

# Diel variability of school structure with special reference to transition periods

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Pelagic fishes generally disperse at dusk and aggregate in schools at dawn. The dynamics (duration, variation in school number, and characteristics) of these two behavioural processes have been studied during a 26 h survey in a small area of high fish abundance in the Catalan Sea (Spain). The dynamics of aggregation and dispersion were investigated using a dual-beam vertical echo-sounder (BioSonics) connected to a special school integrator software package (INES-MOVIES-B) which estimates school parameters in terms of size, geometry, and density. This study shows that, during the night, fish dispersion is limited and schools can still be observed. They are characterized by a highly skewed distribution of the cross-sectional area (many small schools plus a few medium and large schools), low values of packing density and biomass, and irregular shape, while during the day there are only a few schools which have a lower variability of the area, high values of packing density, and a more regular shape. The dynamics of schooling are different between dawn (fast aggregation) and dusk (slower dispersion).

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## Introduction

Schooling behaviour has been studied since the beginning of this century, but most of the work deals with the description of fish schools in tanks or aquaria (see the review in Pitcher, 1993). Field studies began in the 1970s, with the development of acoustic methods (MacLennan and Simmonds, 1992). Nevertheless, very little work has been done on the temporal dynamics of aggregative behaviour, except to show that pelagic fishes generally disperse at night and aggregate in schools during the day. Blaxter and Holliday (1969) reviewed the stability of shoals and noted the view of most authors that schooling behaviour ceases in darkness. Azzali *et al.* (1985) proposed a model of the aggregative behaviour for clupeoids, mainly from a theoretical standpoint, and Fréon *et al.* (1993) studied the diel variability of acoustic abundance estimates, concluding that the aggregative behaviour and the lateral avoidance of schools during the day was responsible for substantial bias and error.

A big pelagic school can hold several hundred thousands of fish in a limited volume (Fig. 1a). How long does it take for so many individuals to aggregate and disperse? Other social animals display a diel aggregative pattern (e.g. ants, bees, and birds), but they have a meeting point, unlike pelagic fish which have a habitat

but no “home”; they must identify and join a moving target: the school. This paper describes the diel variability of schooling from *in situ* observations using a vertical sounder together with an automatic school identification method.

## Materials and methods

We used a 38 kHz dual-beam sounder (BioSonics model 102) with a pulse duration of 0.4 ms and a ping rate (PR) of  $2\text{ s}^{-1}$ . The narrow and wide beam angles at  $-3\text{ dB}$  points are  $\alpha=10^\circ$  and  $\alpha'=25^\circ$  respectively. The INES-MOVIES-B system (Weill *et al.*, 1993) connected to the sounder consists of a data logger combined with an echo-integrator which enables integration by school and calculates several school descriptors. In this paper we have used: the deviation (Qd), which is the integration of the backscattered energy in  $\text{mV}^2$  proportional to the ensonified school biomass; the volume backscattering coefficient ( $R_v$  in  $\text{dB m}^{-3}$ ), which is proportional to the log of the school internal density; the cross-section area (A); the elongation ( $E=\text{length/height}$ ) and the fractal dimension (FD), which is computed from A and the school perimeter P as  $\text{FD}=2 \ln(P/4)/\ln(A)$ . FD is close to 1 for schools which have a smooth outline and close to 2 for very irregularly shaped schools.



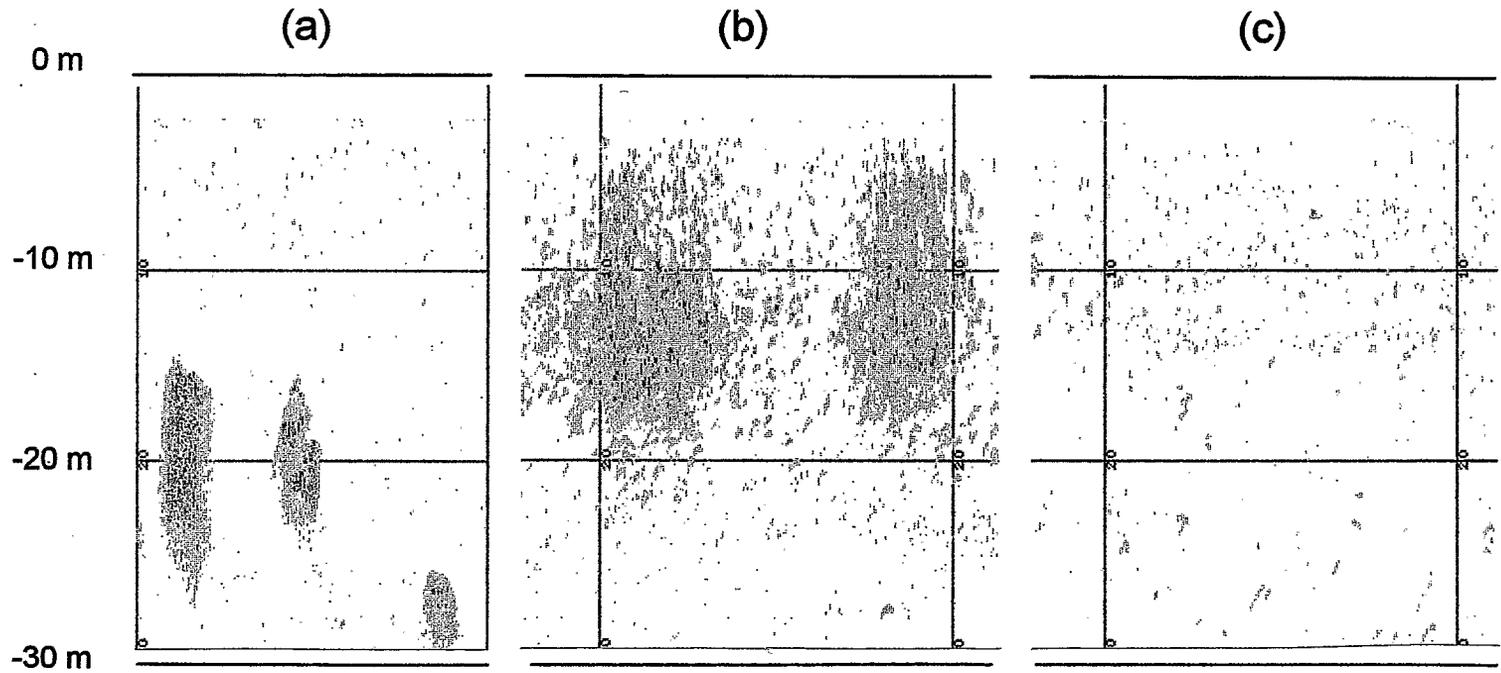


Figure 1. Example of three echograms where the interval between the vertical lines corresponds to 0.1 nmi: (a) typical day schools (1027 GMT); (b) layer including two large schools (2028 GMT; similar echograms are observed all night long); (c) layer of dispersed fish during the night (0045 GMT).

From 21 to 22 May 1994, an experiment conducted by RV "Garcia del Cid" along the Spanish Mediterranean coast was designed to study the diel variability of fish gregariousness, removing as far as possible the spatial variability effect. It was performed in a small area, centred on 40°08'N and 00°30'W, where the bottom depth is less than 40 m and where fish concentrations had been previously observed. The vessel followed a rectangular track of 1.5 × 2.5 nmi at four knots over 26 h (13 rectangles of 2 h each; with only a 20 min interruption at 0510 h). Two hauls made on this concentration 4–5 d later, by night and by day respectively, indicated the dominance of small (13 cm total length) *Sardina pilchardus* (Walbaum), which account for 80% and 88% in the two catches, and 18 cm *Sardinella aurita* (Valenciennes). During the experiment, sunrise was at 0445 GMT and sunset at 1909. The moon was in its last decreasing quarter, setting at 0230.

During the playback, MOVIES-B was set with the following thresholds for school identification: successive transmissions (N) > 3, signal digital sampling units (height 10 cm) > 100, and energy > 100 mV<sup>2</sup>. Moreover, during post-processing, we discarded schools with Rv less than -44 dB, which is the lowest Rv value observed by day. Using the Foote (1987) target-strength (TS) equation for clupeoids (TS = 20 log L - 71.9, where L is the body length in cm) -44 dB corresponds to a sardine school having a packing density less than 3 fish m<sup>-3</sup>. These thresholds were empirically chosen to ignore individual fish echoes, tiny patches, or dense layers. Since MOVIES-B does not take account of the beam pattern, we first applied the usual beam correction (Johannesson and Losse, 1977) by removing 2r tan(α/2) from the school length measurement, where r is the depth of the school centre of gravity. Then another condition was added in order to eliminate from the data echoes that were smaller than 1 m long the number of transmissions associated with the school must be higher than the number of transmissions required to cover, at speed V, a distance equal to the beam width at the minimum school altitude (AMin), plus 1 m: N > 1 + (2 AMin tan(α/2)) (1/PR) V. In order to be more conservative, and to maintain an acceptable precision on the other descriptors (A, E, FD), it was empirically decided during post-processing to discard schools with a cross-sectional area less than 5 m<sup>2</sup>.

Despite the careful choice of these thresholds, corrections and filtering, it was obvious that we could not assume that all the objects remaining in the database corresponded at least to one of the common definitions of a school, which are based on the criteria of mutual attraction, polarization, or fish decision (Pitcher, 1993). Instead of schools, these objects might better be considered as simply dense aggregations (especially during the night), which we call "acoustic schools". The

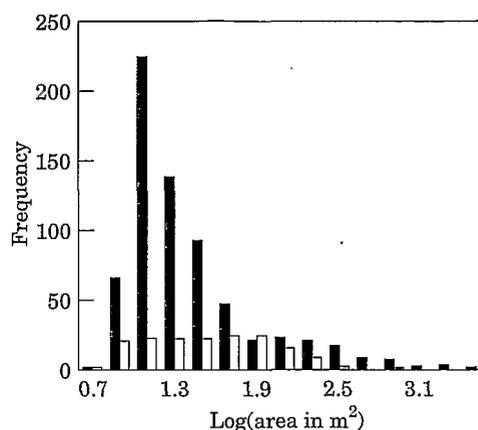


Figure 2. Difference between day (0400 to 2000 GMT; open bars) and night (2000 to 0400 GMT; black bars) frequency distribution of school area estimates (log-transformed) from MOVIES-B connected to the echosounder. n=848.

methodology is mainly intended to quantify the diel changes in patchiness.

The main school descriptors were analysed by multiple analysis of variance (ANOVA) for unbalanced design. The independent class variables were the time, subdivided in 1 h classes (lower class limit of HOUR<sub>i</sub>, i=1→24) and the side of the rectangle (SIDE<sub>j</sub>, j=1→4). The least-squares means (LSMEANS of the General Linear Model procedure in the SAS system) were adjusted for the effect of other terms in the model. The models used were of the form:

$$Y_{ij} = m + \alpha_i + \beta_j + \varepsilon_{ij}$$

where Y is one of the school descriptors (or its log value in the case of A and Qd), m is a constant, and the  $\varepsilon$  are residuals.

## Results

### School cross-section area

The initial number of schools identified by MOVIES-B was 3845, reduced to 847 after filtering. The distribution of the day-time acoustic schools is close to log-normal, while for schools at night it is skewed more toward large values (Fig. 2). Surprisingly, the diel variation of the mean log-transformed area does not show a clear pattern, and the dependent variable HOUR has a low contribution to the total variance in the ANOVA (6%, while SIDE contributes only 2%). This is due to the difference in skewness between day and night values, which appears in Figure 3, especially at HOUR<sub>i</sub> (i=0–2; 20–22) where outlier points are observed.

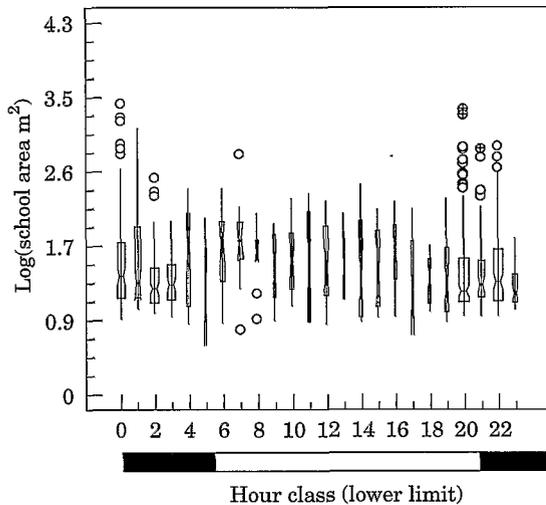


Figure 3. Box-and-whisker plot of the school area (log-transformed) from MOVIES-B over time. The central box covers the middle 50% of the data, between the lower and the upper quartiles. The width of the box is proportional to the square root of the number of observations. The notch corresponds to the width of a confidence interval for the median. The "whiskers" extend out to the values that are within 1.5 times the interquartile range. Outliers are plotted as separate points.  $n=848$ .

### Number of schools

The temporal variability of the number of schools per nmi clearly indicates a large day-night difference (Fig. 4a). The number of schools per nmi decreases suddenly at HOUR<sub>4</sub> and increases more progressively at HOUR<sub>20</sub>. The 2 h periodicity is due to the fact that the boat surveys the same location every 2 h (with an exception at HOUR<sub>5</sub> when the boat was stopped for 20 min).

### School biomass and internal density

The ANOVA results for Rv (proportional to school density) and Qd (proportional to the school biomass) explain 46% and 31% of the variance, respectively. In both cases the HOUR effect (37% and 25%, respectively) is more important than the SIDE effect. As expected, the corrected means (LSMEANS) of these two variables are extremely high during the day when the mean density of sardine schools reached 58 fish  $m^{-3}$ , and low during the night when the mean density decreased to 4 (Fig. 4b). Moreover, the duration of the temporal change is shorter in the morning (1 h) than in the evening (at least 2 h). Despite this clear diel variability of the mean values, the detailed analysis of the Qd and Rv distributions shows that during the night some large schools (area > 400  $m^2$ ) have a biomass similar to the day-time schools, but they usually have a lower Rv. Nevertheless,

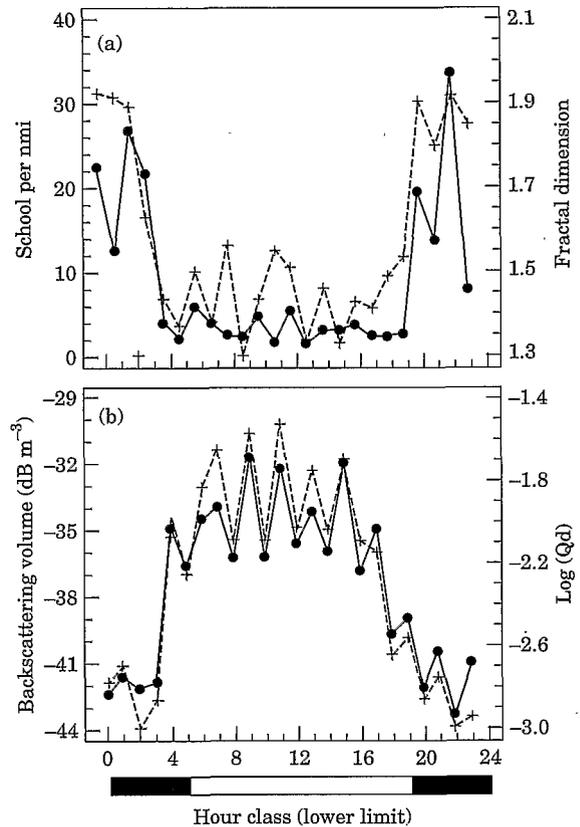


Figure 4. Diel pattern of the number of schools and school descriptors estimated by MOVIES-B. Black bars represented the night and the open bars the day. (a) Number of schools per nautical mile (solid line) and least squares mean of the fractal dimension (broken line); (b) least squares mean of the volume backscattering coefficient (solid line) and of deviation ( $\log(Qd)$ ; broken line).

the density in these large night acoustic schools (Fig. 1b) is from two to three orders of magnitude ~~lower~~ <sup>higher</sup> than that of the dense layers of dispersed fish (Fig. 1c), whose Rv values ranged between -52 and -65 dB.

### Fractal dimension and elongation

The ANOVA on the fractal dimension explains 58% of the total variance, and once more the HOUR effect is predominant (46%). The LSMEANS values of FD also display a clear diel pattern with an abrupt decrease before sunrise and a slower increase 1 h after sunset, which indicates that the school shape is more regular during the day than at night (Fig. 4a). The mean school elongation is also significantly higher ( $p < 0.01$ ) during the night ( $E=4.4$ ) than during the day ( $E=3.0$ ), even though the diel pattern of E is not as clear as for the other school descriptors.

## Discussion

This study indicates that during the night fish dispersion is limited and aggregations are still observed. They are characterized by a highly skewed distribution of the cross-sectional area (many small schools plus a few medium and large schools), low values of  $R_v$  and  $Q_d$ , high values of  $FD$  and  $E$ , while during the day there are only a few schools with a lower variability of the area, high values of  $R_v$  and  $Q_d$ , and low values of  $FD$  and  $E$ . Moreover, the dynamics of schooling are different between dawn (fast aggregation) and dusk (slower dispersion). The diel variability in school numbers and descriptors suggests that daylight is detected by fish long before sunrise owing to their efficient crepuscular vision. This time period should vary according to the season and the latitude (around 1 h in the case of this survey). In the evening, however, the fish react immediately after sunset. The influence of moonlight is not obvious from our data.

Despite the fact that our estimates of  $TS$  and  $R_v$  suffer from the usual technical limitations (MacLennan and Simmonds, 1992), the ratio of mean density inside day-time schools to the mean density inside dense layers during the night can be estimated accurately. Nevertheless, the acoustic data indicate that during the night most of the fishes are still aggregated (we note that 3845 acoustic schools were initially identified). It is likely that during the night these patches still collect isolated fish and could be better described as aggregations. For many years, a generally accepted criterion for school definition was the fact that fish are mutually attracted (Pitcher, 1993). This is obviously the case during the day, but what happens after sunset?

The three main mechanisms enabling schooling are visual contact between individuals, especially at medium distance, local pressure change due to tail movement at short range, and probably auditory cues at long range (Pitcher, 1993). Only the range of vision shows a diel variation even though it is seldom negligible even at night, due to the moon, starlight, or bioluminescence. The large difference between day and night schooling density is due to a change in the volume occupied by the fish, and probably not to an abrupt change in the fish biomass or species in the area. The difference in the densities and shapes of the spatial structures between day and night can help to elucidate the behavioural processes used by the fish when schools form or disperse.

We suggest that the fish swim randomly at dusk, which produces a slow expansion of the school starting necessarily at the periphery, where free space is available. This explains the slow decrease in the volume backscattering coefficient and the deviation in our data (Fig. 4b). At dusk, small day-time schools probably disperse rapidly to form layers of dispersed fishes or to remain in small patches. Our data do not show whether

the fish inside patches are mutually attracted and remain a long time together, or whether they just concentrate temporarily on a source of food. Large schools seem to need more time to disperse, and they probably correspond to the dense layers with large "nuclei" (identified as large and relatively dense schools by MOVIES-B) surrounded by small schools and dispersed fish (Fig. 1b). On some occasions (in the presence of bioluminescence, moonlight, or starlight), this dense nucleus can persist throughout the night. Some purse-seine fisheries take seasonal advantage of this night aggregation behaviour (Marchal, 1993; Fréon *et al.*, 1995).

At dawn, the visual range rapidly increases and the fish can actively aggregate in a short time. The dense nuclei of the largest day-time schools, which persisted throughout the night, are immediately able to form a relatively large school in the morning. Individuals already in "slack" small schools are able to concentrate rapidly and to join neighbouring schools. Finally, fish which are totally dispersed in layers at the end of the night might form small schools and/or join other existing schools. The model of Azzali *et al.* (1985) suggests that, at dusk, the schools dissolve suddenly, while at dawn the reforming of the schools takes longer. This is contrary to our observations. We believe that, from a behavioural point of view, dispersion at dusk is mainly passive, while aggregation before dawn is mainly active.

These results reinforce the view that abundance estimation by acoustic survey is more accurate during the night (excluding the twilight periods) than by day, except in those areas where the echoes from plankton are too strong at night. Nevertheless, fish distribution at night remains highly contagious, which can still introduce substantial bias in the estimates (Fréon *et al.*, 1993). Moreover, the use of school descriptors for automatic species identification would be complicated by diel variability.

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