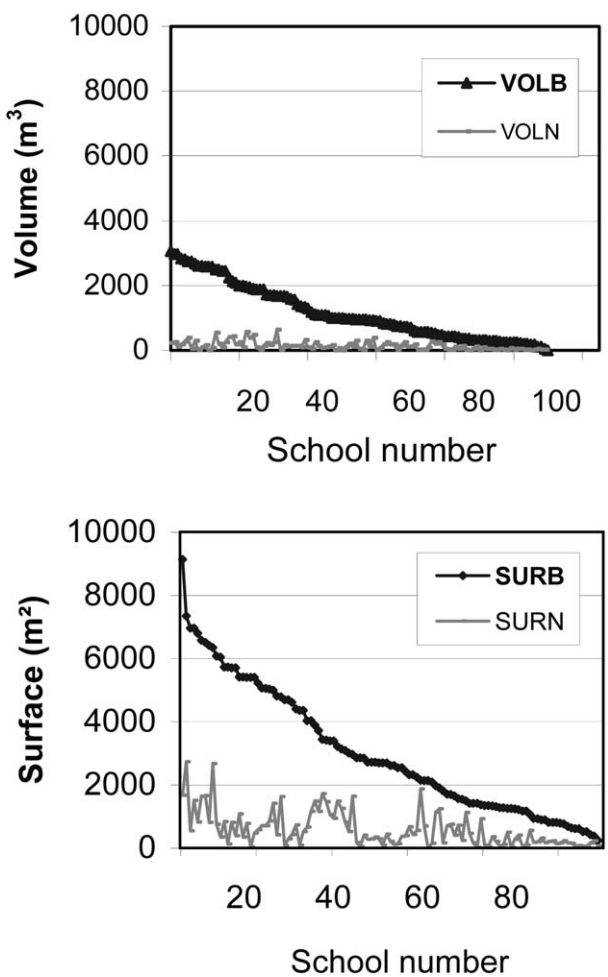

Fig. 4. Volume (above) and surface (below) of nuclei (N) for different values of surface and volume of schools (B). The 15 biggest schools have been removed to make the figure clearer.

Table 6
t-Test matrix on the main characteristics of schools, holes and nuclei. All the *t* tests show significant differences between the variables at $P < 0.001$ (except two pairs, Hon-Ln and Hos-Dn, in italics which are likely artificial similarities). The measurements on holes are done on the whole set of schools (427 individuals); the measurements on nuclei are done on the nuclei extracted in 126 schools

	Ws	Hs	Vs	Ss	Rs	Hos	Ds	Ln	Wn	Hn	Vn	Sn	Rn	Hon	Dn
Ls	14.4	17.4	–8.9	–8.8	19.9	–4.6	–12	14.2	18.4	19.9	–7	–7.4	19.1	3.9	–23.5
Ws	0	14.1	–9	–8.8	22	–5.7	–25.3	–3.2	17.2	21.8	–7.8	–7.6	19.4	–1.3	–35.1
Hs		0	–9	–8.8	16.3	–6	–29.9	–10.8	6.7	13.7	–8.1	–7.6	13.3	–2.7	–39.7
Vs			0	–7.9	9	9.2	8.6	9	9	9	8.6	6.1	9	9.1	8.4
Ss				0	8.8	8.9	8.7	8.8	8.8	8.8	8.7	8.5	8.8	8.9	8.6
Rs					0	–6.3	–34.7	–18.9	–12.8	–9.7	–8.4	–7.7	–17	–4.4	–42.8
Hos						0	2.3	5.5	6.1	6.2	–3.7	–7.4	6.3	6.2	0
Ds							0	24.1	32.2	33.3	–5.1	–7	34	10.6	–19.8
Ln								0	16.2	19.1	–7.8	–7.6	17	–0.8	–35.7
Wn									0	10	–8.2	–7.7	8.8	–3.5	–40.9
Hn										0	–8.3	–7.7	3.9	–4	–42.4
Vn											0	–7.3	8.3	8.9	3.2
Sn												0	7.7	7.8	6.6
Rn													0	–4.1	–42.5
Hon														0	–18

W, weight; H, height; V, volume; S, surface; R, roughness; Ho, hole number; D, density; L, length; s, school, n, nuclei.

3.2.2. Nuclei

The first analysis was to measure the existence of a non-random patchiness inside the schools. For this purpose, we measured an omnidirectional (horizontal) variogram on all of the 427 schools. On all of them, a bounded variogram was calculated, with a nugget presenting in average 66% of the sill and a mean range of 9.3 m (Fig. 3) indicating a patchy school distribution. Based on our definition of a nucleus, as a structure of more than 1 m vertical × 3 m horizontal dimensions, 126 structures were extracted and the global characteristics of the nuclei are presented in Table 6. The overall dimensions of a nucleus are on an average, 12.6 m long, 8.7 m wide, 5.7 m height. The mean elongation (ratio width/length) is 0.7. We compared the main parameters of the nuclei, which showed a series of significant correlations, indicating that these structures were not random.

The relationships between the nuclei and the schools have been considered by comparing the main morphological characteristics, specially the surface and volume (Fig. 4). When plotting a nucleus dimension with the similar dimension of its school, several significant relationships appear (e.g. surface of the nucleus vs. surface of the school: $r = 0.78$, $N = 126$, $P < 0.05$). Nevertheless, these relationships are mostly artificial and likely due to two facts: (1) a nucleus cannot be bigger than a school, (2) the variability of nucleus dimension increases when the dimensions of the schools increase. This is clear when we sorted the school dimension (surface or volume) from the smallest to the biggest, and plotted the corresponding values of the nuclei (Fig. 4). The relationship was tested using two methods. After sorting the data according to the school surface, we cut the data base into five classes (1-5, from very small to very large schools) of 25 data (26 for class 5), then compared the surface means between the schools and the nuclei for these five classes. The result is given on the Fig. 5. We did the same with the volume and obtained a similar result.

This figure shows several phenomena.

- By construction there are significant differences in the mean surface of schools in the five classes.
- The classes 1 and 5 of nuclei are significantly different from the three others and between them. This is due to the two following facts that we described above: (1) the

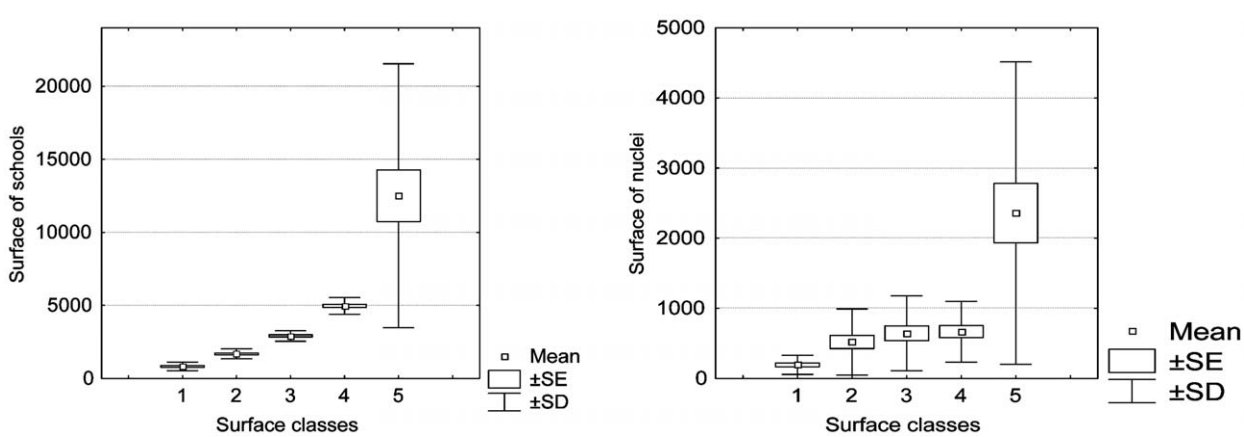

Fig. 5. Box-plot of the mean surface of schools and nuclei for five surface classes.

dimension of the nucleus is limited by the dimension of the school; (2) the class 5 is made of very large schools, most of them with several nuclei, and may represent a particular case that will be discussed below.

- The three other classes present no significant difference in the mean ($P < 0.35$).

A second test was to calculate the Pearson's correlation coefficient between the surfaces of schools and nuclei, and between the volumes of schools and nuclei for the 75 schools included in these three central classes, where the effect of the two above-mentioned artificial relationships are unlikely to bias the results. In this data set, the schools varied between 1300 and 5700 m^2, 260 and 3000 m^3. The correlations were, respectively, $r = 0.19$ for the surfaces and $r = 0.22$ for the volumes, showing no significant relationships ($P < 0.05$) between the corresponding dimensions in schools and nuclei for this set of data.

Therefore, we can conclude that there is no actual correlation between the surface and volume of the school and the surface and volume of its nuclei. Once the school is large enough, the nuclei maintain a relatively constant shape and dimension, with some increasing variability when the school is very large.

4. Discussion

Since the early 1990s, the importance of fish school behaviour and structure has been recognised as critical by fisheries acousticians (Anonymous, 1993), for several reasons, such as predation avoidance, physiologic facilitation, feeding, mating, etc. (Parrish and Turchin, 1997; Pitcher and Parrish, 1993), and effects of human pressure, which takes advantage of the schooling behaviour of the fish to increase the catch (Fréon and Misund, 1999). Until now, most of the works on fish structure and organisation inside a school have been performed at two scales:

- An individual scale (Radakov, 1973; Breder, 1976; Partridge et al., 1983; Pitcher and Parrish, 1993, etc.), with good results on the understanding of the collective behaviour inside a school, and the mechanisms that permit to maintain cohesion within the group. Successful individual-based models on fish schooling have been published at this scale (Huth and Wissel, 1993; Vabø and Nøttestad, 1997; Couzin et al., 2002).
- A global scale (Reid, 2000), where the whole structure of the school is studied and considered as an individual. At this level, successful results have been obtained on the possibility to identify a species using the school shape (Rose and Leggett, 1988; Scalabrin, 1997).

Although some attempts were made to model the school structure at an intermediate "collective" scale (Mackinson, 2000), the results that we present here are likely the first exhaustive observation on large schools in situ allowing for the analysis of their collective mechanisms. From these results, we may draw two main hypotheses.

The first one is that our observations are consistent with those at individual and global scales. We confirmed the existence of strong anisotropies between the three dimensions of the schools that was pointed out by numerous authors (e.g. Fréon and Misund, 1999). For instance, schools are much more extended in the horizontal dimension (L) than in the vertical one (h), and the overall height represents 39% of the length and 65% of the width in our data base. Nevertheless variations in these relationships may occur. We found a rather different ratio L/h than Oshihimo (1996) on anchovy, for instance, as the Sardinella schools have an $L/h = 2.6$, compared with the $L/h = 5$ calculated by this author. This indicates that although the horizontal dimensions are always larger than the height, they vary according to the species. But more likely, this anisotropy is linked with the horizontal dimensions of the schools: the Sardinella schools are rather small schools (mean diameter 23 m in our data set), while some schools studied in the literature are much wider (between 100 and 1000 m). The height cannot increase proportionally to the diameter, for biological, hydrological and geographical reasons. This shows that the differences are quantitative and adaptive to the local condition of the ecosystem. For instance, there is a neat effect of the distance to the vessel, which indicates that the schools we observed were under a dynamic process (avoidance). Concerning the effect of the distance, our results must be considered as preliminary, as the data base is small, but they are not contradictory with those of Soria et al. (1996): schools change their dimensions according to the distance from the vessel. Fig. 6 shows the values of length and width in relation to the distance for the whole data set.

These results are not in opposition with the conclusion that, although they have no regular morphology, schools are consistent structures that maintain some permanent feature and shape. From this observation, we may draw a first hypothesis: most of the small pelagic species develop similar mechanisms to maintain their cohesion inside a social structure and these mechanisms are the base of the school. Therefore, the results that we present on *S. aurita* are applicable to most of the Clupeids and other pelagic families.

The second kind of result is that schools are heterogeneous in their internal structure and that this heterogeneity is the consequence of an organisation. This observation leads to different conclusions than Parrish et al. (1997) who consider that schools are defined, among five criteria, by the fact that

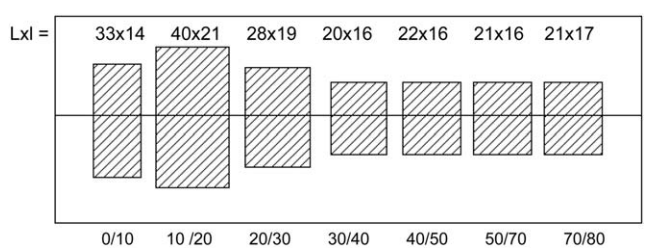

Fig. 6. Diagram of the relations length/width (Lxl. in m) for different classes of distance to the vessel (in m). This diagram is calculated on the whole data base (427 schools).

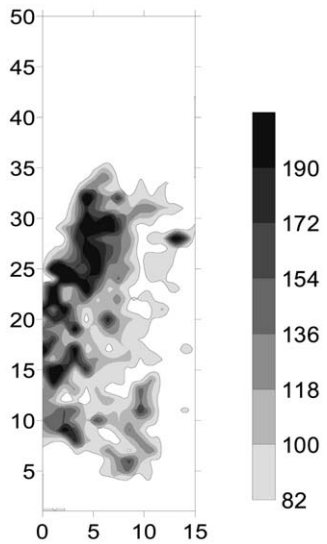

Fig. 7. Horizontal view of the distribution of mean density of fish in school # 770 (see Fig. 2). A nucleus is identified on the upper left part of the diagram. Small dense aggregates can be observed in the low density area (down right). Holes or vacuoles (mean density lower than 50) can be observed as well. Density in relative units on a scale 0-255. Dimensions in m. The density is calculated as the mean of the density on the vertical column below the point drawn on the figure. The threshold and the upper limit of the school densities are not those used for the extraction of the school and nucleus and are defined for the better visibility of the school heterogeneity.

"Many types of animal congregations have fairly uniform densities". Actually, this criterion is relevant for small groups of fish (even inside a larger school) and for small schools, especially when they are moving fast (Soria et al., 1996), but is no more valid for large concentrations of fish. The hypothesis that we propose to explain this apparent contradiction between permanent cohesion and global heterogeneity is the following. Fish tend to maintain a cohesive structure, which is ruled by the inter-individual distance, as observed by numerous authors. When the inter-individual distance is maintained, the school presents a high density. Inside these high density volumes, the fish must present a cohesive and polarised behaviour, otherwise the structure itself collapses. The mechanism that allows for maintaining this structure although the volume of the school is permanently changing, is the construction of vacuoles, which allow for the increase of the global volume of the school, with a local high permanent density of fish (Fréon et al., 1992; Soria, 1994). But such cohesive behaviour implies that the communications of information and decision on changes in the direction of the movement are quasi-instantaneous. Some of these mechanisms, such as the "wave of agitation" (Radakov, 1973), are well known. When the dimensions of the school increase, the quasi-instantaneity in the reactions is not possible anymore. Therefore, the dense structure is not cohesive above certain dimensions, and it must split. We believe that the nucleus represents the compromise between the need to maintain cohesive inter-fish distance and the delays in the transmission of dynamic instructions: for dimensions above 15-20 m, the nucleus cannot maintain its cohesion. This leads a part of the fish to stay in the "low density" volume, where either they tend to gather a nucleus or to build one. In fact, we may find numerous "pre-nucleus' structures, i.e. dense small patches of fish, inside the "low density" volume (e.g.Fig. 7).

In the case of very large schools (or when two schools are merging), two or several large nuclei can merge for a short period, due to the natural attraction of fish to any dense structure. But these "macro-structures" are not able to maintain their cohesion along a large period. This explains why the 10% larger ranges are above 18 m in our data set.

One interesting conclusion that can be drawn from these results is that the idea of a self-organisation of fish inside schools is confirmed: nuclei and vacuoles are emerging structures arising from elementary reaction of individuals (Soria, 1997). The combination of individual attraction, polarisation, synchronous reactions and delay of information transmission between the individuals implies the existence of dense nuclei and correlated empty vacuoles in a large aggregation of fish. This is what we observed in our 3D exhaustive observation of the internal structure of *S. aurita*.

Acknowledgements

This work is part of the Magister thesis of J. Paramo, University of Concepcion, Chile. The authors are grateful to an anonymous referee for the important remarks, which allowed for improving the statistical calculations, and for the edition of the text.

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