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Effect of external factors (environment and survey vessel) on fish school characteristics observed by echosounder and multibeam sonar in the Mediterranean Sea

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Abstract

The size of pelagic fish schools depends on several parameters related to internal factors such as species, number of fish, fish swimming speed and physiological status and to external factors, such as hydrological factors and presence of predators. In order to better understand these relations, results coming from echosounder and multibeam sonar databases are analysed. Field data are collected during four acoustic surveys in the Mediterranean Sea in two different areas (Catalan and Adriatic Seas). The analysis shows differences between the two areas regarding size and position in the water column: schools are deeper and their mean size is lower in the Catalan Sea in comparison with Adriatic Sea. The differences in size of schools are mainly related to differences in school length. Moreover, the elongation of schools seen with the sonar is greater than one and half higher in the Adriatic Sea than in the Catalan Sea, whereas one would expect similar values for the two areas. The results are discussed in terms of environmental influence, avoidance reaction and acoustic capabilities of both tools. A hypothesis is proposed: the variation of school length and consecutively the variation of the correlated dimensions is first related to the strength of the avoidance reaction in front of the vessel and this effect can be reinforced depending on the environmental conditions. The model takes into account the effect of the boat, the vertical constraints undergone by the schools, and the internal requirements of the schools, such as the necessity for fish to keep visual contacts and the cohesion of the group.

Keywords: Acoustic; Multibeam sonar; Echosounder; Fish school behaviour; Avoidance; Environment

1. Introduction

Spatial dynamics are of paramount importance to the understanding of the forces governing population dynamics. In the particular case of fish stocks, studying the factors inducing and maintaining the aggregation of fish within schools could be helpful to better understand the spatial heterogeneity of small pelagic fish populations and the mechanisms that lead to the particular mode of distribution of schools (Pitcher et al., 1996; Mackinson, 1999; Fréon and Misund, 1999; Booth, 2000). Moreover, schooling behaviour is a powerful mechanism to sort fish by length (Fréon, 1984, 1985), an improved understanding of the mechanisms driving space-time variations in school size should greatly improve the estimation of demographic parameters. According to previous investigations, the size and the shape of pelagic fish schools depend on several parameters related to internal and external factors. Among the internal factors, the most commonly quoted are the species (Partridge et al., 1980; Misund, 1993a; Maes and Ollevier, 2002), the swimming speed or the body length of fish (Hara, 1987; Peukhuri et al., 1997; Dagorn et al., 1997; Hoare et al., 2000), the foraging behaviour (Pitcher and Partridge, 1979; Pitcher and Parrish, 1993; Mackinson et al., 1999) or the physiological status (Morgan, 1988; Robinson and Pitcher, 1989; Robinson, 1995). With regard to the external factors, related literature reports the influence of the stock abundance (Misund, 1993b; Petitgas and Lévénez, 1996; Petitgas et al., 2001), the interactions between species like the presence of predators (Fréon et al., 1992; Parrish, 1992; Krause and Godin, 1995; Pitcher et al., 1996) or the trophic competitors (Massé et al., 1996),

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the environmental conditions such as thermocline depth (Swartzman et al., 1994), the food availability and the food density (Nøttestad et al., 1996) or the specific disruptive events like strong gales (Scalabrin and Massé, 1993) or the arrival of a boat (Olsen et al., 1983; Gerlotto and Fréon, 1992). Finally, an important phenomenon must be pointed out: the avoidance behaviour of the schools, which has an impact on factors such as catchability and abundance estimates. The recent development of 3D acoustic technology might lead to a better accuracy of school size estimations and to a better understanding of adaptation mechanisms of schools to local variations (Gerlotto et al., 1999; Misund and Coetzee, 2000; Mackinson et al., 1999). In order to study this issue, we analysed the morphological and spatial characteristics of schools measured by echosounder and multibeam sonar during acoustic surveys in relation to the external conditions measured in the near field of these schools. We focus on both environmental changes occurring during the day in the vertical plane (thermocline, halocline and chlorophyll concentration) and local perturbations induced by the vessel. Data composed of two species (sardine and anchovy). Two surveys were conducted during successive years (1994, 1995), using the same research vessel in two different areas of the Mediterranean Sea showing different environmental conditions. Based on our database and on previous studies (Bahri and Fréon, 2000), the object of this paper is to compare the school characteristics in these two areas, measured with two acoustic devices, so as to test the hypothesis that the differences are related to environmental conditions and to the impact of the vessel.

2. Materials and methods

2.1. Survey designs

The surveys were carried out during 1994 and 1995 in Catalan Sea (39–41°N/0–2°E) during spring, and in Northern Adriatic Sea (43°30'–45°30'N/12°15'–13°30'E) at the end of summer (Fig. 1). In Catalan Sea, the studied area is characterized by a wide continental shelf (30–40 nmi wide by 90 nmi long) and receives in its northern part freshwater from Ebra River. Two back-to-back coverages of the zone were performed during each of the two cruises. In the North Adriatic, the area includes the plume of the Pô River characterized by turbid freshwater. A single coverage was performed during each of the two cruises. The surveys were all performed aboard the R/V *García del Cid*, in the framework of the European programme T-ECHO (AIR1 CT92 0314). For both zones, the vessel's track was designed as parallel transects separated by 7 nmi, roughly perpendicular to the coastline (from 15 to 100 m isobath). Vessel speed was about 5–7 knots. A CTD cast every 7 nmi was performed.

2.2. Acoustic instruments

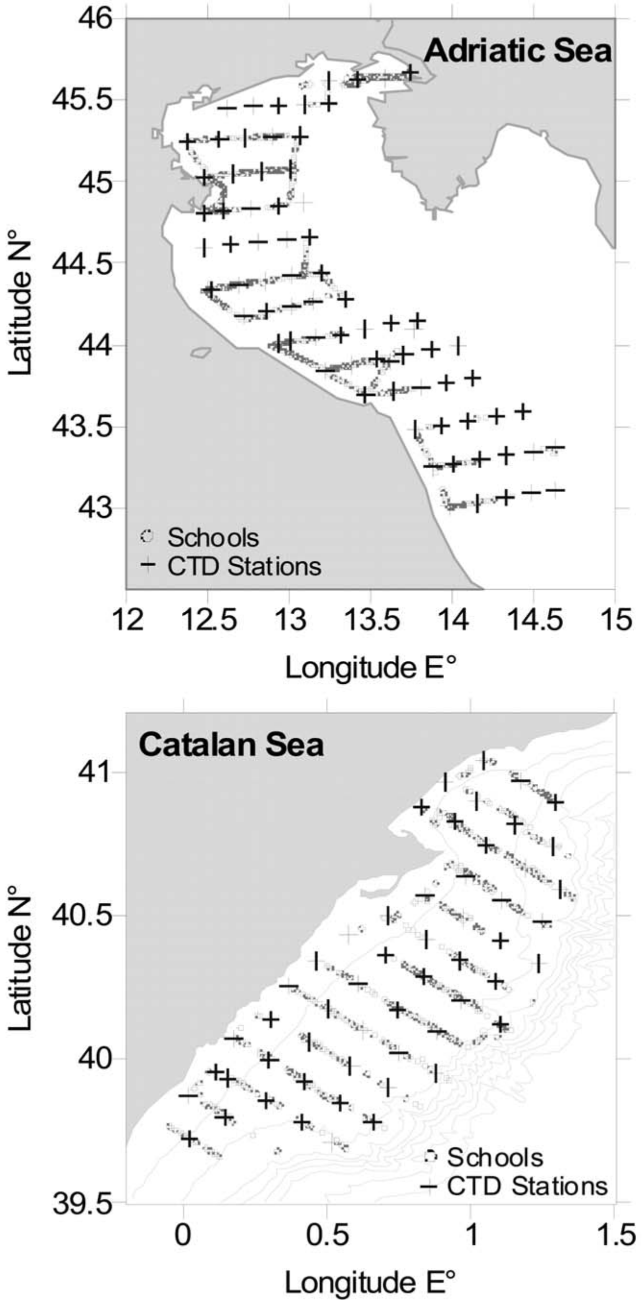

Fig. 1. Sampling design in the areas surveyed during the T-ECHO Project (50 m isobaths are shown in Catalan Sea).

The echo-integration was performed utilizing a 38 kHz dual beam echosounder BioSonics operating at 2 s ping rate and 0.4 ms pulse rate. The beam width was 10° between the –3 dB points on the narrow beam. The transducer was mounted on a V-fin body, towed at 4–6 m depth. The sonar recordings were made by a 455 kHz multibeam sonar Reson SEABAT 6012 with a pulse length of 0.06 ms and with a total receiving beam angle of 90° (60 beams of 1.5° each) in the vertical plane and 21° in the perpendicular direction. The 60 beams were simultaneously updated seven times per second using the 100 m range. The efficient range was 80 m due to the background noise. The sonar was mounted on a vertical pipe along the vessel. The transducer was at 4 m depth and oriented transversally to the boat in order to scan the side of the vessel route and exhaustively explore the water volume (Bahri et al., 1997; Soria et al., 1997; Gerlotto et al., 1999).

2.3. Databases

2.3.1. Schools

An acoustic data processing system, INES-Movies-B (Weill et al., 1993; Diner et al., 1994), was connected to the echosounder and allowed for the extraction of acoustical and morphological characteristics of schools. Thresholds, corrections and filtering used in this analysis were chosen empirically in order to take into account the specific acoustical conditions met during the surveys.

According to several authors (Kieser et al., 1993; Fréon et al., 1996; Patty, 1996; Scalabrin et al., 1996; Bahri, 2000; Bahri and Fréon, 2000), we defined an acoustic pelagic school using the following four settings.

(1) For echosounder, a school was defined as a set of pings having amplitude values above the processing threshold. The value of this threshold was chosen in order to avoid possible detections through the side lobes of the acoustic beam. Depending on the background noise, the value was ranged between 50 and 100 mV. The samples must also satisfy a contiguity law, both for vertical and horizontal axes.

(2) INES-Movies-B was set with the following thresholds: successive pings > 3, signal digital sampling units (height 10 cm) > 30, backscattering energy > 100 (in mV^2). These thresholds were empirically chosen in order to discriminate individual echoes from patches on the echogram.

(3) As during night time, fish tend to disperse in layers and few schools were observed, only daytime data were taken into account. Dawn and dusk have not been included in the database. According to Fréon et al. (1996) and Beare et al. (2002), school formation and school dispersion dynamics during these periods are very specific. Diffuse layers observed during daytime, very likely containing a mixture of plankton and fish, have been discarded from the school dataset on the basis of length and density criteria.

(4) The minimum area and volume of a school were set, respectively, to 5 m^2 and 5 m^3. Echoes smaller than 2 m long, 2 m wide and 2 m high were eliminated from the datasets. Since we considered that pelagic fish schools in contact with the bottom had a greater vertical dimension than demersal species schools, a school was considered as being pelagic when the distance between the seabed and the top of the school was greater than or equal to 6 m.

Due to the lack of calibration procedure of the sonar, neither precise absolute values of the echo-signal nor comparable inter-survey relative measurements could be provided. Therefore, the morphological parameters were the only usable data, they were measured manually on the video screen in our laboratory, after the survey (Soria et al., 1996). The school descriptors are listed (Appendices 1 and 2). School size corrections were based only on nominal beam opening, despite the low accuracy of this type of correction (Diner, 2001). This correction still provided negative length values for few schools that were removed from the database.

2.3.2. CTD data

In addition to the collection of acoustic data, vertical profiles of hydrological data were also collected during CTD stations. In order to analyze relationships between school characteristics and environmental parameters, and because of the inertia of environmental characteristics of the water column, each school was associated to the closest CTD cast. The measured values were: thermocline depth, halocline depth, first fluorescence peak depth and second fluorescence peak depth, we considered both absolute and relative depths (in percentage relative to the bottom depth). We calculated the vertical distance between the fish schools and the thermocline, the halocline and the fluorescence peaks, and we assigned either positive or negative sign, depending on whether the school is above (positive distance) or below (negative distance). Spatio-temporal descriptors were also attributed to each school (longitude, latitude, date and time, vessel speed, bottom depth).

2.3.3. Biological sampling

Biological sampling was also performed, using pelagic trawls, in order to identify fish species and size composition. The main species were sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*). The two occasional species were the gilt sardine *Sardinella aurita* in the Catalan Sea and the sprat *Sprattus sprattus* in the Adriatic Sea (Bahri and Fréon, 2000).

2.4. Statistical analysis

The comparison between areas and between acoustic tools of the main school descriptors was done using a *t*-test for independent samples by groups.

A principal component analysis (PCA) was performed in order to reduce the number of variables and to identify components, which best explain the observed variability, thereby making it possible to describe differences between the geographical areas. The analysis was performed for each acoustic device. A varimax-normalized rotation was applied in order to maximize the variance. Eigenvalues were calculated and factor coordinates of variables were plotted.

In order to evaluate the contribution of environmental variables to the variability of the school size (see results), a multiple ANOVA was performed on sonar and echosounder data. Since the effect of the predictors on the dependent variable may not be linear in nature, relationships cannot adequately be summarized by a simple linear equation, and categorical predictor variables were then computed. Effects for these variables are represented using the sigma-restricted parameterization. The backward stepwise method was used to select the best model. Intercept is included in the model. In addition to environmental variables, the vessel speed and the lateral distance of the school to the boat were taken into account at the initial step of the process.

Table 1
Summary statistics of survey characteristics

Survey	Covered distance (nmi)	Sonar		Echosounder	
		Number of schools	School density (Nb nmi^{-1})	Number of schools	School density (Nb nmi^{-1})
Catalan94	534	380	0.71	307	0.58
Catalan95	595	158	0.27	310	0.52
Total Catalan	1129	538	0.48	617	0.55
Adriatic94	303	333	1.10	87	0.29
Adriatic95	298	599	2.01	156	0.52
Total Adriatic	601	932	1.55	243	0.40
Total	1730	1470	0.85	860	0.50

3. Results

3.1. Survey characteristics

General survey characteristics are indicated (Table 1). First, we noted a difference between the density of schools recorded by the sonar in Adriatic Sea in 1994 and 1995 (respectively, 1.1 and 2 school nmi^{-1}). This difference can be partly due to the change in the image smoothing rate (from 4 to 2). Nevertheless, this interpretation is minimized by the fact that similar results are obtained with the echosounder (0.3 and 0.5 school nmi^{-1}, respectively). Since the sonar has a greater sampling area, the number of schools was expected to be higher than echosounder schools. This is not the case in Catalan Sea: differences are surprisingly weak in 1994 (Nb_{sonar} = 380, $Nb_{echosounder}$ = 307) and in inverse order in 1995 (Nb_{sonar} = 158, $Nb_{echosounder}$ = 310). On the one hand, this could be due to a lower reception gain of the sonar in 1995 in comparison with 1994 (4 vs. 5); this, implies that the size of schools in 1995 should be smaller than in 1994 and that a lower number of small schools should be detected in 1995 in comparison with 1994. On the other hand, the differences in detection thresholds and acoustic properties of the echosounder and the sonar, imply that the sonar does not detect small schools and therefore underestimates the number of schools (MacLennan and Simmonds, 1992; Misund and Coetzee, 2000). This last hypothesis is confirmed by the analysis of morphological characteristics of schools detected in Catalan Sea. The mean size of schools, recorded in Catalan Sea by the sonar in 1994, is similar to those recorded in 1995 (e.g. on an average: area in 1995 = 63 m^2 and area in 1994 = 64.6 m^2; t-value = 0.98, $P = 0.32$), whereas the mean size of schools, recorded by the echosounder in 1995, is smaller than those recorded in 1994 (mean area = 195 m^2 in 1995, and mean area = 355 m^2 in 1994; t-value = 9.4, $P < 0.0001$). Moreover, mean school sizes of schools recorded by the echosounder in Catalan Sea are higher than mean school sizes of schools recorded with the sonar (e.g. mean $length_{echosounder}$ = 24.5 m and mean $length_{sonar}$ = 9.7 m; t-value = –18.5, $P < 0.001$). Therefore, the data cannot be compared between years and acoustic device. The analysis was performed separately on the two database, and the years were not take into account.

3.2. Morphological and spatial characteristics of schools and environmental parameters

Table 2 shows, for each acoustic device, the results of the comparison between the two areas for selected variables describing morphological and spatial characteristics of schools and environmental parameters. Student t-tests reveal significant differences between the areas for all the descriptors. Regarding morphological parameters, the difference of school size recorded by the sonar is mainly dependent on the variation of the school length. Moreover, the mean school length is significantly higher in Adriatic Sea than in Catalan Sea. This difference is also observed with the echosounder. The other parameters are significantly different, even though they show less striking results. The most important result concerns the elongation (ratio length/width) of schools recorded with the sonar. The mean value is twice higher in Adriatic Sea than in Catalan Sea, whereas similar values were expected. The value of this ratio was expected to be 1. This is not observed in Adriatic Sea, where the average value is 1.5, which means that in this area, schools are in average more or less half longer than wide. Regarding external factors, mean bottom depth of Adriatic Sea is lower than in Catalan Sea. This induces differences between the means of related factors, such as the school depth and vertical distance between the schools and the thermocline, the halocline or the depth of the fluorescence peaks. The comparison of the mean relative depth of the schools indicates that schools in Adriatic Sea tend to occupy the upper part of the water column compared to those of Catalan Sea. The mean lateral distance to the boat might reflect the horizontal avoidance reaction of the fish to the vessel. This distance is significantly greater in Adriatic Sea than in Catalan Sea. Moreover, the vessel sailed faster in Adriatic Sea than in Catalan Sea.

3.3. Principal component analysis

The PCA of the correlation matrix allows for the description of the linear interactions between descriptors of schools and environmental parameters. Analysis of echosounder data (Table 3) showed that the variables, describing school characteristics, are grouped into three sets (morphological, acoustical and environment-related descriptors). Respec-

Table 2
Means of selected variables describing morphological and spatial characteristics of schools and environmental parameters for each area and each acoustic tool, *P* value is the level of significance of student *t*-test

Variables	Sonar			Echosounder		
	Catalan Sea	Adriatic Sea	$P < 0.05$	Catalan Sea	Adriatic Sea	$P < 0.05$
Nb School	538	932		617	243	
Boat speed (knot)	6.6 ± 0.1	6.7 ± 0.1	*	6.3 ± 0.1	6.5 ± 0.2	*
Bottom depth (m)	60 ± 4	27 ± 2	*	78 ± 4	36 ± 4	*
School depth (m)	29 ± 3	11 ± 1	*	53 ± 4	18 ± 4	*
Relative depth of the school (%)	50 ± 4	36 ± 3	*	67 ± 3	46 ± 5	*
Length (m)	10 ± 2	18 ± 2	*	25 ± 3	29 ± 6	*
Height (m)	8 ± 1	6.2 ± 0.5	*	12 ± 1	9 ± 1	*
Ratio length/height	1.6 ± 0.3	3.3 ± 0.5	*	2.4 ± 0.2	3.5 ± 0.6	*
Area (length × height) m^2	64 ± 16	95 ± 17	*	274 ± 69	252 ± 87	*
Thermocline depth (m)	12 ± 1	12 ± 1	*	13 ± 1	16 ± 2	*
Halocline depth (m)	19 ± 3	9 ± 1	*	20 ± 3	12 ± 2	*
First fluorescence peak depth (m)	6 ± 1	8 ± 1	*	6 ± 1	8 ± 1	*
Second fluorescence peak depth (m)	38 ± 2	24 ± 2	*	44 ± 2	27 ± 4	*
Relative depth of the thermocline (%)	22.3 ± 2.3	42.8 ± 2.8	*	19.2 ± 2.4	44.3 ± 4.8	*
Relative depth of the halocline (%)	31.8 ± 3.9	28.9 ± 2.8	*	27.8 ± 3.3	30.8 ± 4.3	*
Relative depth of the first fluorescence peak (%)	11.7 ± 2.4	20.7 ± 2.6	*	8.3 ± 1.5	21.3 ± 4.0	*
Relative depth of the second fluorescence peak (%)	62.5 ± 2.6	75.0 ± 2.3	*	58.9 ± 2.7	71.7 ± 4.9	*
Distance to the thermocline (m)	–17 ± 3	2 ± 1	*	–40 ± 4	–2 ± 3	*
Distance to the Halocline (m)	–10 ± 4	–1 ± 1	*	–33 ± 5	–6 ± 3	*
Distance to the first fluorescence peak depth (m)	–23 ± 3	–3 ± 1	*	–47 ± 4	–9 ± 4	*
Distance to the second fluorescence peak depth (m)	9 ± 3	11 ± 2	*	–9 ± 4	9 ± 3	*
Integrated back-scattered energy (relative value)				131 ± 67	684 ± 317	*
Volume reverberation index (dB m^{-3})				–54 ± 1	–40 ± 2	*
Roughness				1.4 ± 0.03	1.4 ± 0.04	*
Perimeter (m)				196 ± 57	147 ± 49	*
Width (m)	14 ± 1	14 ± 1	NS			
Volume (m^3)	729 ± 267	1 291 ± 394	*			
Ratio length/width	0.8 ± 0.1	1.4 ± 0.2	*			
Ratio width/height	2.1 ± 0.3	2.7 ± 0.3	*			
Lateral distance to the boat (m)	34 ± 3	42 ± 2	*			

tively to Adriatic and Catalan Seas, the first component explained 42% and 49% of the total variance, the second component 19% and 18% and the third component 14.5% and 16%. In both areas, the first component is highly correlated with the environmental-related descriptors, the second component to morphological descriptors, and the third to acoustical characteristics of schools associated with the roughness. This result indicates that the morphological and acoustical characteristics (related to internal density and biomass) of schools are independent from the variations of environment-related parameters. Nevertheless, the PCA allows for a classification according to the environmental conditions measured near the schools. Moreover, the factor coordinates of the schools were plotted for each geographical area, according to the two components representing environmental conditions and school morphology. Variations along

Table 3
Factor loadings of the principal components extracted from the echosounder data set and percents of variance explained

Class of descriptors	Variable	Factor loadings (varimax-normalized)					
		Adriatic Sea; Nb = 243			Catalan Sea; Nb = 617		
		Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
Environmental-related descriptors	Relative depth of the school	**0.82**	–0.29	0.05	**0.81**	–0.42	0.13
	Distance to the thermocline	**0.96**	–0.03	0.07	**0.94**	0.05	0.15
	Distance to the halocline	**0.95**	–0.04	0.09	**0.88**	0.15	0.23
	Distance to the first fluorescence peak	**0.94**	0.04	0.20	**0.94**	0.04	0.20
	Distance to the second fluorescence peak	**0.61**	–0.39	–0.13	**0.92**	0.06	0.23
Acoustic descriptors	Integrated back-scattered energy	–0.11	0.57	**–0.68**	–0.16	0.31	**–0.92**
	Volume reverberation index	–0.18	–0.07	**–0.75**	–0.19	–0.09	**–0.94**
Morphological descriptors	Roughness	–0.05	0.29	**0.81**	0.22	0.25	**0.58**
	Height	–0.02	**0.81**	0.12	–0.21	**0.85**	0.03
	Length	–0.19	**0.79**	0.09	0.30	**0.82**	0.03
	Percentage of inertia	41.7	19.3	14.6	49.4	17.7	16.2

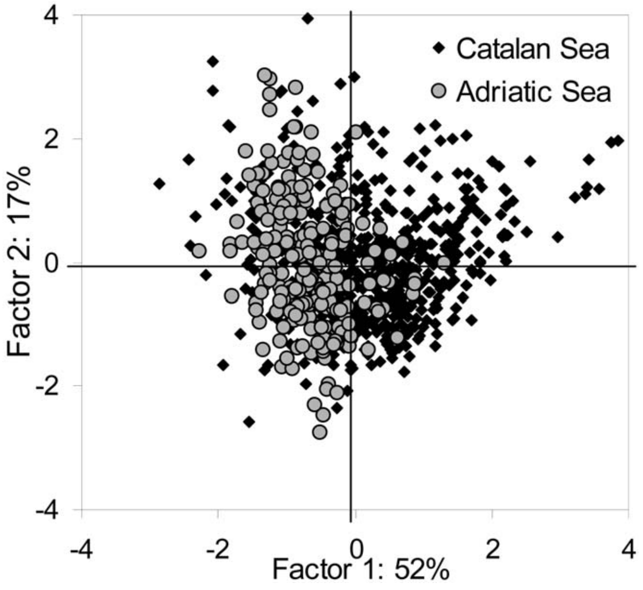

Fig. 2. Scatter plots of the schools detected in both geographical area and for echosounder, according to the two components representing environmental conditions (factor 1) and school morphology (factor 2).

the horizontal axe induced two separated clouds of points (Fig. 2), which means that the first component discriminates the two geographical areas. Concerning sonar school data, the main result is similar to the one obtained with echosounder data: morphological characteristics of schools are independent of environmental parameters. Nevertheless, the factor coordinates of the schools of each geographical area, plotted on the first plane, induced two superposed clouds of points.

3.4. Multiple analysis of variance

Results of analysis on sonar and echosounder are shown (Tables 4 and 5). The variables explaining the variance of the school length are similar in Adriatic and Catalan Seas. They regard parameters related both to the influence of the vessel (vessel speed and lateral distance to the boat) and to the vertical stratification of the water column (principally parameters related to the thermocline and the halocline). Nevertheless some differences appear. First, in Catalan Sea the most important variables of the model are: the vessel speed, the distance of schools to the thermocline or the relative depth of the thermocline and the relative depths of the first and second fluorescence peaks. In Adriatic Sea, the most important variables of the model are: the lateral distance to the boat, the distances of the schools to the halocline and to the second fluorescence peak and the relative depths of the first and second fluorescence peaks. These variables enter both in the sonar and echosounder models. Secondly, the most important difference between sonar and echosounder models is that variables related to the seabed (bottom depth, relative depth of schools and altitude) have significant influence on the length of schools recorded with the echosounder, whereas this influence is not marked on the length of schools recorded with the sonar. A consequence of this influence is a higher multiple correlation coefficient for echosounder model than for sonar model (Tables 4 and 5). However, despite the low values shown by the sonar model, statistical analysis suggests relations between the size of fish schools and vertical distribution of schools, strength of the vertical stratification of the water column and intensity of the vessel perturbation.

In order to visualize the results of the MANOVA, we drew the 2D-categorized box plots of the school mean length vs. the relative school depth, the lateral distance to the boat, and the vessel speed (Fig. 3), the distances of the schools to the thermocline, the halocline and the second fluorescence peak (Fig. 4). Three conclusions can be drawn: (i) in both areas, the higher is the vessel speed, the greater is the school length (Fig. 3c); (ii) the schools close to the surface or above the thermocline, the halocline and the depth of the second fluorescence peak are longer than those far from the surface or below the thermocline, the halocline and the depth of the second fluorescence peak (Figs. 3a and 4); (iii) in Adriatic

Table 4
Results of the MANOVA performed on sonar data. Contributions of variables to the variability of the school length in Adriatic and Catalan Seas

	Sonar				
	Sum of squares	d.f.	Mean square	F	*P*
Catalan Sea ($r^2 = 0.17$)					
Intercept	402.6	1	402.6	4993	* * *
Vessel speed	1.70	3	0.57	7.02	* * *
Distance to the thermocline	2.87	9	0.32	3.95	* * *
Relative depth of the first fluorescence peak	1.93	9	0.21	2.67	* *
Relative depth of the second fluorescence peak	2.15	9	0.24	2.97	* *
Error	40.64	504	0.08		
Adriatic Sea ($r^2 = 0.20$)					
Intercept	74.4	1	74.4	682	* * *
Lateral distance to the boat	5.39	9	0.60	5.49	* * *
Distance to the Halocline	3.60	9	0.40	3.66	* * *
Distance to the second fluorescence peak	3.09	9	0.34	3.15	* *
Relative depth of the first fluorescence peak	1.86	8	0.23	2.13	*
Relative depth of the second fluorescence peak	1.98	7	0.28	2.59	*
Error	67.06	614	0.11		

Table 5
Results of the MANOVA performed on echosounder data. Contributions of variables to the variability of the school length in Adriatic and Catalan Seas

	Echosounder				
	Sum of squares	d.f.	Mean square	F	*P*
Catalan Sea ($r^2 = 0.48$)					
Intercept	873.2	1	873.2	31904	* * *
Vessel speed	0.48	3	0.16	5.87	* * *
Relative depth of the school	1.40	9	0.16	5.67	* * *
Relative depth of the thermocline	1.05	9	0.12	4.27	* * *
Relative depth of the halocline	0.49	9	0.05	2.00	*
Relative depth of the first fluorescence peak	0.52	9	0.06	2.09	*
Relative depth of the second fluorescence peak	1.37	9	0.15	5.56	* * *
Altitude	0.96	9	0.11	3.89	* * *
Error	14.67	536	0.03		
Adriatic Sea ($r^2 = 0.37$)					
Intercept	380.8	1	380.8	7178	* * *
Bottom depth	1.01	9	0.11	2.11	*
Distance to the thermocline	1.97	9	0.22	4.13	* * *
Relative depth of the first fluorescence peak	1.59	8	0.20	3.75	* * *
Altitude	2.54	9	0.28	5.33	* * *
Error	10.93	206	0.05		

Sea, there is a negative correlation between school length and lateral distance to the boat, and this is not observed in Catalan Sea (Fig. 3b).

4. Discussion and conclusion

Few restrictions must be done regarding our database. We did not use the algorithm proposed by Diner (2001) in order to “correct” school length, because as stressed by this author, schools resulting from complex shapes and varying internal densities do not fill the conditions for the use of the algorithm, and this was the case for most of the schools of our database. Besides, as usual in fisheries acoustics, the change of settings may have a dramatic effect on the results, mostly by changing the actual sampled volume and the echo threshold. This was the case in our surveys, where some important changes in the settings were decided. Therefore, a careful check must be done prior to any analysis, to see whether the possible differences in the results (from one year to the other and/or from one acoustic device to the other) are due to the settings. The preliminary analysis of our data regarded the number and size of schools detected by each acoustic device and in each zone. We checked that the differences observed were not due to changes in the settings from one year to the other. Moreover, it appeared that the properties of each acoustic device did not allow for a global analysis of the whole dataset, and we therefore decided to perform separate analysis.

The comparison of the characteristics of schools in the two areas evidenced important differences: it appears that, observed with the sonar, schools in the Adriatic Sea are longer, tend to occupy the upper part of the water column and are detected further from the boat. In this area, the vessel showed higher sailing speed compared to the Catalan Sea.

The PCA indicated a clear independence between environmental, morphological and acoustic descriptors in each zone. The main difference between sonar and echosounder data is that environmental factors of the two zones can be discriminated only in echosounder dataset (Fig. 2).

The variability of the length of schools appears to be mostly explained by the vessel speed, the lateral distance to the boat and the thermocline and halocline depth. In addition, echosounder schools’ length is sensitive to parameters related to the bottom depth and to variables related to the bottom, which is not the case for sonar schools. This is very likely due to the range of the device which enables the detection of deeper schools in comparison with the sonar. In this respect, the echosounder allows the analysis of the depth effect on school characteristics, which is not the case of the sonar, as this device has a much more limited vertical range. On the other hand, the lateral range of the sonar allows for the analysis of the boat effect on schools size (as evidenced by the multiple analysis of variance). Therefore, our results show in which way these two devices can be complementary.

The PCA indicated that the components were explained by distinct sets of descriptors. Nevertheless, this classification does not allow for the discrimination of sonar schools between the Adriatic and Catalan Seas, despite their morphological differences and does not allow the relation of morphological differences of echo-sounder schools between the Adriatic and Catalan Seas with the differences of their environmental-related factors. These results are similar to those obtained by Coetzee (2000) on the sardine schools along the South-African coasts. This suggests that variability of school size is governed by specific factors not taken into account in our analysis. These factors could be related to the physiological status and motivation of individuals, such as feeding motivation (Mackinson et al., 1999) or to the species composition of schools and size of fish. These behavioural and biological characteristics imply different capabilities of reaction and different types of internal organization in terms of structural homogeneity, minimum approach distance or

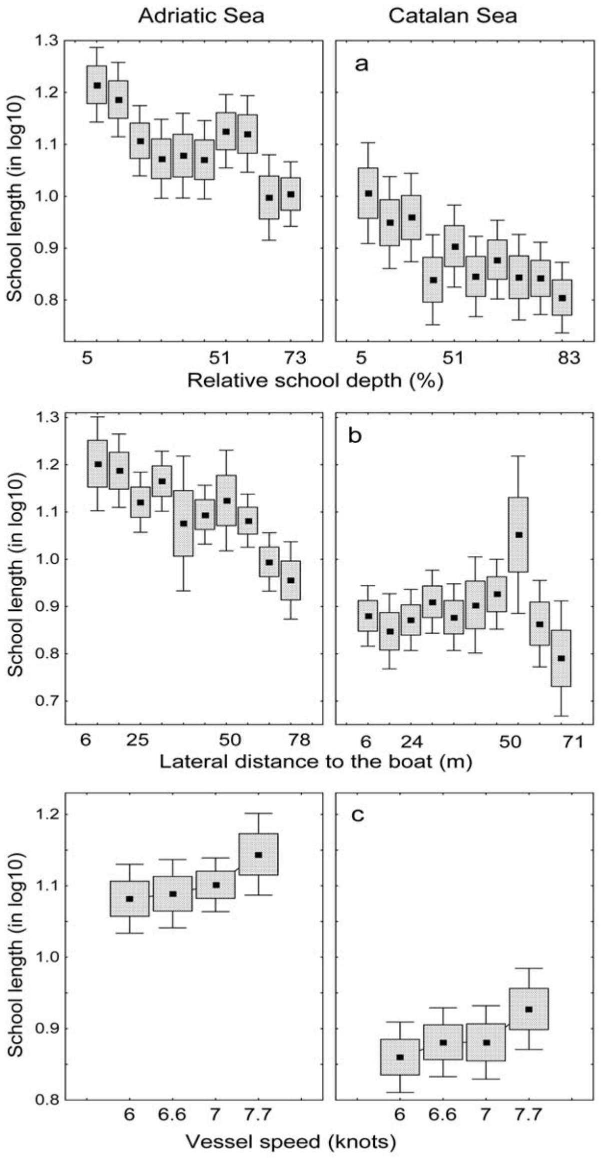

Fig. 3. Categorized box plots of the school mean length vs. the relative school depth (a), the lateral distance to the boat (b) and the vessel speed (c).

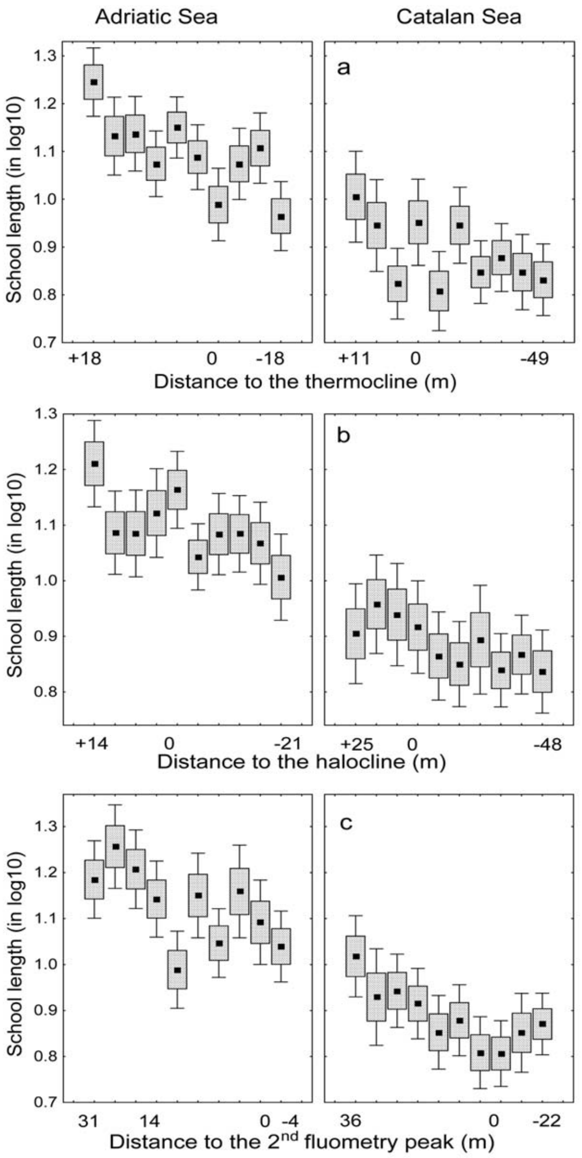

Fig. 4. Categorized box plots of the school mean length vs. the distance of the schools to the thermocline (a), the distance of the schools to the halocline (b), the distance of the schools to the second fluorescence peak (c).

swimming speed and polarization, which have positive relationships with school size (review in Hoare et al., 2000). Near environmental field conditions such as the presence of predators can also influence the behavioural dynamics of pelagic schools and contribute to the variation of their size (Swartzman et al., 1994; Massé et al., 1996; Pitcher et al., 1996; Misund et al., 1998). This analysis is in agreement with those done by other authors (review in Fréon and Misund, 1999), and confirms the necessity to go deeper in to the behavioural observations at micro-scale.

The difference in the length of schools between Adriatic Sea and Catalan Sea, is the most surprising result, since this dimension represents the horizontal dimension of the schools along the vessel track. No bias was found regarding the beam correction, vessel speed estimation and sonar settings for image acquisition. According to several authors, environmental factors such as temperature, bottom depth (Swartzman, 1997), or biological factors such as species and interactions between species (Massé et al., 1996) may explain variations observed in morphological parameters of schools. Neural networks developed by Haralabous and Georgakarakos (1996), or the linear discriminant model approach proposed by Scalabrin et al. (1996) take into account school descriptors extracted from echo-integration data. Our analysis validates these works, however, we suggest an alternative to the hypothesis of a direct influence of these factors on school morphology: the variation of school length and consecutively the variations of the correlated dimensions in 2D and 3D are first related to the intensity of the avoidance reaction in front of the vessel and this effect can be reinforced depending on the environmental conditions.

Our investigation focuses on the differences, between two areas, of the mean school length measured by the sonar and

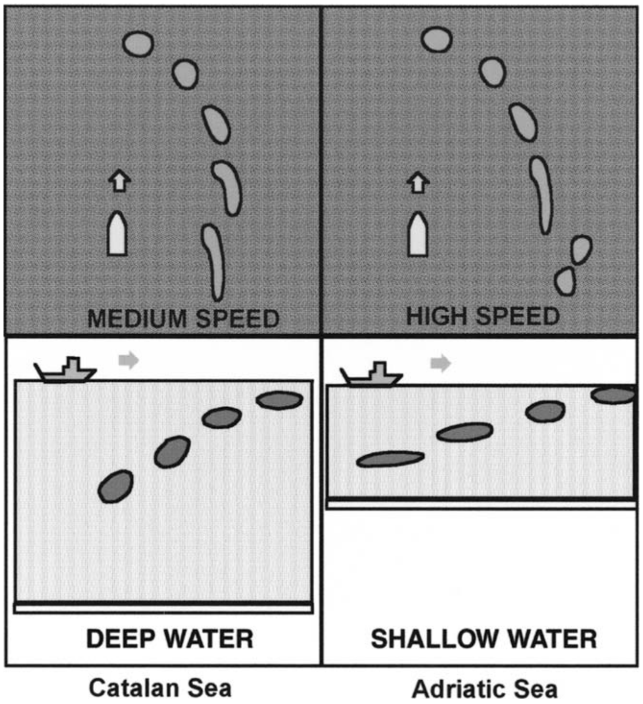

Fig. 5. Schematic diagram of the behavioural mechanism, that may explain differences of school length and elongation between the Catalan and Adriatic Seas (see text).

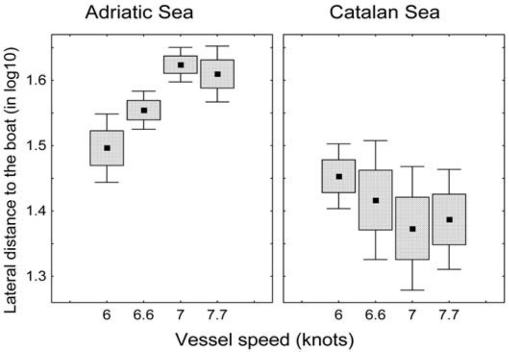

Fig. 6. 2D categorized box plots of the mean lateral distance to the boat vs. the vessel speed.

the echosounder. The MANOVA shows that, depending on the geographical zone, the school length may be explained alternatively by the schools' position in the water column, their lateral distance to the boat, the vessel speed and the vertical stratification of the water column. Due to the high variability of the measured values, the sonar model applied on Adriatic and Catalan database did not explain more than 20% and 17% of the variation observed. However, the echosounder model and the analysis of the box plots (Figs. 3 and 4) confirm the results of the sonar model and allow for proposing a behavioural model of avoidance (Fig. 5). School avoidance occurs both in the horizontal and vertical plans (Olsen et al., 1983; Soria et al., 1996; Misund et al., 1998; Misund and Coetzee, 2000). In the absence of vertical constraints, fish far away from the boat are disturbed by the noise of the vessel and react by polarizing their swimming. This polarization induces a fast compression and enables the fish to avoid the vessel laterally and vertically by a fast and coordinated movement of the school (Pitcher and Parrish, 1993; Fréon et al., 1993; Soria et al., 1996). We assume that under shallow water conditions and environmental constraints related to the vertical distribution of temperature and/or salinity, vertical movement of fish is restricted. Since the mean bottom depth, the halocline depth and the depth of the second fluorescence peak are lower in Adriatic Sea than in Catalan Sea (Table 2), pelagic fish schools in Adriatic Sea tend to stay in subsurface area and disturbed schools escape rather in the horizontal direction than in vertical one. Fish are forced both by the vertical constraint and by the necessity of keeping visual contacts and minimum inter-distances in order to maintain the cohesion of the group. After the works of Radakov (1973), Breder (1959), Shaw (1978), Fréon et al. (1992) and Soria (1994), we assume that these constraints induce a stretching of the schools in the field of the lowest gradient of disturbances. Since this field is parallel to the vessel path, the school elongation is expected to be greater than in non-disturbed conditions. This effect can be amplified by vertical restrictions, such as the depth of the halocline and/or the depth of the thermocline, which could play the role of horizontal fences. This hypothesis is supported by the environmental characteristics of the two prospected zones during our sampling periods: in September, Northern Adriatic Sea shows a strong thermal stratification (Russo and Artegiani, 1996), whereas the stratification is still weak in the Catalan Sea at the beginning of spring, both for temperature and salinity (Castellón et al., 1985). Following the schematic pattern of gradual reaction of fish, the more they detect external stimuli, the stronger is their reaction. Then there is evidence that this reaction is proportional to the vessel speed (Fig. 3c). This hypothesis is validated by the analysis of the relationship between the mean lateral distance to the boat and the vessel speed (Fig. 6). The vessel speed has no effect on the lateral position of schools in Catalan Sea, while in Adriatic Sea the highest lateral distances to the boat were recorded for schools, detected at the highest vessel speeds. Nevertheless, above a threshold of disturbance, the cohesion of a school cannot be kept and the schools might split. This last hypothesis could explain the highest number of small schools observed far from the boat in Adriatic Sea. An alternative explanation is that schools furthest from the vessel are relatively undisturbed and then fish gather again and form small schools in length with a more regular shape (Fig. 7).

The above results allow to improve our knowledge on the vertical and lateral avoidance patterns of schools in relation to their position in the water column, and allow for describing the influence of external factors on school characteristics. After our results, it seems very hazardous to estimate fish biomass from size of schools. Nevertheless, we need more information to be able to quantify the impacts of avoidance reaction on size of schools and biomass estimates. In order to establish the relations between the intensity of factors, like

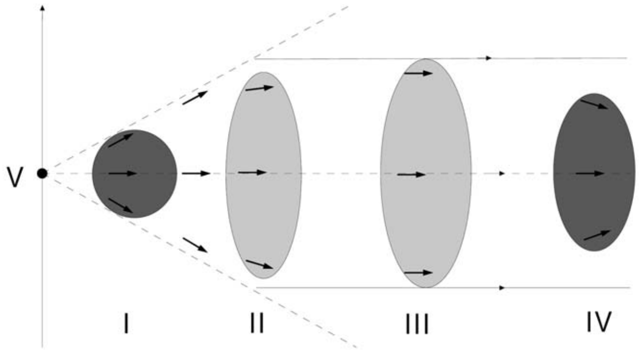

Fig. 7. Diagram presenting the dynamics of a school avoiding a source of noise. In this scheme, we have identified three fish represented by darts, at two sides and in the centre of the school. Dotted lines represent the noise vectors; solid lines the maximum length of the school. (a) At the beginning of the noise emission, the school is circular, each fish tends to escape, following the line of maximum noise avoidance (i.e. in direct opposition to the source). (b) The inter-individual distance increases; if the stress is not too strong, the gregarious tropism will allow the fish to maintain contact. The volume of the school has increased, i.e. fish are on an average at larger inter-individual distances from each other. (c) The inter-individual distance reaches the maximum and the school is not stretching anymore; if the dispersal effect of the noise is stronger than the gregarious behaviour of the fish, the school will split. Otherwise, it will maintain this anisotropic shape until the noise becomes lower and fish may closely aggregate again. (d) The school is at enough distance from the source of noise and goes back to its original shape, i.e. roughly circular. (e) Vessel route (source of noise). This example is presented as if the vessel was static and began to transmit noise close to the school. The reality is slightly different, due to the slow approach of the vessel, all schools already present an elliptical shape when the vessel approaches.

the bottom depth or the vessel speed and the intensity of the stretching behaviour of schools, more investigations are required. Moreover, environmental factors like the thermocline depth or the halocline depth and the chlorophyll concentration seem to have an effect on this behaviour and should systematically be taken into account when observing schools. Several scientists have noted that the aggregation of schools in clusters is a key factor, affecting both precision of acoustic surveys and catchability in the fishery (Fréon and Misund, 1999; Booth, 2000; Petitgas et al., 2001). From our point of view, the spatial dynamics of fish at a micro-scale (e.g. at the level of the school), could be a key factor affecting both precision of acoustic surveys and catchability in the fishery, at the same level of importance than the dynamics of clusters.

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Annex 1. List of school descriptors of the echosounder database (see Weill et al., 1993)

Descriptor (abbreviated)	Signification and unit	Calculation method
H	Maximum height (m)	
L	Maximum length (m)	The beam pattern effect on length estimation was taken into account by removing $2R \tan(\alpha/2)$ of the maximal horizontal length, where R is the depth of the gravity centre of the school; and α the beam angle (Johannesson and Losse, 1973).
Elong	Elongation	Ratio maximal length (L) to the maximal height (H).
Ar	Area (m^2)	Ar = $\pi/2(HL)$ assuming that the schools have an ellipsoid shape.
RO	Roughness	RO = 2 ln(Per/4)/(ln(Ar). RO is close to 1 for schools having a very smooth outline shape and close to 2 for the very irregularly shaped schools.
Per	Perimeter (m)	Corrected from the beam angle error.
MinDep	Minimum depth (m)	Distance between the sea surface and the upper limit of the school.
RelDep	Relative depth (m)	RelDep = 100(MinDep/depth), where: MinDep is the minimum depth of the school (distance between the water surface and the upper limit of the school). Depth is the bottom depth.
σ_s	Integrated back-scattered energy (relative value)	It is the sum of squared echo amplitude computed with the samples used to define the school detection. This value is proportional to the total biomass of the school. $\sigma_s = 1/\varepsilon \sum_{j=1}^{N} S_j \quad T_j \sum_{i=1}^{n} V_{ij}^2$ where ϵ = number of samples per meter, N is the number of pings over the integrated school length, n is school sample number integrated for each ping, S is vessel speed (ms^{-1}), T is ping period in seconds, V is the integrated sampling amplitude, measured in volts.
	Volume reverberation index (dB m^{-3})	Sv = 10 log(σ_s/A), where A is the school area (m^2). This value is proportional to the mean density of the school.

Annex 2. List of school descriptors of the sonar database

Descriptor	Signification and unit	Calculation method
H	Maximum height (m)	
L	Maximum length (m)	The maximum horizontal length of each school is the maximum dimension of the school along the vessel path. It is estimated using parameters of image acquisition (Gerlotto et al., 1994). The same beam correction applied on the echosounder school lengths was used
W	Maximum width (m)	Perpendicular to the vessel path
Elong1	Elongation 1	Ratio maximum length (L) to the maximal height (H)
Elong2	Elongation 2	Ratio maximum length (L) to the maximal width (W)
Elong3	Elongation 3	Ratio maximum width (W) to the maximal height (H)
Ar1	Area 1 (m^2)	$\pi/2(LH)$, calculated assuming and ellipsoid form of the school
Ar2	Area 2 (m^2)	$\pi/2(LW)$, calculated assuming and ellipsoid form of the school
Ar3	Area 2 (m^2)	$\pi/2(WH)$, calculated assuming and ellipsoid form of the school
V	Volume (m^3)	$V = 4/3\pi(HWL/2)$, calculated assuming and ellipsoid form of the school
MinDep	School depth	Distance between the sea surface and the upper limit of the school
RelDep	Relative depth	RelDep = 100(MinDep/depth)
LatDiB	Lateral distance to the boat (m)	Horizontal distance from the school centre to the vertical line under the boat

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