Changes in school structure according to external stimuli: description and influence on acoustic assessment[1]

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ABSTRACT

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The study of the internal school structure and behaviour of pelagic fish provides interesting information in relation to acoustic surveys, especially when comparing the undisturbed structure with the structure observed beneath a vessel passing over a school. The methodological approach involves in situ observations and combines acoustic and visual (aerial and underwater) techniques.

The internal school structure is heterogeneous, including vacuoles, and this structure changes when the school is overpassed by a vessel during the day. In this case compression of the upper layer of the school is observed. The influence of this school structure on the variability of the density estimation has been studied. For the subsurface schools, the usual rate of sampling may be too low for some heterogeneous schools. Other consequences of the school structure on acoustics are discussed.

INTRODUCTION

The structure of a fish school can generally be described by three parameters: (1) the mean density of the whole school; (2) the arrangement of individual fish inside this structure (e.g. homogeneity of the density, variations in the relative position of the fish, variation in the relative and absolute tilt angles); (3) the external shape of the school.

These parameters are governed by numerous factors, either internal (i.e. relative to the fish itself, such as species or maturation stage) or external. These external factors can be divided into two subgroups: environmental con-

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[1]This paper is mainly based on two talks which were given at the ICES meeting held in Bergen in 1988 (Fréon and Gerlotto, 1988; Gerlotto and Fréon, 1988).

ditions (e.g. temperature, light intensity, availability of prey), and external stimuli such as visual or auditory stimuli coming from a natural predator or from a vessel.

All these internal and external factors interact in a complex way; therefore modelling school structures and behaviours — or, generally speaking, pelagic fish behaviour — represents a challenge, the answer to which unfortunately is at present out of our reach. This paper intends to present information on changes in the structure and behaviour of tropical pelagic schools in relation to two sources of external stimuli: predator and vessel.

This information, even though representing only a few pieces of the puzzle, is interesting in the case of acoustic surveys because the school characteristics may have an important influence on the results, as they may introduce some biases and errors in the biomass estimation or in species identification.

Undisturbed structures of wild schools were compared with disturbed ones, when a research vessel or the shadow of an aeroplane is passing over a school. The methodological approach involves in situ observations and combines visual and acoustic techniques. Some hydroacoustic observations were carried out from a small dinghy or from a sailing-boat using sails and motor alternately, and some others from a research vessel. Visual observations, both underwater and aerial, were also made. Most of the experiments were performed in the Eastern Caribbean, the others in West Africa; all of them concern small tropical clupeoids.

MATERIALS AND METHODS

Hydroacoustic observations

Three sets of observations were recorded and processed. The first two sets were obtained using a Simrad EY-M portable sounder (70 kHz) with a narrow beam transducer (11° at -3 dB point), and the data recorded on a portable Digital Audio Tape recorder (DAT, Sony). The equipment was powered by a 12 V battery; no electric plant was used in order to limit the noise. Later, in the laboratory, the signal was processed for each individual transmission using the echo integrator AGENOR with narrow depth integration intervals (1 m or 1.4 m). The third set of observations was obtained using a Simrad EKS echo sounder (120 kHz) with a hull-mounted transducer (10° at -3 dB point); the accessory equipment was identical.

The first set of hydroacoustic observations is called 'drifting observations' in this paper. These observations were made from a drifting dinghy; the transducer was installed starboard, 50 cm below the surface. The dinghy was stopped ahead of the school as observed at the sea surface (Fréon and Gerlotto, 1988). Several schools belonging to three different tropical sardine spe-

cies were recorded: *Sardinella aurita* off Venezuela, *Sardinella maderensis* off Cameroon and *Harengula clupeola* off Martinique (French West Indies). Only one example of each species is presented in Fig. 1. The data from each transmission were integrated separately. School A was recorded for 87 s using a high sampling rate (180 transmissions min^{-1}). All the other schools were
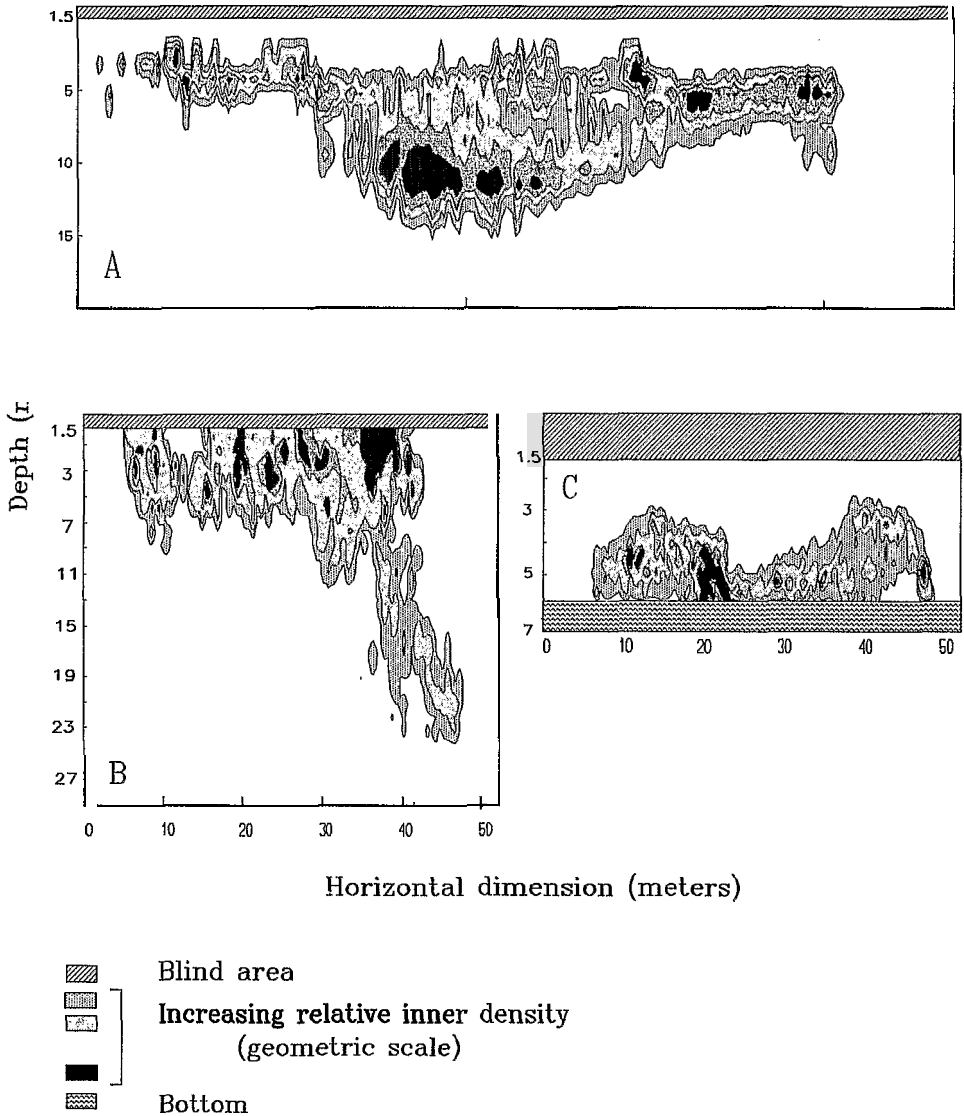

Fig. 1. Internal density structure in some undisturbed tropical pelagic schools (vertical cross-sections): (A) *S. aurita* (Venezuela), (B) *S. maderensis* (Cameroon), (C) *H. clupeola* (Martinique).

recorded using a more usual sampling rate (90 transmissions min^{-1}). Analysis of the internal structure of schools using acoustics must be approached cautiously. An individual sample has to be considered as being drawn from a distribution of possible values. Therefore the figures represent the results after smoothing the values from three successive transmissions.

The second set of observations is called 'stress observations'; these were obtained using two similar approaches. In the first, a dinghy, equipped as previously and towing a lure (a 60 cm bonito) at 50 m behind it, overpassed several times the same school of *H. clupeola* in Martinique. Several sets of observations were recorded at different periods and one typical result is presented here. In the second approach, a 16 m overlength sailing-boat, with 116 h.p. inboard diesel motor, was used off Venezuela. The transducer was installed starboard at 7 m from the stern and at 1.5 m below the surface. A single school of young *S. aurita* was overpassed three times consecutively at intervals of a few minutes. This surface school was initially detected by sight and overpassed at 1.5 knots using sails the first time (in fact, as the wind was very weak, the motor was also used for propelling the boat and it was stopped around 100 m before reaching the school). The second time the school was overpassed, the motor was running at 800 rev min^{-1} (about 3.5 knots), and the third time at 1400 rev min^{-1} (about 6 knots). Because of the impossibility of encountering these favourable experimental conditions again, this observation was not repeated.

The third set of observations ('survey observations') was made by the R/V Capricorne (46 m overall) during conventional echo surveys off Venezuela. They concern mainly *S. aurita*.

Visual observations

A school of *H. clupeola* was observed and photographed during five 1 h surveys (at a few months' interval) in a bay off Martinique, simultaneously underwater by a swimmer and from an ultralight aeroplane flying at an altitude set between 60 and 90 m. Although during the last 4 days of the survey acoustic observations were performed at the same time, these sets are regrouped under the single name 'visual observations'. The schools of *H. clupeola* are usually small compared with those of other clupeoids (from 1 to 5 tons). A Nikonos V camera with a 28° lens was used for the underwater sights and a reflex camera with a 100–200 mm zoom and a polarizing filter was used aboard the aeroplane. In both cases 400 ASA films were used. The aerial pictures, taken more or less vertically above the school, are used for estimating its surface. The water transparency and the shallow depth of the area allowed us to observe the whole water column. The size of the swimmer gave the scaling factor.
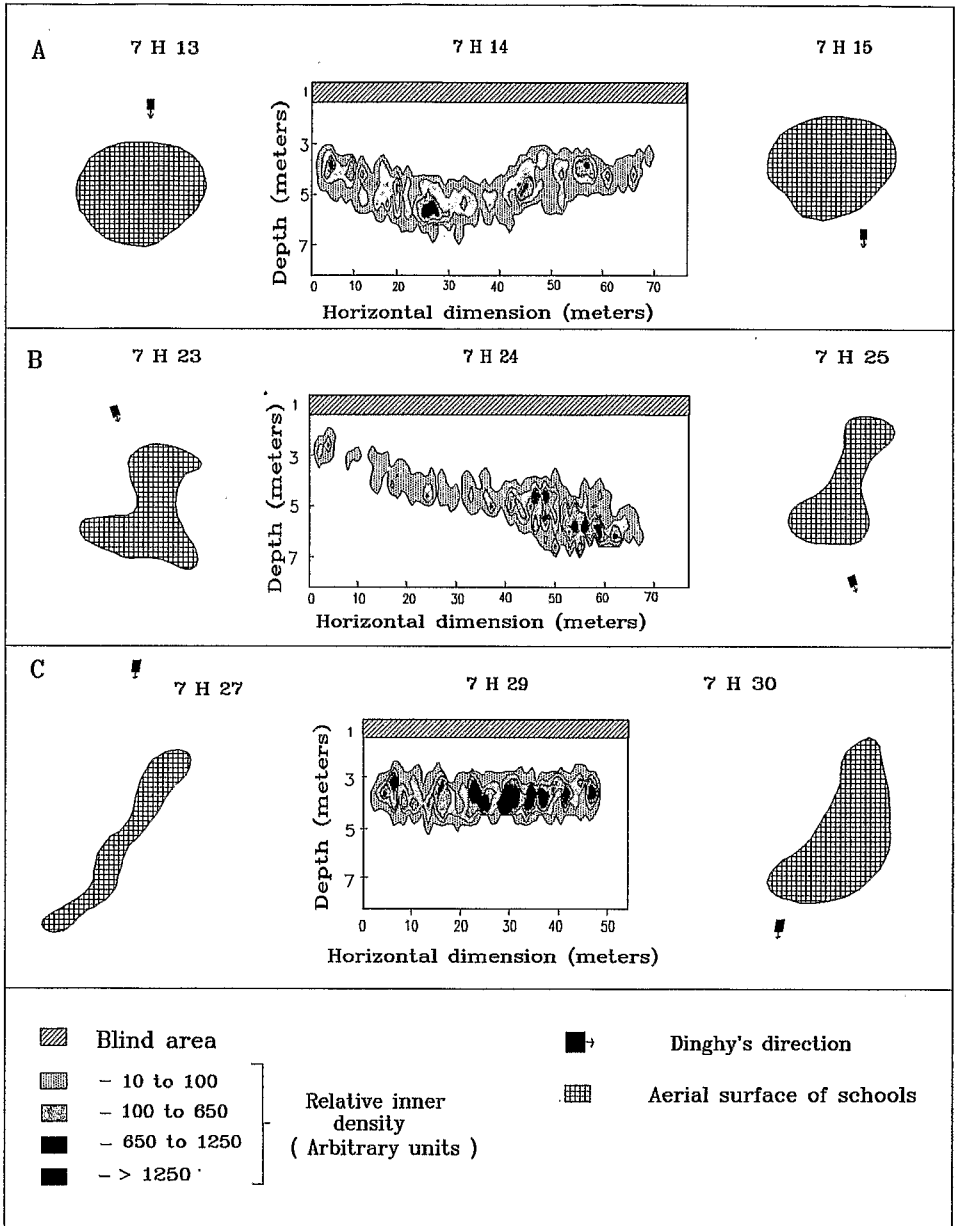
Fig. 2. Internal density structure (acoustic vertical cross-sections) and surface (aerial observation) of the same *H. clupeola* school overpassed three times by a dinghy towing a lure: (A) before the lure passage, (B) after the first lure visual contact, (C) after the second lure contact.

RESULTS

Hydroacoustic observations

The school structure resulting from the drifting observations or from the first transects of the stress observations are taken to represent an undisturbed situation. They all show strong and irregular spatial density variations (Figs. 1, 2(A), 3 and 4(A)), and in some cases 'vacuoles' appear in different layers (Figs. 1(A) and 1(B)). As no target strength determination was possible, the results are presented in empirical density units, using a geometric progression scale. Note that, although saturation of the echo reception appeared for the highest voltages recorded in some cases, the range of densities inside a single school changes by a factor of 500 (without taking into account the vacuoles).

In the stress observations, the three-times overpassed school showed a reduction in its geometrical cross-section in the vertical dimension which may be a reaction to the vessel stimulus (Figs. 3 and 4(B)). Moreover, the mean depth increased, especially between the first cross-section and the second, as a result of the diving reaction of the subsurface fish (which was visible by eye below the transducer during the first transect, and disappeared completely later, even around the boat). In the last cross-section the school seemed to be split into two 'subschools' at slightly different depths. The stress observations made in Martinique from a dinghy towing a lure over *H. clupeola* schools indicated that the same kind of reaction occurs, although the shallow depth limited vertical avoidance (Fig. 2(B)).

The volume occupied by a school is often irregular in shape. As the sounder provides a distribution pattern only in two dimensions, the observed differences could be because of a different location of the geometrical cross-section inside the school and/or a real change in its shape and location during the time elapsed between two successive transects. Analysis of the signal confirmed that the schools actually increased their internal mean density when stressed. The mean density of the samples low-pass filtered to eliminate the samples below a threshold (in this case 50 mV) provides a good dispersion index of the individuals (Marchal, 1988). It was calculated as 58 (arbitrary units) in the first sailing-boat cross-section and 100 in the third (because of a technical problem, the signal of the second cross-section was not recorded); during the dinghy observation the data series were 46, 45 and 100. Moreover, the internal structure of the school shows a high variability in all figures but in different ways (Figs. 2 and 4). During the unstressed transects (Figs. 2(A) and 4(A)) and at the beginning of stress (Fig. 2(B)) the structure showed large areas of low density. In Figs. 2(B) and 4(A), the right-hand side of each diagram, which corresponds to the end of the transects by the sailing-boat or the dinghy, is deeper than the left part. This may reflect the beginning of a
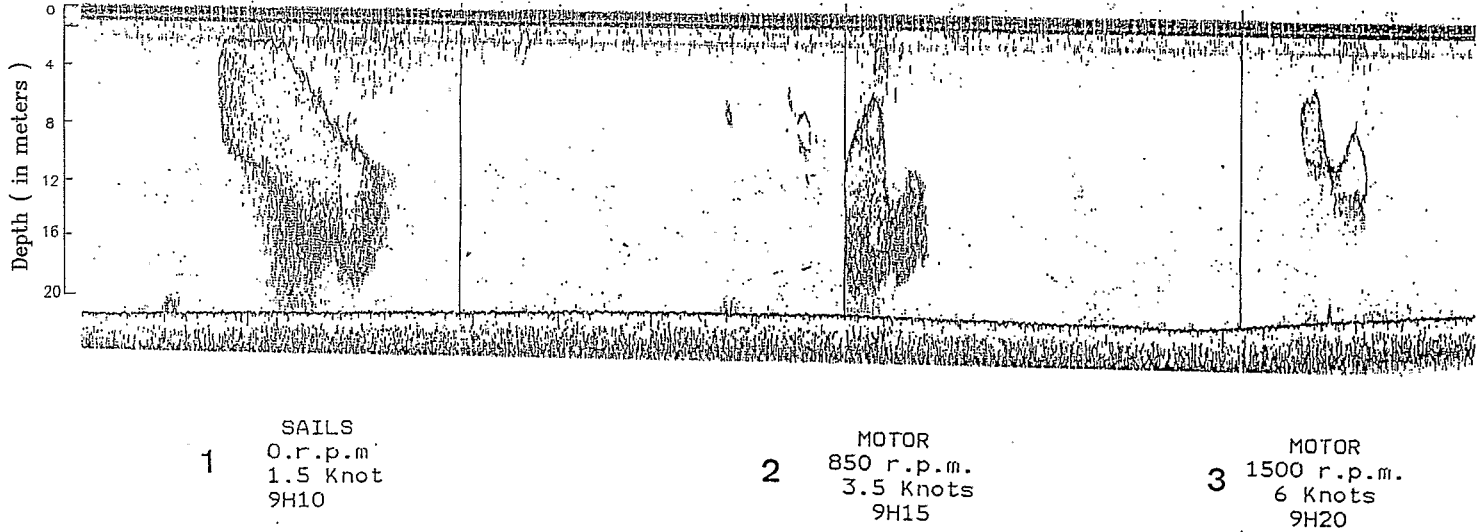
Fig. 3. Echogram of the school overpassed three times by the sailing-boat, using first sails then two different motor speeds.
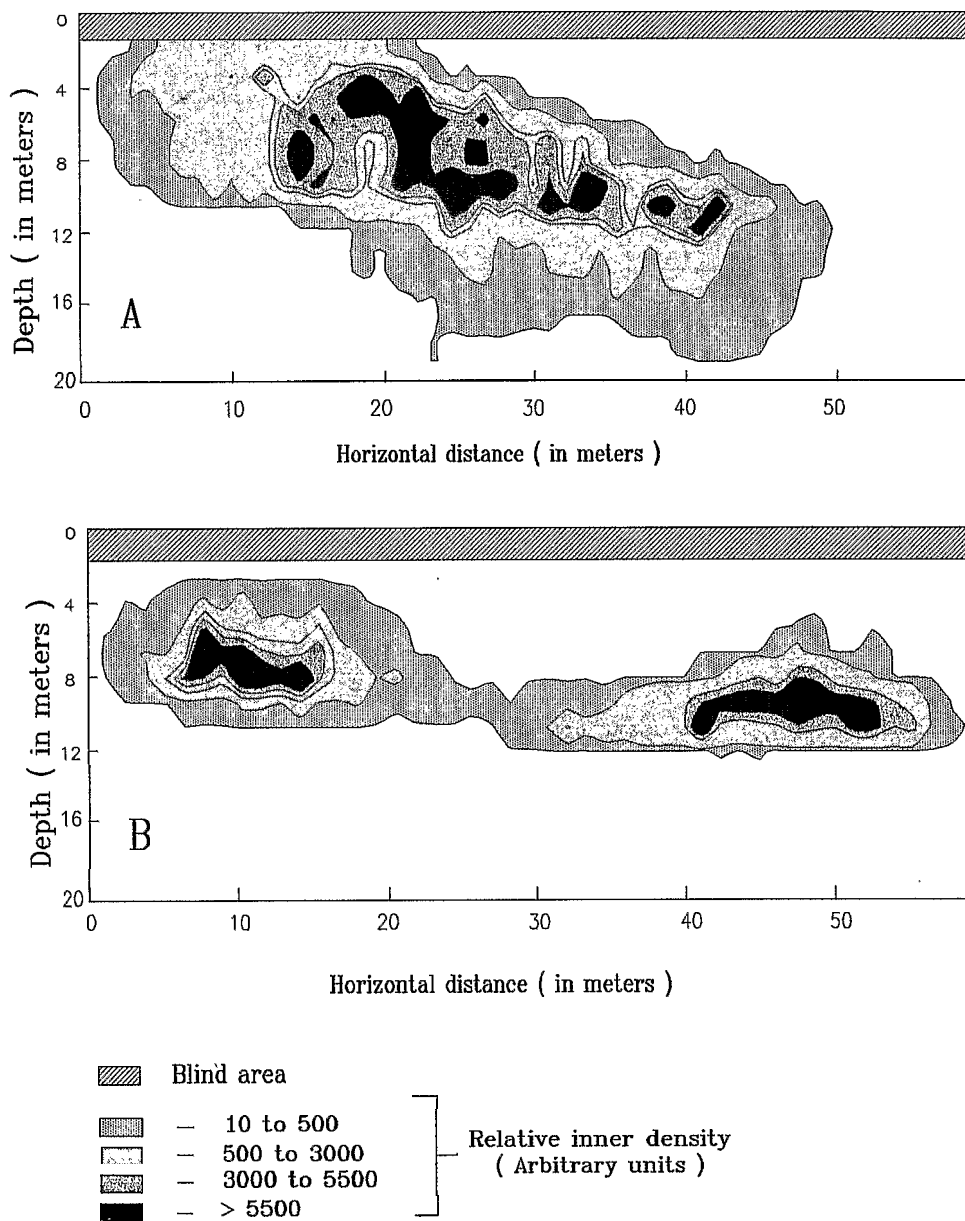
Fig. 4. Internal density structure (vertical cross-sections) in the same *S. aurita* school over-passed twice by the sailing-boat using first sails (A) then motor (B).

diving avoidance reaction which could be a consequence of a contagious and fast propagation of a 'wave of agitation' inside the school (Radakov, 1973) initiated by the arrival of the boat. The difference between Fig. 4, where the

diving reaction is immediate, and Fig. 2, where it occurs only during the second transect, may be because of the difference in the intensity of the stress (visual and/or auditive) between the large sailing-boat and the small dinghy.

During the last transects (Figs. 2(C) and 4(B)) the distribution of the density was different from the first ones. The surface of the low density area was smaller than previously observed. In Fig. 4(B) it corresponded first of all to the 'neck' between the two constitutive 'subschools'. In both figures the distribution of the density is much more homogeneous than previously, with few maximal values and a strong density gradient around these points compared with the larger dispersion observed in the first cross-sections.

In order to obtain a horizontal and linear external contour of the school under the surface, we arbitrarily defined as the upper part of the school the first layer of each transmission for fish detection; the following layers were assigned the numbers 2, 3, 4, etc. Finally, all the transmissions having the same layer number were placed on a common horizontal line to allow a homogeneous presentation of all the results. However, the densities of the different schools in layer 1 cannot be taken into account because this layer is generally not completely occupied by fish.

The data for the three large schools presented in Figs. 1(A), 1(B) and 4(A) were processed (Fig. 5(A)) and compared with the density distribution obtained from seven schools recorded beneath R/V Capricorne steaming at 7 knots during the survey observations (Fig. 5(B)). These latter schools show a unimodal distribution where the highest density was observed in the upper layers, which is completely different from the vertical structure of the so-called undisturbed schools which do not show a particular distribution in relation to depth. Three additional schools were also observed near the bottom by R/V Capricorne. They were not included in the data set because their vertical migration was naturally limited by the sea bed, which probably explains their bimodal vertical density distribution (Gerlotto and Fréon, 1988).

Visual observations (aeroplane and underwater)

The five aerial survey observations indicated that the shape of a school and the horizontal surface it occupied were highly variable with time, as has been observed by other authors in different areas (Bolster, 1958; Hara, 1985; Squire, 1978). During the first survey the surface varied within a range of 1–4 (Fig. 6). The observed shapes can be subdivided into two types: (1) amoebiform type, where the school looks slack and unstructured (Figs. 6(A)–6(C)); (2) egg-shaped type, where the school is homogeneous and dense (Figs. 6(D)–6(F), 7 and 8). The simultaneous underwater observation in-
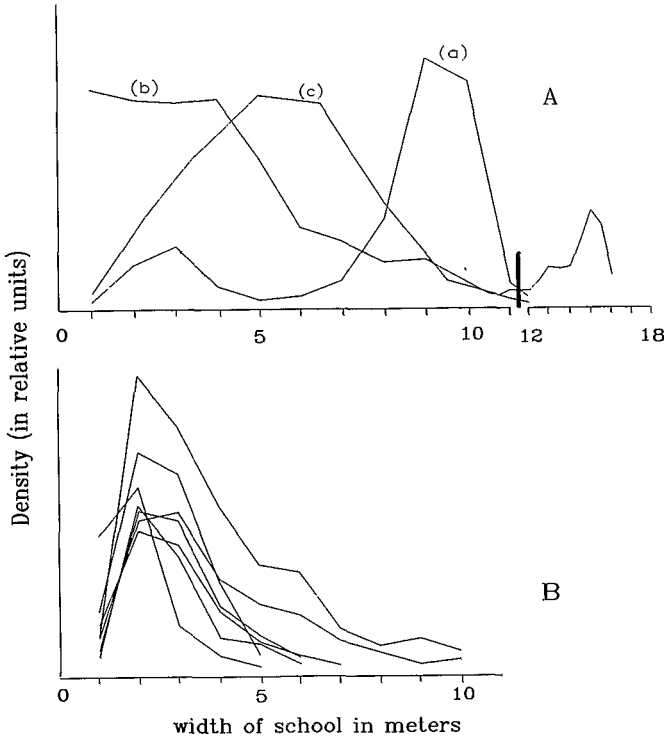
Fig. 5. Vertical density profile of pelagic fish schools: (A) undisturbed schools ((a) and (b) refer to Fig. 1, (c) refers to Fig. 3(B)). (B) disturbed schools (during a survey).

dicates that this type of shape coincides with the arrival of a group of predators: *Elagatis bipinnulatus* (in another similar observation, the same reaction was produced by the presence of small hunting bonitos).

The second visual survey of a school gave the same kind of result: at the beginning of the observation the school presented an irregular shape and provided plume-like pictures (Fig. 9), and vacuoles in its internal structure (Fig. 10). During the survey, the school crossed the bay and presented a compact structure with egg-shaped limits, with a denser nucleus (Fig. 11). A few minutes later the shape was the same but the internal structure was irregular with a low density in the centre and a high density at the periphery, suggesting a circular movement (Fig. 12) typical of a 'mill' structure observed in tanks (Pitcher, 1986), which could represent defensive behaviour against predators or the shadow of the aeroplane.

The observations made during three additional aerial surveys confirm the high variability of the school structure and the concentration of the school after the passage of the lure. Simultaneous underwater and acoustic observations confirm the existence of two typical internal structures: dense (Figs. 2(C) and 8) with a regular interfish distance (at least within the field of view of the camera), or comprising intermingled fish columns separated by large vacuoles (Figs. 2(A) and 10).
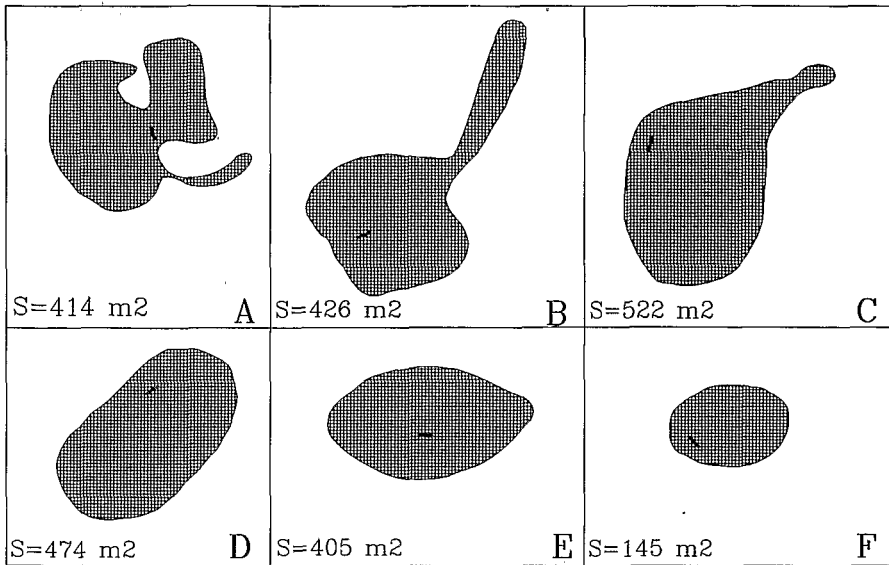
Fig. 6. Variation of school surface during a 1 h aerial survey (the thick bar represents the apparent size of the surface observer).

DISCUSSION

Limitations in the data sets

Two possible limitations in the interpretation of our results have to be studied in the three acoustic observations: (1) the representativeness of a single transmission as an independent sample (drifting, and sailing-boat observations), and (2) acoustic limitations (all observations).

(1) Because of the shape of the transducer beam, the sampling volume increases with depth; this has three consequences. First, below a few metres' depth, the first two or three and the last transmissions have a high probability of sampling only the edge of the school, where the density will therefore be underestimated. Secondly, the heterogeneity of the school is better described in the upper layer than in the deepest layer, which probably explains the vertical gradient in the homogeneity. Thirdly, an increasing overlap of the sampling volumes occurs with depth: when retaining the − 3 dB point, under the conditions of the experiment the overlap starts at 1 m and is 50% at 2 m (under usual survey conditions these will be 10 m and 20 m, respectively, because of the speed of the vessel and the lower sampling rate). The consequence of both phenomena is a horizontal smoothing effect of the school's
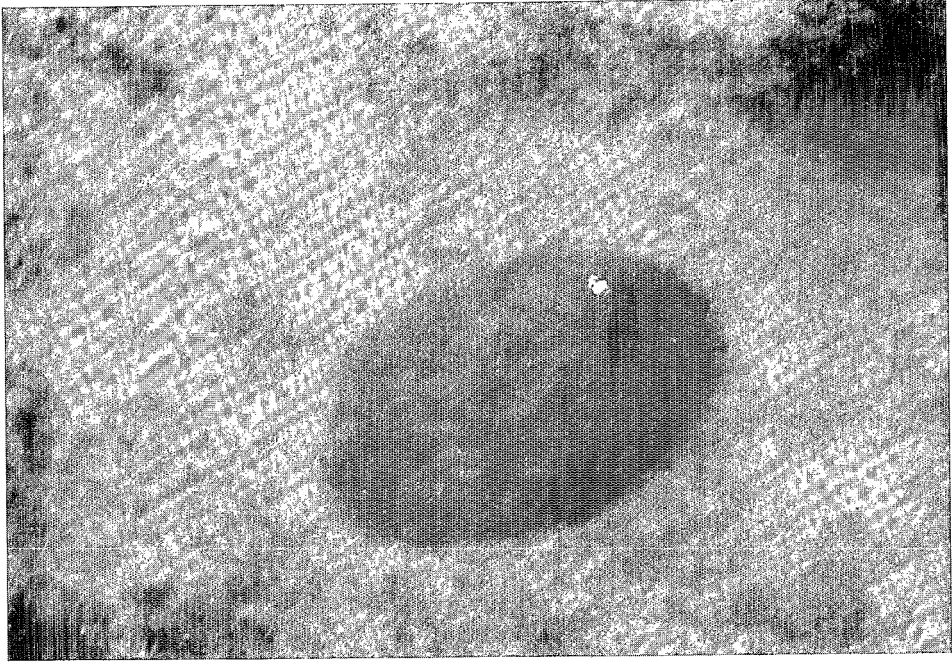
Fig. 7. Egg-shaped structure of the dense and homogeneous school of *H. clupeola* during the first visual survey (the white dot is the surface observer).
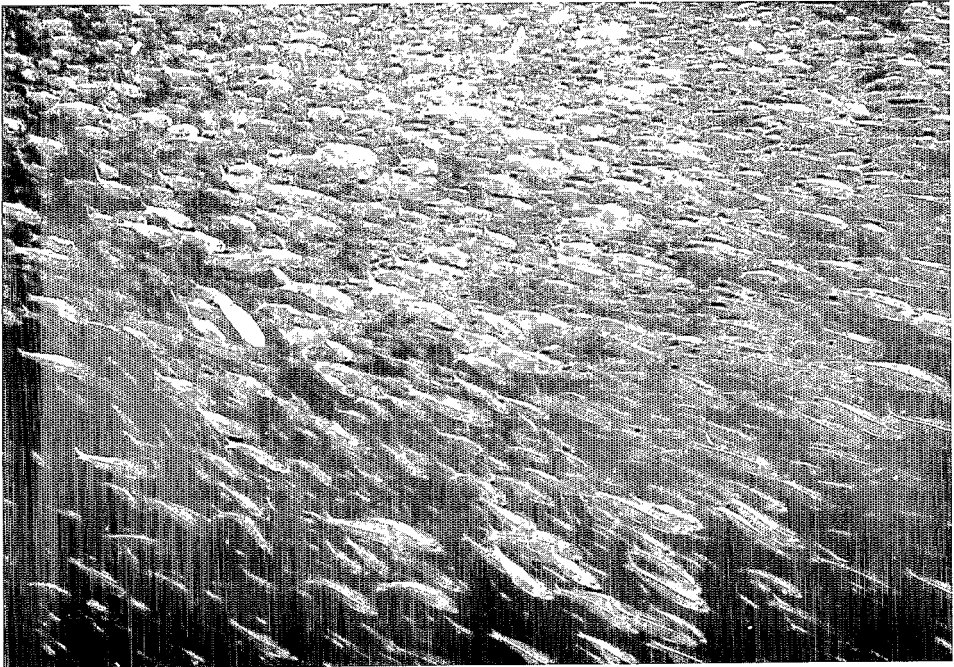

Fig. 8. Underwater photograph of flight reaction of the *H. clupeola* school to predators during the first survey.

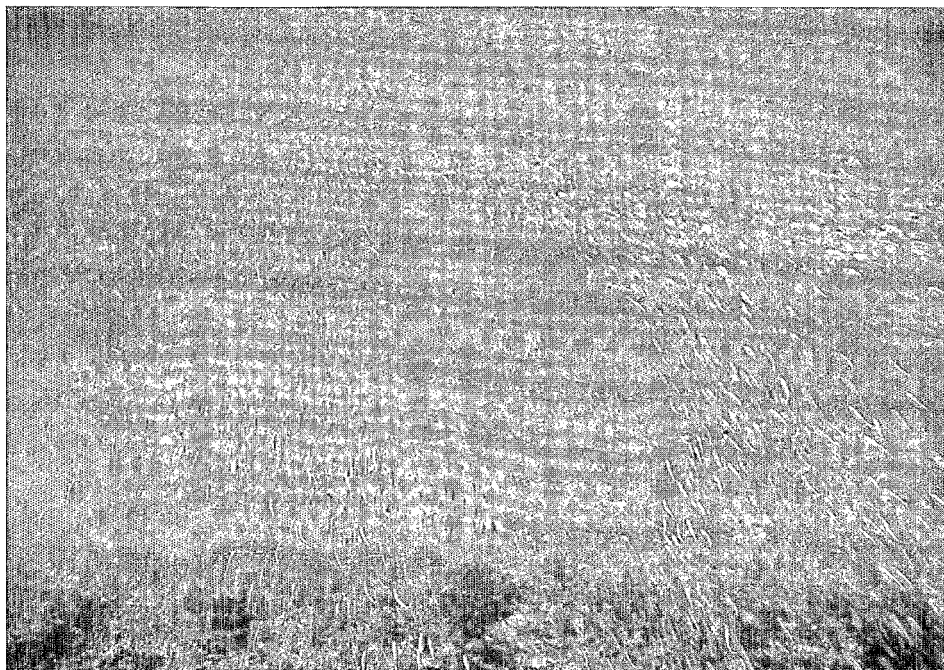Fig. 9. 'Plume-like' structure of the *H. clupeola* school during the second visual survey (middle of the photograph).

Fig. 10. Underwater photograph of column-shaped structure of *H. clupeola* separated by large vacuoles.
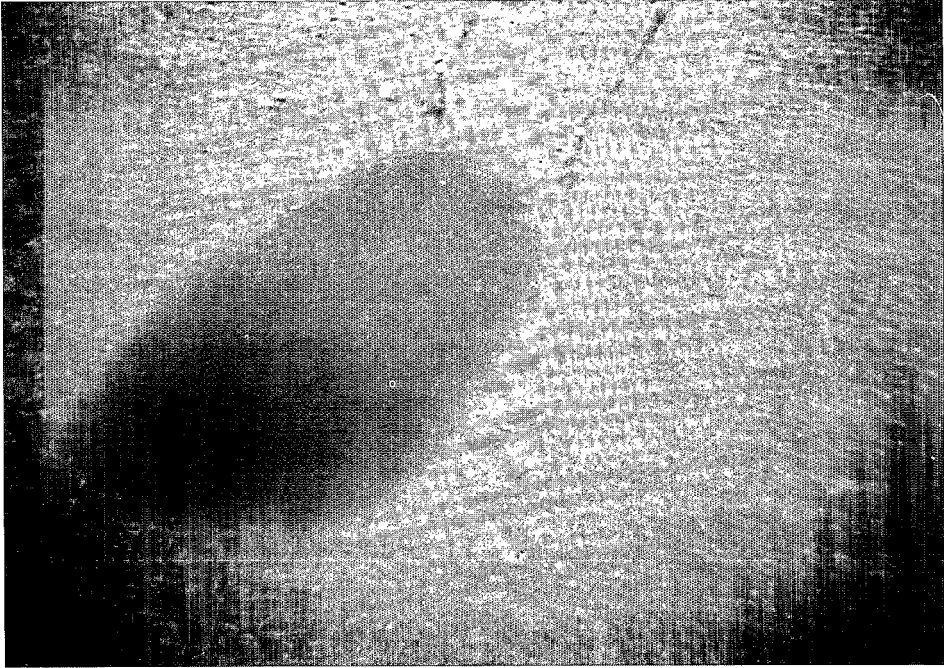
Fig. 11. Egg-shaped structure with a nucleus of the *H. clupeola* school during the second visual survey.
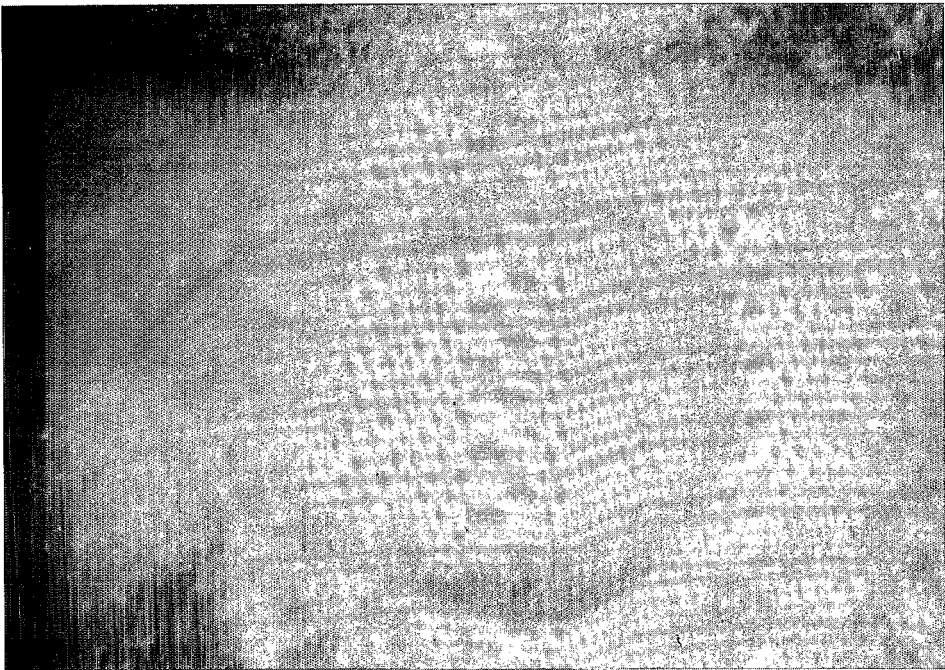

Fig. 12. 'Mill' structure of the *H. clupeola* school during the second visual survey.

structure, especially in the deepest layers, which means that heterogeneity could be greater than stated.

(2) Among the numerous acoustic limitations resulting from absorption, multiple reflections, fish behaviour or physiology, etc. (MacLennan and Forbes, 1982), the most important could be the 'shadow effect'. Following the authors who studied this problem after Röttingen (1976), such as Lytle and Maxwell (1983), Olsen (1986) and Foote (1978, 1982, 1990), this shadow effect occurs in schools in which the density is greater than 3 kg m^{-3} and the width greater than 20 m. Some calculations on the density of tropical schools have shown that these cases are very rare in our regions, and negligible in the observations presented here (even though the density inside a small nucleus overpasses 3 kg m^{-3}). This is also the case for most northern species (Misund, 1990).

Concerning the in situ visual observations, the usual limitation is the influence of the observer on fish behaviour. In Martinique *H. clupeola* is not exploited and, since the area of observation is a seaside tourist resort, the fish are accustomed to swimmers and are not afraid of them as long as they keep swimming slowly at the surface. Active feeding behaviour was frequently observed and recorded at less than 1 m from the camera operator. The effect of floating objects and swimmers on the schools was recorded during several underwater observations. When the observer is moving nervously, the usual concept of flight distance applies; this distance is around 6 m. Around objects, or a slow moving observer who does not change his swimming behaviour, the fish maintain a 'security distance' of 1 m. Therefore it can be stated that a quiet observer did not influence the school.

Compressing/stretching and stretching/tearing hypothesis

Most studies on school structure deal with the mean distance between neighbours and their spatial distribution, but a few deal with the heterogeneity of the distribution and its significance. This spatial heterogeneity inside wild fish schools was first mentioned by Cushing (1977) who studied the horizontal distribution of the fish inside sprat and sandeel shoals using a scanning narrow beam sonar. Reviewing the different hypotheses (dissipation of dissolved oxygen within the school, 'functional' or 'core' units inside the school, etc), Misund (1990) found them inappropriate. From observations of herring schools and applying our approach (Gerlotto and Fréon, 1988), he proposed a 'moving mass dynamic' hypothesis which describes the situation.

We propose here two complementary hypotheses of aggregating behaviours in order to explain the mechanism of the internal variability of density inside a school. In both cases, the school is compared with a sponge where the large holes would be vacuoles and the flesh would be a continuum of fishes maintaining visual (or other) contact. We assume that inside this continuum there

is a variable distance between neighbours depending on different internal or external factors inducing particular behaviours such as feeding, fright, etc., but that this distance varies within a narrow range (Fig. 13(A)). The compressing/stretching behaviour concerns mainly the description of the fish
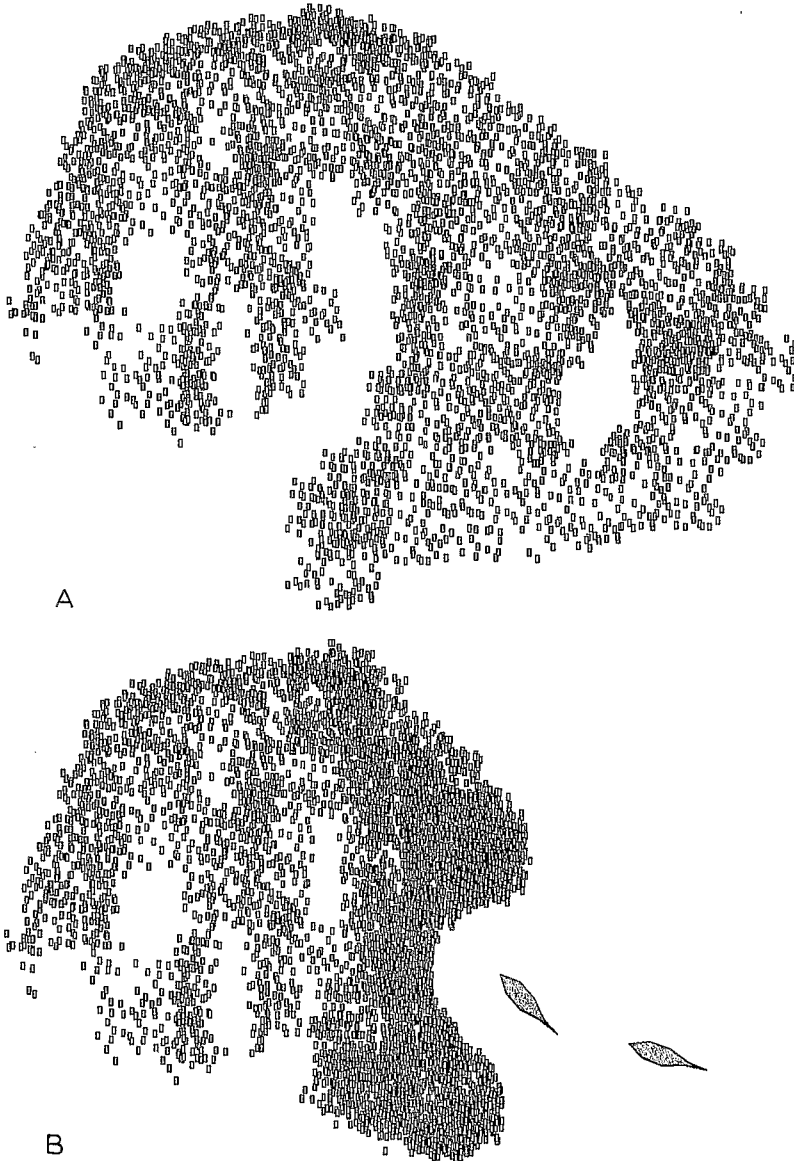

Fig. 13. Scheme illustrating the compressing/stretching hypothesis: (A) undisturbed school with vacuoles, (B) local compression by an external stimulus, (C) almost total compression after several external stimuli.

Fig. 13 (continued).

density inside the continuum: in unstressed situations (feeding behaviour, individuals in safety in the centre of the school) the distance may be large and the polarization low, but when confronted by a real or potential danger this distance becomes shorter (individuals located on the periphery of the school, especially in the front and rear parts, as confirmed by visual observations but not by acoustics, as mentioned above). When the stress is very strong and/or concerns a large portion of the school, the interfish distance rapidly reaches its lowest limit (the minimum compressing distance) and in that part of the school all the vacuoles quickly collapse (Fig. 13(B)). Of course, as a school of pelagic fish is always moving, there is a high dynamic in the system and the propagation of the phenomenon is very fast from one part of the school to another (Radakov, 1973). Nevertheless, this propagation is rapidly attenuated in large schools and we observed that several repeated stimuli are necessary to compress the school as a whole (Figs. 2(C), 6(F) and 13(C)).

From this compressed structure, which is reassuring (possibility of efficient defensive manoeuvres; Pitcher, 1986), but probably uncomfortable (higher swimming speed), the dense fish continuum first stretches and individual exploratory behaviours start to take place. For instance, typical feeding behaviour was often observed during the visual survey. The school volume increases and at some point the interfish distance reaches its upper limit (the maximum stretching distance). Then the stretching/tearing phenomenon occurs: a given individual must choose which fish it has to join on its right or its left (or above/below) in order to maintain this maximum stretching distance within the normal range, and a small vacuole appears (Figs. 14(A) and 15). The individual following the first 'disrupting' fish then faces the same problem with a greater intensity because the possibility of keeping
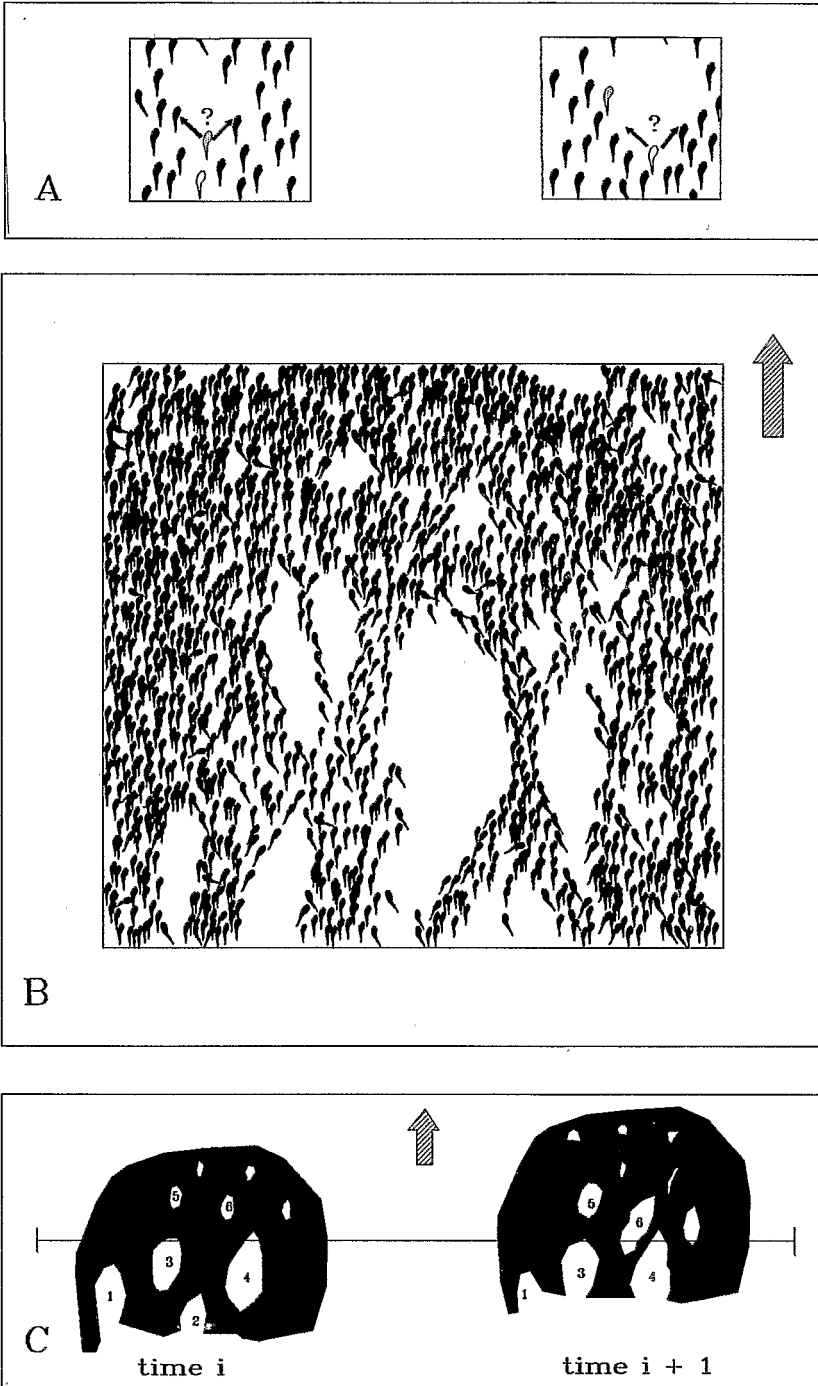
Fig. 14. Scheme illustrating the stretching/tearing hypothesis: (A) initiation of a vacuole, (B) vacuoles inside the school, (C) migration and enlargement of the vacuoles inside the school.
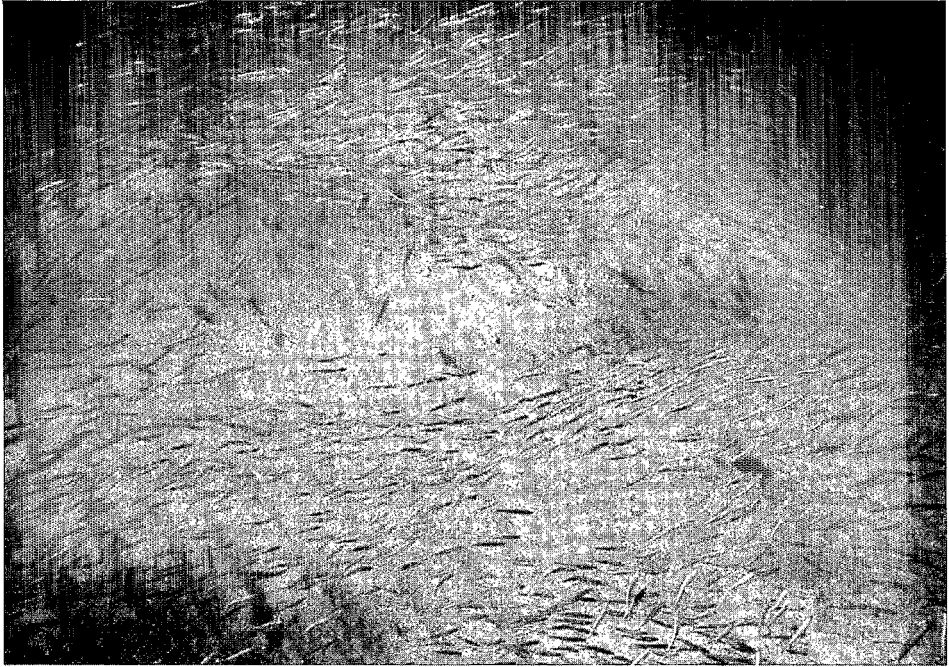
Fig. 15. Initiation of a vacuole and 'disrupting fish' behaviour in a *H. clupeola* school.

an equal distance from neighbours means a greater withdrawal from each of them. As a consequence, the vacuole enlarges; the 'sponge' swells, tears in rags and functional units appear (Fig. 14(B)). Here the comparison with a sponge shows its limitations: we observed, in fact, that the vacuoles were not moving with the school—the fish move around them like a river flows around rocks. It seems that these empty volumes represent insecurity areas, which generally increase in size when overpassed by the school (Fig. 14(C)). The school, as a whole, finds a temporary equilibrium in its increase in volume and then the mean size of the vacuoles becomes stable. This stretching/tearing hypothesis explains how, paradoxically, a strong individual aggregative behaviour may lead to heterogeneity and disruption of the school without strong external stimuli such as predation, which generates other well-known mechanisms of disruption (e.g. the fountain effect).

Consequences for acoustic surveys

The heterogeneity of density inside the schools has two main consequences with respect to acoustic surveys: first, it increases substantially the confidence limits of the abundance estimation if the sampling rate is too low; second, it invalidates some estimations of school biomass or density based on school size or on average interfish distance.

It is well known that, during daytime surveys, most of the biomass of pe-

lagic species is present in schools. So it is important to verify that the sampling rate of the school is high enough to provide a reasonable confidence limit of the school's biomass. In order to investigate this, we have simulated different sampling rates for the school presented in Fig. 1 (A) and studied the variability of the results. Considering the conditions of observation it can be assumed that the sampling rate was very high compared to a routine survey. The different systematic sampling rates were obtained by using successively one transmission every 2, 5, 10, 15, 20 of the 264 transmission data sets (Fig. 16). Under normal conditions of an acoustic survey (8–10 knots, 90 transmissions min^{-1}), the same school would have been sampled at a 1/10 rate and the maximal error would have been 54%. For deeper schools, considering the overlap of the transmissions, this error would be much lower.

In order to overcome the limitations of the vertical sounder when used for acoustic survey (avoidance, limited sampled volume) different authors have tried to estimate abundance by using the number and volume of schools detected by a lateral or multibeam sonar or to combine horizontal sonar and vertical sounder observations (Lamboeuf et al., 1983; Misund and Beltestad, 1988). Estimations of fish density inside layers were obtained by combining acoustic and photographic measurements (Buerkle, 1987), or using the relationship between average interfish distance and average fish length (Serebrov, 1976; Misund and Beltestad, 1988). These methods are based on the assumption that the mean density of a school detected by a sonar is the same as when detected by a sounder, and/or that the interfish distance is homogeneous.
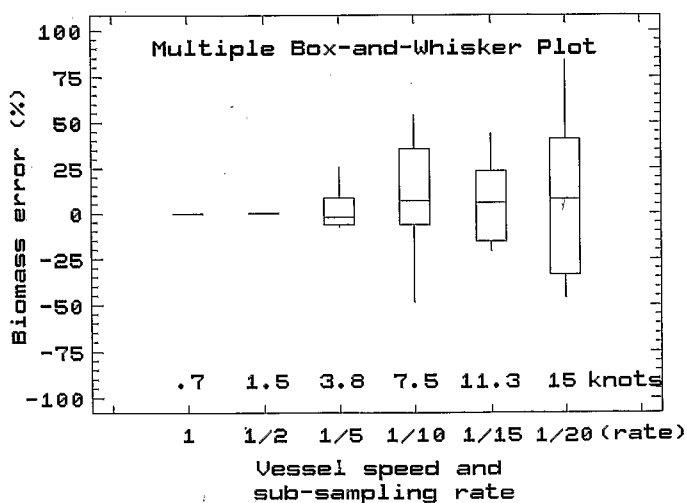

Fig. 16. Simulation of the mean biomass estimates of a school at a usual sampling rate (90 transmissions min^{-1}) according to the boat speed, from the data collected during an oversampling (1.5 knots, 180 transmissions min^{-1}).

Numerous potential reasons for departure from these two assumptions have been identified by Misund and Ovredal (1988). Our results confirm the limitations of these approaches, at least in the particular case of our observations (species, environment). The homogeneity of interfish distance was generally observed on small schools in a tank (Van Olst and Hunter, 1970; Weihs, 1973; Breder, 1976), but it seems that this regular structure is relevant in situ only on a small scale inside a large school; this presents several lacunae as mentioned by various authors as recorded by Pitcher and Partridge (1979) and Pitcher (1986).

CONCLUSION

The observations made on tropical clupeoid schools indicate some similarities and some discrepancies with similar studies carried out on temperate species.

The internal school structure is heterogeneous, including large vacuoles and nuclei of high density, and may change when the school is overpassed by a vessel by day. In this latter case compression of the upper layer of the school is observed, resulting from the collapse of the vacuoles and the decrease in the interindividual distance. This school structure has a consequence on the variability of the density estimation, especially for the subsurface schools. The usual rate of sampling (90 transmissions s^{-1} at 8–10 knots) may be too low for some heterogeneous superficial schools. Nevertheless, this result is based on unstressed schools. The fact that stressed schools show a more homogeneous internal structure must reduce the confidence interval of sampling results.

Considering the fact that usually tropical pelagic schools are rather small, this behavioural response is then, as a whole, favourable to conventional acoustic estimation of the biomass; when schools are bigger, this behaviour leads to underestimation because of acoustic shadows and saturations.

On the other hand, the heterogeneity of the school structure leads to difficulties in the estimations of school biomass based on external volume (multibeam sonar) and density estimations using visual counting or a distribution model.

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