Available online at www.sciencedirect.com

Waves of agitation inside anchovy schools observed with multibeam sonar: a way to transmit information in response to predation

François Gerlotto, Sophie Bertrand, Nicolas Bez, and Mariano Gutierrez

Gerlotto, F., Bertrand, S., Bez, N., and Gutierrez, M. 2006. Waves of agitation inside anchovy schools observed with multibeam sonar: a way to transmit information in response to predation. – ICES Journal of Marine Science, 63: 1405–1417.

Most pelagic fish live in schools. To allow fast reactions, for instance to predator attacks, these collective structures require behavioural mechanisms authorizing fast, coordinated movements. Considering the large number of individuals constituting a school of small pelagic fish, a crucial premise to coordinated movements and school reorganization is an ability to transfer quickly and efficiently information across the whole collective structure. We observed anchovy school movements and reactions to sea-lion attacks while the ship was drifting in Peruvian waters. The main process of information transfer we could observe was that of waves of agitation crossing large anchovy schools. The average speed of these waves (7.45 m s⁻¹) was much greater than the average 0.3 m s⁻¹ school speeds measured during this experiment. The internal organization of each school modified dramatically after the waves of agitation had crossed them. Changes in school external morphology and internal structure were described and measured using geostatistics. Our results show that information transfer is a crucial process for the cohesion and plasticity of schools. As such, it allows efficient reactions of schools of pelagic fish to variations in their immediate environment in general, and to predation in particular.

© 2006 International Council for the Exploration of the Sea. Published by Elsevier Ltd. All rights reserved.

Keywords: anchovy, communication, fish behaviour, pelagic, predation, schooling, sea lions.

Received 31 October 2005; accepted 30 April 2006.

F. Gerlotto, S. Bertrand, and N. Bez: IRD, CRHMT, Avenue Jean Monnet, BP 171, 34203 Sète Cedex, France. M. Gutierrez: IMARPE (Marine Institute of Peru), Esquina Gamarra y Gral. Valles s/n, Chucuito, Callao, Lima, Peru. Correspondence to F. Gerlotto: tel: +33 4 99 57 32 00; fax: +33 4 99 57 32 95; e-mail: francois.gerlotto@ird.fr.

Introduction

Fish schools have been mainly studied from two perspectives (Parrish *et al.*, 1997). A bottom-up approach considers schools as collective structures emerging from the sum of individual fish interactions: schools are therefore defined as groups of fish characterized by polarized, equally spaced individuals swimming synchronously (Breder, 1976; Pitcher, 1983; Pitcher and Parrish, 1993; Pedersen, 1996), in which the inter-individual distance is usually less than one body length (Pitcher and Partridge, 1979). Such definition allows the consideration of a school as any "group of three or more fish that constantly adjust their speed and direction according to the other school members" (Partridge, 1982). These types of studies rely mostly on *in situ* visual recordings and aquarium experiments (Robinson and Pitcher, 1989; Herskin and Steffensen, 1998; Svendsen *et al.*, 2003), or on individual-based modelling (IBM). A second type of approach works at a larger scale and focuses on the specific properties of the individually school immersed in its natural environment. Such analyses require field observations including fishing data and underwater acoustics (see Fréon and Misund, 1999, for a synthesis). In this case, the definition of a school relies more on the geometric properties of the fish aggregation, the existence, for example, of clear edges around a group of thousands or up to millions of fish concentrated in a reduced volume. In the same sense, an acoustic school is defined as "a multiple aggregation of acoustically unresolved fish" (Kieser *et al.*, 1993).

Field observations on the internal structure and reorganization of fish inside a school were rare and difficult before the late 1990s. Fréon *et al.* (1992) used coupled visual observations (aerial and underwater) and acoustic recording to study in situ the internal structure of schools of tropical clupeids (Harengula sp.). They demonstrated the existence of vacuoles and dense structures. Axelsen et al. (2000) described the complex behaviour of herring schools during spawning, using modern echosounders. Multibeam, omnidirectional sonar allowed dynamic observations and was used to display reactions of schools to predation (Misund, 1993; Nøttestad and Axelsen, 1999; Brehmer, 2004). Recently, new acoustic instrumentation has allowed better description of school internal structures in 2D and 3D (Gerlotto et al., 1999; Mayer et al., 2002; Foote et al., 2005; see Reid, 2000, for a synthesis), and their evolution through time (Misund and Coetzee, 2000; Axelsen et al., 2001; Misund et al., 2005). Applying such tools to tropical clupeids, it has been shown that in many cases, a school's external morphology is liable to vary greatly while the internal structure remains unchanged (Gerlotto et al., 2004). Using multibeam sonar, a specific internal structure, the "nucleus", was described for several species and areas (Gerlotto and Páramo, 2003; Gerlotto et al., 2004).

Many authors state that schooling may constitute an adaptation to predation (Magurran, 1986; Magurran et al., 1993; Pitcher and Parrish, 1993). If such a statement is true, we should observe mechanisms in the behaviour of schools that facilitate collective reactions to the presence of predators, such as better avoidance (Pitcher et al., 1996). Radakov (1973) described and named several of them, among which the wave of agitation (WA) could be a good candidate to transfer information within a large school. A wave of agitation is the result of individual rolling movements producing a "flash" of light when the silver underside of the fish becomes illuminated. Each neighbour receiving this flash repeats the movement, and the synthesis produces a flash frontline crossing the whole school. This can be seen also in many other groups of animals (e.g. in flocks of birds; Heppner, 1997). Such a pattern, also called the "Trafalgar effect" (Webb, 1980), is described by Axelsen et al. (2001) for herring as "intraschool density propagation". Any change of fish angle referred to the transducer gives a strong change in its backscattering cross-section (see Simmonds and MacLennan, 2005, for a synthesis), especially when observed horizontally, as is the case with multibeam sonar. For instance, Kubecka (1996) recorded horizontal target-strength changes attributable to fish position, and found more than 20 dB difference for a fish 19 cm long facing the transducer, or perpendicular to it. Therefore, the collective reaction of fish during a WA is easily recorded by acoustic devices through changes of the general backscattering strength, either as a highly reflective area or as a shadow on the school image.

The objective of this work was to observe whether WAs were generated in schools suffering some predator attack, and to determine whether this type of transfer of information had a significant impact on the dynamics of school structure and morphology. In an experiment conducted on a small school of *Atherinomorus* sp. (300 individuals) in a tank, Radakov (1973) showed that fish appeared to be more homogeneously organized after the passage of the WA than before, suggesting perhaps that the mechanism is directly related to subsequent school reorganization. If such a phenomenon appears also in large schools in the wild, we would argue that WAs constitute a crucial mechanism of transfer of information inside fish schools and are a key anti-predator response.

Material and methods

Data

Behavioural investigations are not easy to perform on fish in the wild, because the scientist is not able to experiment *per se*, depending instead on the natural conditions. It was essential to find a favourable area for our observations. The large biomass of anchovy (*Engraulis ringens*), and the presence of populations of sea lions (*Arctocephalus australis* and *Otaria byronia*), which prey on anchovy (Arias-Schreiber, 2000; Hückstädt and Antezana, 2003) make the coastal waters of central Peru ideal for such research. This encouraged the Marine Institute of Peru (Instituto del Mar del Peru, IMARPE) to plan, in cooperation with the French Institut de Recherches pour le Développement (IRD), a dedicated survey to be carried out aboard IMARPE's RV "Jose Olaya Balandra" from 17 to 26 November 2004.

The survey consisted of two phases. First, while the vessel covered an area of 4 square nautical miles at 8 knots, the sonar was set perpendicular to the vessel, covering a vertical plane from the surface to the vertical line below the vessel (Gerlotto *et al.*, 1999). This experiment provided 3D snapshots of the shape of the schools present in the study area. School length, width, height, depth, volume, surface, and roughness were extracted for each school, as well as their distance from the vessel (Gerlotto and Páramo, 2003). In the second phase, the ship was held on station at $12^{\circ}35'S$ 76°50′W, for 36 h with the sonar beam set in a horizontal plane. This drifting experiment followed the method design of Axelsen *et al.* (2001), and was intended to study the evolution of school structure over time.

The main observation tool was a multibeam sonar RESON type Seabat 6012 (Gerlotto and Páramo, 2003), of frequency 455 kHz. Calibration of multibeam sonar is not easy (Simmonds and MacLennan, 2005), and this particular one has only been calibrated once, in 1999 (Simmonds *et al.*, 1999), essentially to evaluate the beam angle. (The calibration appeared to be different from the manufacturer's specification: 22° instead of 15°.) In this case, the point of using the instrument was to observe the morphology and dynamics of fish schools and, because actual echo energy is not used for absolute measurements, there was no need for another calibration. The sonar transducer covered an overall angle of 90°, with 60 beams of $1.5^{\circ} \times 22^{\circ}$ each. Observation was to be horizontal, the sonar transducer being submerged

4 m deep, and the overall beam axis was set perpendicular to the vessel axis, to starboard. The ping rate was 3.5 pings s^{-1} and the range was set at 100 m, giving a permanent surveyed surface of 7850 m². Video images of the data (Figure 1) were recorded continuously. Digital, raw acoustic data were only recorded during the presence of fish or sea lions inside the sampled volume. Using this method, acoustic data on all detections during the sampling period were stored. Observations during the first part of the survey revealed no schooling by night, so no recording was made after dark. The observation periods were 24 November, 04:00-12:00 and 13:00-18:00, and 25 November, 04:00-12:00. Except for the period 12:00-13:00 on the first day, an operator was present constantly recording when needed. Therefore, we assume that the 231 min of acoustic recording represents the duration of the presence of fish or sea lions or both in the insonified volume during the total 21 h 52 min observation period.

Processing

The speeds of fish, sea lions, and WA were calculated from the video images as the linear distance covered by the subject during 30 s (schools and sea lions) or 15 s (attacks and WA). For schools and WA, the point of reference was the centre of the frontline. Wind conditions throughout were light to calm, so no correction for vessel drift was made, drift being considered negligible compared with the speeds of fish and sea lions. Measurements of speeds of vacuole edges involved measuring the movements of fish on the border of a vacuole created around a sea lion inside a school. Measuring speeds of vacuole edges is a method for calculating the real avoidance speed of the anchovy. School speed is not appropriate for this evaluation, because a school is much slower than the fish contained in it. We observed that, at the moment of attack, school speeds dropped and even stopped. On the contrary, the vacuole edge represents the riskiest place for a fish to be if the vacuole is produced by a sea lion, and its speed represents the actual individual avoidance reaction.

Acoustic data were processed with the software SBI Viewer (Gerlotto and Páramo, 2003). We selected the most remarkable and longest sequence of predation (sequence 1762, 24 November, 09:21, $13^{\circ}39.70'S76^{\circ}37.63'W$), which took place on one of the densest abundances of anchovy, to monitor the spatial structure of the schools present in the recorded area before, during, and after a predatory attack. The total duration of the selected sequence was around 94 s (335 images recorded). We selected one in ten images, i.e. one every 3.5 s.

For each of these 33 images, a 2D horizontal matrix was formed from the raw (radial) acoustic data, creating square pixels of 0.20 m side, a density value for the corresponding acoustic data closest to the centre of the square pixel. Empirical variograms were computed and fitted by eye with a combination of spherical or linear models (Figure 2). The large number of data in a single image allowed calculation of very accurate values for the experimental variograms, because no lag value in any image was supported by less than 10 million pairs of points. Such accuracy



Figure 1. Video images of fish distribution in a horizontal plane on the side of the ship as observed using multibeam sonar (Reson SEA-BAT 6012). Scale 100 m. Densities in levels of grey (over a relative scale of 256). The sequence is 4 s, and anchovy schools, sea lions, vacuoles, and the displacement of waves of agitation (WAs) can be seen.



Figure 2. Example of density distribution as viewed after transformation in Surfer 7^{\odot} : density scale from blue (0) to red (255), scale in pixels (1 pixel size = 0.20 m); and an experimental variogram and nested spherical models fitted onto it. Lags in pixel distance (0.2 m). Minimum number of pairs for one lag: 28.10⁶; maximum nb: 738.10⁶.

allowed the fitting of nested models on the experimental points. Once the variogram models had been defined for each image, they were compared from one image to the other, in order to describe the variation of spatial organization in the schools. To account for differences in overall variance between images, variograms were compared relative to the coefficients of variations calculated on the density distribution of the pixels. Distances were expressed in the same units as the 2D matrices. Two types of variograms were computed. First, regional structures, i.e. the variogram for all possible distance lags, were computed for the 2D matrices regularized by blocks of $4 \times 4 = 16$ pixels (16P variograms). Second, the smallscale structures were investigated on the raw $(1 \times 1 \text{ pixel})$ 2D matrices (1P variograms). 16P variograms are less sensitive to small-scale heterogeneities, and present lower nuggets but smoothed slopes, while 1P variograms are adapted to observe these small-scale internal structures.

For the latter, an artificial small structure is anticipated in directions perpendicular to the beam axes, for the following reason. Raw data are organized in 60 sectors (acoustic beams), and the sample surface changes with the distance to the transducer: an acoustic sample represents a surface of $0.05 \times 0.013 = 6.5 \times 10^{-4}$ m² at 5 m from the transducer,

and of $0.05 \times 2.6 = 13 \times 10^{-2} \text{ m}^2$ at 100 m. Then, at large distances from the transducer, sets of neighbouring pixels perpendicular to the beam axis represent the same portion of a beam and are identical (Figure 3), because of the beam pattern. This induces a small structure in each empirical variogram, but as this is an artefact, this structure is not discussed further. Nevertheless, this led us to check whether any small-scale structure was present, using a bias-free method. We first selected a threshold to discard data outside the school detections. Then we calculated for each beam of a given image, the variogram of the raw polar acoustic data in one direction parallel to the beam axis. Finally, we computed a mean variogram for the 60 beams. This was repeated one in every 50 images. Such an approach is supposed to prevent the introduction of any artificial structure but cannot give 2D information; only structures that are present along the beam axis can be observed.

Results

3D characteristics of schools

In all, 63 schools were recorded, but after correction for the beam angle (Johannesson and Losse, 1977), we retained



Figure 3. Schematic description of data transformation. Left, acoustic data obtained through a 0.06 ms acoustic pulse scanning the area, with dimension along beam axis = 5 cm, and dimension across beam axis variable with distance to the transducer (diagram not to scale). A square grid is shown at the remotest point of the diagram: at this distance to the transducer, the same acoustic data are represented in several square pixels. Right, an example of actual data in the square grid 100 m from the transducer. Circles are proportional to density. Scales on the *x*- and *y*-axes are the number of pixels (distances to the transducer in metres can be obtained by multiplying the pixel number by 0.2).

just the 55 schools with positive length for shape measurements (e.g. school length, volume, and surface). Indeed when a school is small compared with the beam diameter, the correction may be bigger than the measured length of the school, and the corrected value becomes negative. The statistics are given in Table 1. It is of interest that mean school length (horizontal dimension parallel to the vessel route) and width (dimension perpendicular to the route) were not significantly different (at p < 0.01), indicating that anchovy were not avoiding the ship (Gerlotto *et al.*, 2004). Schools were, on average, 18 m diameter, with minimum and maximum diameters of 4.6 m and 52 m, respectively. They were located close to the surface (average depth of the geometric centre of the school was 10 m and mean height was 12.8 m). The average distance from the centre of the school to the transducer was 38 m. Considering these features, the total distance covered by the sound pulse from the target to the transducer when reflected by the surface was calculated to be 38.5 m. Given that the echo reflected from the surface from a target located at 38 m from the transducer was received at 11.8° from the beam axis, i.e. at 4 dB less than the on-axis sensitivity according to the directivity diagram of the transducer, such echoes were 2.5 times lower than the direct echo. Therefore, the overall effect of the indirect echo (in dimension and energy) was considered negligible, and we did not

Table 1. Descriptive statistics for 3D school structures. Density in relative units coded on a 256-level scale. Distance to vessel represents the distance of the gravity centre of the school; depth is the depth of the upper part of the school; length is the horizontal distance parallel to the vessel route; width is the horizontal dimension perpendicular to the vessel route; height is the maximum height of the school. The length is corrected from the beam-angle effect, and schools with negative value for corrected length were discarded (eight schools) for this particular and correlated dimension.

Parameter	n	Mean	Confidence interval (-95%)	Confidence interval (+95%)	Minimum	Maximum	Variance	s.d.
Distance to vessel (m)	63	38.0	34.4	42.7	9.9	77.2	289	17.0
Depth (m)	63	10.0	8.6	11.3	2.5	27.7	28	5.3
Length (m)	55	17.4	13.5	21.3	2.32	77.0	206.6	14.4
Width (m)	63	18.2	15.6	21.0	4.6	52.6	112	10.6
Height (m)	63	12.8	10.9	14.6	3.3	37.7	54	7.35
Volume (m ³)	55	1843.0	979.2	2 706.8	28.5	15282.1	1.002×10^{7}	3164
Surface (m ²)	55	5357.0	3 276.8	7 438.0	152.4	33 969.0	5.811×10^{8}	7 6 2 3
Density	63	66.6	60.7	72.4	34.1	164.1	540	23.2

take this possible bias into consideration in other calculations.

Schools and their speeds

Anchovy schools gathered from 04:00 to 06:00 and were observed for 3 h 51 min of the 21 h 52 min spent observing (i.e. during 17% of the experiment; Figure 4). Sea lions were observed in 58% of the images with fish schools, and occasionally when there were no fish. They were usually observed in groups of 3–10. On one occasion we observed and recorded a group of nine sea lions swimming in V-formation, as do some migrating birds. During our survey, sea-lion attacks on anchovy were mainly between 08:00 and 10:00 and early in the afternoon (Figure 4). We were able to make 275 measurements of speed on schools (separating schools with and without predation), 19 on sea lions, 22 on WA, and 12 on vacuole edges.

The average school speeds were 0.48 m s⁻¹ under predation, and 0.28 m s⁻¹ without predation (significantly different at $p < 10^{-2}$). School-speed distribution was centred on 0.25 m s⁻¹ for schools without predation, and varied between 0.25 and 0.75 m s⁻¹ when under attack (Figure 5). For seven schools continuously targeted for predation, usually small schools, we measured the speed before, during, and after the instant of contact between the anchovy and the sea lion(s) (Figure 6). In all cases, school speed dropped at this contact instant from an average speed of 0.44 m s⁻¹ $(n = 102, \sigma = 0.273 \text{ m s}^{-1})$ to almost zero. For the 12 cases allowing measurements, the mean speed of vacuole edges was estimated at 1.6 m s⁻¹. The average speed of a WA was 7.45 m s⁻¹ (n = 22; $\sigma = 3.5 \text{ m s}^{-1}$), with a maximum at 14 m s⁻¹, and the speed of sea lions was measured at 1.2 m s⁻¹ (n = 12; $\sigma = 0.84 \text{ m s}^{-1}$).

School structure during predation

Three periods (before, during, and after attack) were visually defined from the video sequence, by taking the first image of a WA as the start of predation, and the end of the WA period as the end of predation. Before attack was described by images 1-110, during attack by images 111-220, and after attack by images 221-330 (Figure 7). The relative regional variograms of the images for a given group reflected great similarities (Table 2). Before the attack, relative 16P variograms had a range of 150 unit distances (around 30 m) and were stable around the sill. During the attack, the situation was similar except that the behaviour of the 16P variogram at long distances was no longer stable, depicting clear waves around the sill associated with the WA (wavelength of 150 unit distance, i.e. \sim 30 m). The slopes of the 16P variograms at the origin, indicating the degree of spatial structure, were similar for these two groups. A systematic inflection around 70 unit distance (~ 14 m) and a 10% nugget effect were also common to all these variograms. After the attack, the 16P



Figure 4. Frequency of events per hour (from 04:00 to 19:00; no sampling before 04:00 and between 12:00 and 13:00). Above, a number of images with anchovy schools; middle, images with sea lions present; below, sea-lion attacks.



Figure 5. Histogram of measured school speed (in m s⁻¹) for free schools (left) and schools under attack (right).

variograms showed a completely different structure, with weak nugget effect and a linear tendency for the slope to be smaller than observed before and during the attack.

The 1P variograms suggested a split of the sequence of images into four periods instead of the three phases, based on the visual observation of WA (Table 2, Figure 8): (i) a first period (images 10-80) showing general stability of both the relative nugget, which represented 40% of the overall variability, and the slope; (ii) a second period (images 90-170), where the slope remained rather stable and the nugget increased regularly up to 55% of the total variability; (iii) a third period (images 180-220), marked by strong variability in both nugget and slope; (iv) a fourth period (images 230-320) during which the nugget value decreased to the original value of period 1, and with a decreasing slope.

Slopes were estimated by fitting the experimental variograms with models made of a nugget effect and a linear component, and were compared with the coefficients of variation of the density values in each image (Figure 9). During the first period, both indicators showed good stability. During the second period, they behaved differently, the slope



Figure 6. Variation in school speed for seven schools suffering one or two sea-lion attacks, measured at intervals of 15 s. t_0 was set on one attack for all sequences. Two schools have suffered two successive attacks: in both cases (visible at time +45 s and -105 s), speed dropped to zero.

remaining stable and the CV decreasing significantly. During the third period, they showed both strong and quasierratic changes, with an increasing CV and a decreasing slope. Finally, during the fourth period, they still had symmetric variation, the CV increasing slowly up to its value before the attack and the slope continuing to decrease, but at a much slower rate than during the third period. In most of the images, but not all, where we calculated the variogram at small scale along the axis of individual beams (images 50, 100, 150, 200, 250, and 300), a small structure (range around 0.5 m) was found (Figure 10).

Discussion

Sea-lion attacks

Anchovy are relatively slow fish, especially compared with clupeids $(1.24 \text{ m s}^{-1} \text{ for Sardinella aurita; Misund et al.,}$ 2005). As for most fish, anchovy do not have the physiological capacity to maintain high speed even under attack (Videler and Wardle, 1991; Axelsen et al., 2000, 2001). Fréon and Misund (1999) reported that, "Fish are able to rely on 'anaerobic metabolism' to cover high short-term energy requirements such as burst swimming in response to a predator attack." We calculated that the vacuole edges may move at 1.6 m s^{-1} , but such effort cannot last more than a few seconds. If we consider the average speed of sea lions (1.2 m s^{-1}) , it is clear that they are much faster than anchovy schools, and above all are able to maintain high speed for longer. When approaching a school, they swim even faster, and in a few cases we saw sudden acceleration followed by predation on very small groups of fish that had become separated from the main school. However, such events were too short to allow the measurement of speed from the acoustic images. Moreover, we noted that when a sea lion was in contact with a school, it practically stopped. No coherent movement in a given direction can be decided by the school at such a time.

Waves of agitation

This pattern is common, and we saw a great number of WAs during most of the attacks. We did not measure all



Figure 7. Examples of images from before, during, and after attack phases, with their respective variograms (sequence 1762).

of them, because very often they took place in small schools and were very brief. When WAs were noted in large schools, their speed was regularly 7.5 m s⁻¹, occasionally much faster. This series of values is close to the 11-15 m s⁻¹ measured by Radakov (1973) for a school (300 fish) of Atherinomorus sp. Although they do not give any quantitative estimate, Axelsen et al. (2001) note also that WAs of herring schools being attacked by puffins are very fast. They show also that WAs can be seen in any school, regardless of its dimension (from $<50 \text{ m}^2$ to $>500 \text{ m}^2$), consistent with our observations. In our example, we observed several WAs crossing the whole aggregation of fish from one side of the sampling area to the other. In such cases, they were also extremely coherent, expanding in concentric circles around the excitation source (a sea lion; Figure 1). This means that the impulse produced by a sea lion can be perceived at distances of >100 m after 13 s. Moreover, there is no distortion in the signal: WAs cross the aggregation at constant speed and in a constant direction. This is an important result, because it shows that the same information is transmitted to the entire school, regardless of distance from the source. Through WAs, fish can assess precisely the direction of the sea lion. Whether they receive other information, such as distance to the predator, cannot be determined from our data.

Effect on nuclei and school internal organization

A nucleus is defined as a small volume of the school with a greater density than the average, and with dimensions independent of the school itself. Gerlotto and Páramo (2003) hypothesized that such a self-organized structure was the result of two contradictory processes inside the school: a need for fish to behave in synchrony with others, and the maximum overall dimensions of the fish aggregation above which fish from the two sides of the aggregation cannot swim synchronously (Viscido *et al.*, 2005). Under such conditions, the maximum dimension of the nucleus, which was estimated through geostatistics to be around 10 m (horizontal diameter) for *Sardinella aurita* schools, would represent the maximum volume within which simultaneity is possible.

If such a hypothesis is correct, it means that the formation of internal structures, and particularly nuclei, requires a mechanism for transmitting information from one side of the school to the other (Aoki, 1980). Through WAs, transfer of information inside a 10-m diameter nucleus takes approximately 1.5 s. At an average school speed of 0.3 m s^{-1} , this means that one side of the nucleus has moved 50 cm (here, four body lengths) before the other side becomes aware of a change.

Table 2. Parameter values of nested 1P variograms for images 10–320, sequence 1762. Ranges are given in number of pixels (1 pixel = 0.2 m).

Image	Nugget	Sill 1	Range 1	Sill 2	Range 2	Sill 3	Range 3	Slope
10								
20	300	30	90			680	140	
30								
40	300	110	80			790	150	
50	350	110	60			780	150	
60	350	120	70			860	150	
70	400	160	70	220	120	650	170	
80	350	60	70	320	110	540	170	
90	350	50	60	450	100	500	180	
100	330	50	60	250	100	430	160	
110	320	50	50	200	80	390	160	
120	320	40	50	100	90	450	140	
130	270	60	60			330	120	
140	360	30	60	60	85	490	145	
150	290	40	55	95	90	135	125	
160	410			80	95	390	125	
170	290	45	40	95	90	90	140	
180								
195	260	70	40	230	110			
200	350	50	45	50	120	470	220	
210								2.23
220	550	30	50	50	130	740	210	
230								
240								
250	550			250	150			3.3
260								
270	480			180	125			3.15
280								
290	450							3.47
300	435							3.34
310								
320	420							3.15



Successive variograms have been shifted to clarify the figure. The *x*-axis displays the image number for each variogram

Figure 8. Evolution of nugget and slope during the predation event. Periods 1-4, see text for detail.



Figure 9. Comparison of the CVs and the slopes.

The variograms (Figures 7 and 8) confirmed that, as in the case of the experimental results of Radakov (1973), the internal organization in a school changes completely after a WA has crossed it, with fish distribution becoming more regular and homogeneous. In fact, the two main structures present in the area disappeared progressively and the variograms became practically linear. Although we cannot show any analysis after image 330, because part of the biomass left the area, video recordings of the sequence seemed to indicate that it took several minutes before these small-scale structures appeared again. It is therefore clear that a WA transmitted explicit information within a fish school, allowing the whole group to adopt a different spatial organization.

Existence of "micro-groups"

A small structure was observed on several images, with a range of some 0.5 m (Figure 10). This dimension is close



250, and 300.

to those of "micro-groups" in herring schools described by Zaferman (2003, 2005) from echo soundings. In some cases, the small structure was only represented by the first lag of the variogram. In this case, the structures are doubtful, so we interpret the first point on the images with caution (Rivoirard et al., 2000). Nevertheless, for some images, three out of six, the small structure is clear, so some micro-group structure may exist at a small scale. We do not have sufficient results to understand what these micro-groups mean, but are aware that many observations by other authors, for quite different aspects of a school's life, show that patterns can be observed at this dimension (Zaferman, 2003). Griffiths and Magurran (1997), for instance, show the existence of some familiarity inside a small group of six guppies. More generally, this bears on the hitherto unsolved question of the fidelity of pelagic fish to a single school. It is unlikely that the hundreds of thousands or millions of fish constituting a school, which scatter by night, would be able to gather again to form exactly the same school. Dispersion cannot permit such reconstruction. However, micro-groups, if they exist and are stable, would probably not scatter completely by night. Then some interindividual fidelity might exist, forming durable groups of a few fish in a school. Such fidelity has been observed by several authors. Using acoustic tags and fish tracking, for example, M. Soria (pers. comm.) on horse mackerel Selar crumenophtalmus and L. Dagorn (pers. comm.) on yellowfin tuna Thunnus albacares showed that these pelagic fish sometimes left and rejoined fish-aggregation devices (FADs; floating for tuna, an artificial reef for horse mackerel) in small groups of the same individuals. The possible existence of micro-groups would reinforce the idea of the possible transmission of information between schools through learning. Soria et al. (1993) showed that clupeids were able to learn to react to fishing activity and to transmit this knowledge to "naïve" fish. This work was done in a tank, but its conclusions are directly applicable to a large school: if a few experienced anchovy react strongly to an approaching fishing vessel, their reaction would be transmitted to the whole school. WAs favour the efficiency of fish learning functions.

Communication inside schools

Communication, which includes the transmission of information, can be defined as a process in which two or more individuals interact (McFarland, 1987). Could we therefore consider a WA to be a communication process? It is certainly a transmission of information. Communication is less obvious, because there is no visible feedback message. Nevertheless, the fact that a strong change in structure appears means that, once the signal is transmitted, fish change their behavioural pattern and adopt new rules of aggregation. Communication then seems likely. Further, although no clear change in organization is visible on the first images we classified in part as before attack (images 90–140; Figure 7), fish reacted to the presence of a predator before the passage of a WA: that is why we found four periods using detailed analysis instead of three with simple visual observation. We have no idea about the signal received before the WA. It is likely that a sea lion produces sounds when swimming, hunting, or breathing, which may alert anchovy from a considerable distance. The result of such preliminary information is greater heterogeneity at a small scale, as shown by the increasing nugget value. The role of a WA is then to inform the fish of the location of the sea lions and to give a coordination signal for new spatial organization. After the passage of a WA, the overall structure changed, and the distribution became more homogeneous. This reinforces the hypothesis that an elaborate system of communication is needed to maintain some form of spatial structure in a school, and we follow Soria (1994) in believing that collective dynamics require a "reciprocal reinforcement of stimuli" (Baerends and van Rhijn, 1975) to produce adaptive changes. In this case, auditory information would initially induce a warning position, enhancing the effectiveness of the WA in producing new collective structures. This hypothesis is reinforced by the common, often visual, observation that WAs may appear spontaneously in a school, without predation taking place, but in such cases they tend to abort rather quickly. There is a need for other information about the presence of predators to make these WAs become strong and stable when crossing the whole school. We conclude that WAs are just one of the actual mechanisms that allow schools to change their morphology and structure in response to predation.

Defining the communication characteristics from field observations is not easy. One approach could be through Individual-Based Models (IBMs) of fish schools. Several models and simulations have been developed (Huth and Wissel, 1992, 1994; Vabø and Nøttestad, 1997; Couzin et al., 2002; Adioui et al., 2003; Viscido et al., 2005). IBMs of schools allow a better understanding of the possible way that fish can adopt a position inside a group in order to produce a cohesive structure. The main factors considered are generally individual fish speed, attraction and repulsion by neighbours, direction, and position (polarization) with reference to a certain number of neighbours (Aoki, 1984; Viscido et al., 2005). Usually self-organization plays a role (Deneubourg and Goss, 1989; Soria, 1997; Théraulaz and Spitz, 1997; Bonabeau et al., 2000; Viscido et al., 2005), collective organization at a given level resulting from individual behaviour patterns at a lower level of organization. There is no need for reciprocal communication in such models, each fish adapting its dynamics and position according to its neighbours. Nevertheless, when increasing the number of individual fish, and particularly the number of nearest neighbours interacting (Viscido et al., 2005), an IBM school simulation becomes less realistic. In particular, no clear internal structure emerges. It could be of interest to test whether some communication process input into the IBMs would improve the results. If so, we would have a demonstration of the importance of communication in a school, as compared with the transmission of information.

Conclusions

We have demonstrated that fish use behavioural functions for transmitting information inside a large group of individuals, and that this information induces important changes in the inter-individual organization of fish in a school, depending on external factors. This result leads to several conclusions.

- (i) The mechanisms identified in this work are typical of self-organization processes (Nicolis and Prigogine, 1977). Self-organization is demonstrated when simple individual actions (in this case, the rolling of fish) produce a complex collective behaviour, i.e. the construction of a WA and the communication of information within a school. Whether the change in school structure is also strictly self-organized is not so clear, and more research will be needed to clarify this point.
- (ii) The changes attributable to sea-lion attacks confirm that schooling is related to predation. However, it is obtained through dynamic behaviour processes that have other effects, particularly the maintenance of collective cohesion and organization (nuclei for instance). Therefore, we cannot conclude that schooling is essentially a predator-induced behaviour.
- (iii) The way an individual reaction is transmitted without attenuation in a large school reinforces the hypothesis of the cognitive function of a school. When a group of experienced fish is present inside a "naïve" school, the reactions of its members when predation is beginning may induce a fast and adapted reaction of the whole school through a wave of agitation.
- (iv) Our last conclusion is that school structure and morphology are the response of fish to their environment. A school under predation has a completely different shape from a school that is not. This observation can probably be extended to other environmental parameters (Bertrand *et al.*, 2006), showing that school typology is an excellent candidate for the role of an indicator describing the condition of a school, and statistically of a population, with respect to the environment. In an ecosystem approach to fisheries, school typology, which is easy to observe acoustically, could help our understanding of the relationships between a population and the ecosystem once a consistent description of types is established.

Acknowledgements

We thank Captain Erik Salazar and the crew of the RV "José Olaya Balandra" for their help during the survey, the IMARPE scientists for participating in the survey and data processing, and Renato Guevara (IMARPE) and Pierre Soler (IRD) for their support. The work was in part funded by the IRD Project "ATI (Action thématique Inter-Départements) on the Humboldt Current System".

References

- Adioui, M., Treuil, J. P., and Arino, O. 2003. Alignment in a fish school: a mixed Lagrangian–Eulerian approach. Ecological Modelling, 167: 19–32.
- Aoki, I. 1980. An analysis of the schooling behaviour of fish: internal organization and communication process. Bulletin of the Ocean Research Institute University of Tokyo, 12: 1–65.
- Aoki, I. 1984. Internal dynamics of fish schools in relation to interfish distance. Bulletin of the Japanese Society for Scientific Fisheries, 50: 751–758.
- Arias-Schreiber, M. 2000. Los lobos marinos y su relacion con la abundancia de la anchoveta peruana durante 1979–2000. Boletín IMARPE, 19: 133–138.
- Axelsen, B. E., Anker-Nilson, T., Fosum, P., Kvamme, C., and Nottestad, L. 2001. Pretty pattern but a simple strategy: predator—prey interaction between juvenile herring and Atlantic puffins observed using multibeam sonar. Canadian Journal of Zoology, 79: 1586–1596.
- Axelsen, B. E., Nottestad, L., Fernö, A., Johannessen, A., and Misund, O. A. 2000. "Await" in the pelagic: dynamic tradeoff between reproduction and survival within a herring school splitting vertically during spawning. Marine Ecology Progress Series, 205: 259–269.
- Baerends, G. P., and van Rhijn, J. 1975. The effect of colour in egg recognition by the black-headed gull. Koninklijke Nederland Akademie, 78(1).
- Bertrand, A., Barbieri, M. A., Gerlotto, F., Leiva, F., and Córdova, J. 2006. Determinism and plasticity of fish-schooling behaviour as exemplified by the South Pacific jack mackerel *Trachurus murphyi*. Marine Ecology Progress Series, 311: 145–156.
- Bonabeau, E., Sylvain, G., Snyers, D., Kuntz, P., and Théraulaz, G. 2000. Three-dimensional architectures grown by simple "stigmergic" agents. BioSystems, 56: 13–22.
- Breder, C. M. 1976. Fish schools as operational structures. Fishery Bulletin US, 74: 471–502.
- Brehmer, P. 2004. Analyse compare des caractéristiques dynamiques et spatiales des bancs de Sardinella aurita (Valenciennes, 1847) de diverses populations: adaptations comportementales face à l'environnement et à l'exploitation, effet sur la capturabilité. Thèse Doctorat ENSAR Université Rennes. 367 pp.
- Couzin, I. D., Krauze, J., James, R., Ruxton, G. D., and Franks, N. R. 2002. Collective memory and spatial sorting in animal groups. Journal of Theoretical Biology, 218: 1–11.
- Deneubourg, J., and Goss, S. 1989. Collective patterns and decision making. Ethology. Ecology and Evolution, 1: 295–311.
- Foote, K. G., Chu, D., Hammar, T. R., Hufnagle, L. C., and Jech, J. M. 2005. Protocols for calibrating multibeam sonars. Journal of the Acoustical Society of America, 117: 2013–2027.
- Fréon, P., Gerlotto, F., and Soria, M. 1992. Changes in school structure according to external stimuli: description and influence on acoustic assessment. Fisheries Research, 15: 45–66.
- Fréon, P., and Misund, O. A. 1999. Dynamics of Pelagic-Fish Distribution and Behaviour: Effects on Fisheries and Stock Assessment. Blackwell, Oxford. 348 pp.
- Gerlotto, F., Castillo, J., Saavedra, A., Barbieri, M. A., Espejo, M., and Cotel, P. 2004. Three-dimensional structure and avoidance behaviour of anchoveta and common sardine schools in central southern Chile. ICES Journal of Marine Science, 61: 1120–1126.
- Gerlotto, F., and Páramo, J. 2003. The three-dimensional morphology and internal structure of clupeid schools as observed using vertical scanning multibeam sonar. Aquatic Living Resources, 16: 113–122.

- Gerlotto, F., Soria, M., and Fréon, P. 1999. From two dimensions to three: the use of multibeam sonar for a new approach in fisheries acoustics. Canadian Journal of Fisheries and Aquatic Sciences, 56: 6–12.
- Griffiths, S. V., and Magurran, A. E. 1997. Familiarity in schooling fish: how long does it take to acquire? Animal Behaviour, 53: 945–949.
- Heppner, F. 1997. Three-dimensional structure and dynamics of bird flocks. *In* Animal Groups in Three Dimensions, pp. 68–89. Ed. by J. K. Parrish, and W. M. Hamner. Cambridge University Press, Cambridge. 378 pp.
- Herskin, J., and Steffensen, J. F. 1998. Energy saving in sea bass swimming in a school: measurement of tail-beat frequency and oxygen consumption at different swimming speeds. Journal of Fish Biology, 53: 366–376.
- Hückstädt, L. A., and Antezana, T. 2003. Behaviour of the southern sea lion (*Otaria flavescens*) and consumption of the catch during purse-seining for jack mackerel (*Trachurus symmetricus*) off central Chile. ICES Journal of Marine Science, 60: 1003–1011.
- Huth, A., and Wissel, C. 1992. The simulation of the movements of fish schools. Journal of Theoretical Biology, 156: 365–385.
- Huth, A., and Wissel, C. 1994. The simulation of fish schools in comparison with experimental data. Ecological Modelling, 75/ 76: 135–146.
- Johannesson, K. A., and Losse, G. F. 1977. Methodology of acoustic estimation of fish abundance in some UNDP/FAO resourcesurvey projects. Rapports et Procès-verbaux des Réunions du Conseil International de l'Exploration de la Mer, 170: 296–318.
- Kieser, R., Mulligan, T. J., Richards, L. J., and Leaman, B. M. 1993. Bias correction of rockfish school cross-section widths from digitized echosounder data. Canadian Journal of Fisheries and Aquatic Sciences, 50: 1801–1811.
- Kubecka, I. 1996. Use of horizontal dual-beam sonar for fish surveys in shallow waters. *In* Stock Assessment in Inland Fisheries, pp. 165–178. Ed. by I. G. Cowx. Fishing News Books, Oxford.
- Magurran, A. E. 1986. The development of shoaling behaviour in the European minnow, *Phoxinus phoxinus*. Journal of Fish Biology, 29A: 159–170.
- Magurran, A. E., Seghers, B. H., Carvalho, G. R., and Shaw, P. W. 1993. Evolution of adaptive variation in antipredator behaviour. *In* Behavioural Ecology of Fishes, pp. 29–44. Ed. by F. A. Huntingford, and P. Torricelli. Ettore Majorana International Life Science Series, vol. 11, Harwood Academic Publishers.
- Mayer, L., Li, Y., and Melvin, G. 2002. 3D visualization for pelagic fisheries research and assessment. ICES Journal of Marine Science, 59: 216–225.
- McFarland, D. 1987. The Oxford Companion to Animal Behaviour. Oxford University Press, Oxford.
- Misund, O. A. 1993. Dynamics of moving masses: variability in packing density, shape, and size among herring, sprat and saithe schools. ICES Journal of Marine Science, 50: 145–160.
- Misund, O. A., and Coetzee, J. 2000. Recording fish schools by multi-beam sonar: potential for validating and supplementing echo-integration recordings of schooling fish. Fisheries Research, 47: 149–159.
- Misund, O. A., Luyeye, N., Boyer, D., Coetzee, J., Cloete, R., Dalen, J., and Oechslin, G. 2005. Observations on the nearsurface behaviour of sardinella schools in Angolan waters. African Journal of Marine Science, 27: 169–176.
- Nicolis, G., and Prigogine, I. 1977. Self-Organization in Non-Equilibrium Systems. Wiley, New York.
- Nøttestad, L., and Axelsen, B. E. 1999. Herring-schooling manoeuvres in response to killer-whale attacks. Canadian Journal of Zoology, 77: 1540–1546.
- Parrish, J. K., Hamner, W. M., and Prewitt, C. T. 1997. Introduction – from individuals to aggregations: unifying properties, global framework, and the holy grails of congregations. *In* Animal Groups in Three Dimensions, pp. 1–13. Ed. by J. K. Parrish,

and W. M. Hamner. Cambridge University Press, Cambridge. 378 pp.

- Partridge, B. L. 1982. Structure and functions of fish schools. Scientific American, 245: 114–123.
- Pedersen, J. 1996. Discriminating fish layers using the threedimensional information obtained by a split-beam echosounder. ICES Journal of Marine Science, 53: 371–376.
- Pitcher, T. J. 1983. Heuristic definition of shoaling behaviour. Animal Behaviour, 31: 611–613.
- Pitcher, T. J., Misund, O. A., Fernø, A., Totland, B., and Melle, V. 1996. Adaptive behaviour of herring schools in the Norwegian Sea as revealed by high-resolution sonar. ICES Journal of Marine Science, 53: 449–452.
- Pitcher, T. J., and Parrish, J. K. 1993. Functions of shoaling behaviour. *In* Behaviour of Teleost Fishes, 2nd edn, pp. 363–439. Ed. by T. J. Pitcher. Chapman and Hall, London.
- Pitcher, T. J., and Partridge, B. L. 1979. Fish-school density and volume. Marine Biology, 54: 383–394.
- Radakov, D. V. 1973. Schooling in the Ecology of Fish. Wiley, New York.
- Reid, D. G. (Ed.) 2000. Report on echo trace classification. ICES Cooperative Research Report, 238. 115 pp.
- Rivoirard, J., Simmonds, J., Foote, K. G., Fernandes, P., and Bez, N. 2000. Geostatistics for Estimating Fish Abundance. Blackwell Science, Oxford. 203 pp.
- Robinson, C. J., and Pitcher, T. J. 1989. The influence of hunger and ration level on shoal density, polarization and swimming speed of herring, *Clupea harengus* L. Journal of Fish Biology, 34: 631–633.
- Simmonds, E. J., and MacLennan, D. 2005. Fisheries Acoustics. Theory and Practice, 2nd edn. Blackwell Science, Oxford. 429 pp.
- Simmonds, E. J., Gerlotto, F., Fernandes, P. G., and MacLennan, D. N. 1999. Observation and extraction of three dimensional information on fish schools. Journal of the Acoustical Society of America, 105: 996.

- Soria, M. 1994. Structure et stabilité des bancs et agrégations de poisons pélagiques côtiers tropicaux: applications halieutiques. Thèse Doctorat Université Rennes 1. 280 pp.
- Soria, M. 1997. Le banc de poissons: expression d'une motivation sociale ou comportement collectif d'un groupe auto-organisé? *In* Auto-Organisation et Comportement, pp. 141–156. Ed. by G. Théraulaz, and F. Spitz. Hermes, Paris. 293 pp.
- Soria, M., Gerlotto, F., and Fréon, P. 1993. Study of learning capabilities of a tropical clupeoid using artificial stimuli. ICES Marine Science Symposia, 196: 17–20.
- Svendsen, J. C., Skov, J. B., Bildsoe, M., and Steffensen, J. F. 2003. Intra-school positional preference and reduced tail-beat frequency in trailing position in schooling roach under experimental conditions. Journal of Fish Biology, 62: 834–846.
- Théraulaz, G., and Spitz, F. 1997. Auto-Organisation et Comportement. Hermes, Paris. 293 pp.
- Vabo, R., and Nøttestad, L. 1997. An individual-based model of fish-school reactions: predicting antipredator behaviour as observed in nature. Fisheries Oceanography, 6: 155–171.
- Videler, J. J., and Wardle, C. S. 1991. Fish swimming strideby-stride: speed limits and endurance. Reviews in Fish Biology and Fisheries, 1: 23–40.
- Viscido, S. V., Parrish, J. K., and Grünbaum, D. 2005. The effect of population size and number of influential neighbors on the emergent properties of fish schools. Ecological Modelling, 183: 347–363.
- Webb, P. W. 1980. Does schooling reduce fast-start response latencies in teleosts? Comparative Biochemistry and Physiology A, 65: 231–234.
- Zaferman, M. 2003. Fish structure of pelagic-fish shoals. ICES Symposium on Fish Behaviour in Exploited Ecosystems, Bergen, June 2003.
- Zaferman, M. 2005. Fine structure of fish aggregation: methods of study, effect on acoustic characteristics and fishing-gear catchability. ICES Document CM/2005/U: 13.