

Variability of *Harengula* spp. school reactions to boats or predators in shallow water

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The internal structure and behaviour of clupeid schools has been observed *in situ* during unstressed periods followed either by natural predation or by applying a controlled stress (a realistically painted model predator). Combined acoustic and visual (aerial and underwater) observation techniques were used. *In situ* observations are characterized by a high variability of fish reactions in space and time. The variability in space is obviously due to the large scale of observation which allows the simultaneous occurrence of different types of behaviour in different regions. The variability in time is probably due to a large number of physiological or environmental influences changing unexpectedly between repeated experiments. The variability of fish reaction depends on the characteristics of the source of the stimuli: some sources (e.g. predators) induce different behavioural patterns according to the number of stimuli; others (e.g. boats) induce a single pattern, varying only in intensity. Consequences for acoustic signal identification are discussed.

using smoothing software (SURFER). Two kinds of visual observation were recorded simultaneously during several one-hour surveys: underwater views recorded by a swimmer and aerial photos from an ultra-light aircraft flying at an altitude of 60 to 90 m. A Handicam video camera (24° lens) and a Nikonos V camera (28° lens) were used underwater and a reflex camera (100–200 mm zoom and polarizing filter) was used onboard the airplane; 400 ASA film was used in both still cameras. The aerial photos were used to estimate the school surface (the boat length served as a scale). They also show variation of opacity in each part of the school, with some dark spots being easy to follow from one view to the next. Movement of these dark regions, associated with the swimming behaviour recorded by the underwater video, can give a good idea of the displacement of fish within the school.

The dinghy, with the echo sounder on board, towed a model predator (a realistically painted, 60 cm long, model of a bonito moulded in fibreglass from a fresh specimen of *Auxis thazard*) at the end of a 50 m nylon line and passed over the same school several times in shallow water (between five and eight metres). From eighteen operations carried out on one day we obtained eight successful sets of observation on the same school, with simultaneous aerial, acoustic and underwater recordings. These observations were compared with those performed one day later, when we were able to record chase and attack by three predators (*Euthynnus* spp.).

Results

The horizontal shapes (i.e. plan views) of the presumably unstressed schools and their surfaces are highly variable in time, as observed by other authors in different areas (Bolster, 1958; Squire, 1978; Hara, 1985). Before the boat crossed them, the schools looked slack and unstructured and their outlines were blurred. The simultaneous underwater observations of internal structure show non-polarized groups of fish in some parts of the school. In other parts or at other instants, synchronized movements of polarized fish take place. Intermingled or parallel and regularly spaced columns of polarized fish may also shape large vacuoles (Fréon *et al.*, 1992).

The two aerial surveys retained for the description of stressed schools are typical of all the observations. They show high variability in response of the school in terms of structure and concentration. During the first transect, school shape did not change throughout the passage of the model predator. From the movements recorded by the swimmer we can assume that the two dark areas in Figure 1 A3 are fish swimming rapidly in opposite directions on each side of the path of the boat and model predator. This displacement is interpreted as a partial fountain effect. After three additional passes the model

induced a reaction of all the school, which adopted a rather compact structure and fled the disturbed area (Table 1A, Fig. 1 A4–A6). During the last transect, the model passed near the periphery of the school and we noted a local compression of the disturbed area followed by compaction of the whole school without shifting (Fig. 1 A7–A9). During this transect, the change in shape and surface of the school (Table 1A) associated with underwater observations strongly suggested that the two dark areas are fish that flock rapidly together.

A systematic diving of the upper layer of schools upon the approach of the boat was displayed during all these experiments (including those not presented here). In contrast, different reaction intensities were displayed upon the impact of the model predator. When the model was in the middle of the water column, we observed typical fountain effects of the fish “visually concerned” (Pitcher and Wyche, 1983). When the model was towed close to the bottom, fish were often structured in layers and avoided it by displaying a dense wall reaction. Finally, all the fish may flee before it with successive waves of agitation which run over the whole school as a shiver.

The diving and fountain effects seen at the approach of the model predator did not induce noticeable instantaneous modification of the horizontal shape of the whole school. Nevertheless, repetition of the stress was likely to induce such modifications. Instead of an expected habituation effect to false alarms, deformations and decreases of the surface were observed. Analysis of the acoustic signal revealed a corresponding increase in internal mean density and homogeneity depending upon the stress intensity, as shown in Figures 2 A1, 2 A2, 2 A3 and in Table 1 A, although these values should also be related to the location of the transect.

During the following day we observed the reactions of another school suffering chases and attacks from live predators (*Euthynnus* spp.). The aerial views showed first the progressive formation of an ovoid shape with sharp outlines, and high peripheral densities. Then the school split quickly into two homogeneous schools (Table 1B), the smallest of which fled the disturbed area and rapidly crossed the bay. The other, after a shorter drift, became compact and circular, and six minutes later split again into two other schools after briefly forming a “neck” (Fig. 1B) as described by Radakov (1973). The simultaneous underwater observations indicated that during predatory chases, the fish displayed several dense wall reactions and successive waves of agitation. When the predators attacked by breaking through the school like an arrow, the school became a compact ball. This compact ball with a high speed of reaction of the fish, and this splitting with a shift of the resulting schools, were never observed in response to the model predator. However, we obtained a similar compact structure after circling the school several times with the dinghy and model in a later experiment.

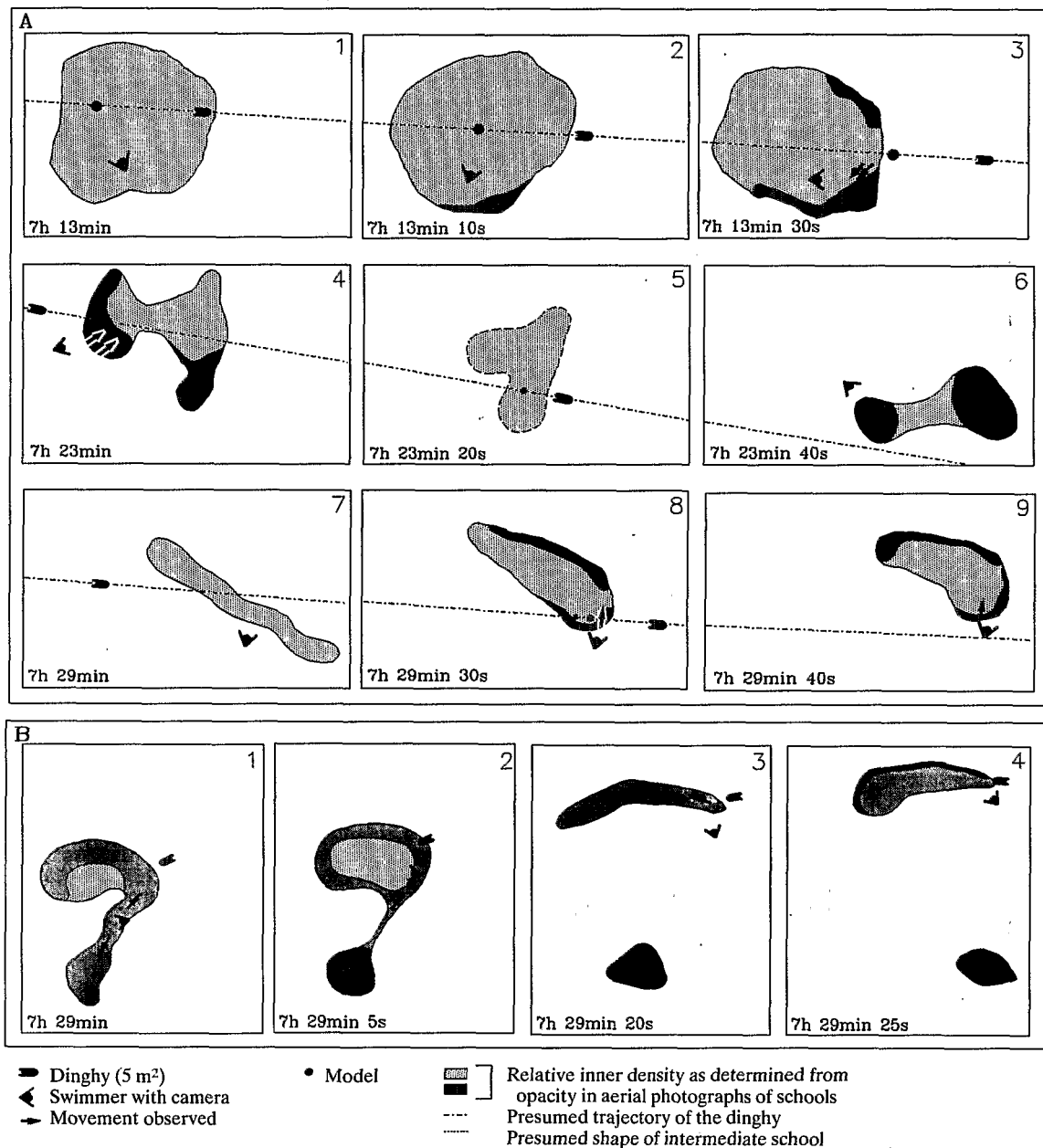


Figure 1. Two aerial observations of school reactions: (A) during three passes of the dinghy towing a model predator above the same school (5 June 1991); (B) during chases and attacks by predators (*Euthynnus* spp.) on a single school (6 June 1991). See also Figure 2.

Discussion

From these observations we can distinguish four types of behaviour: diving, fountain effect, dense wall reaction and waves of agitation. Diving and the fountain effect were always observed as local and instantaneous defensive behaviour. The first appeared just before the impact of the boat, and the second at the moment of visual contact with the model predator. The dense wall reaction and successive waves of agitation were also dis-

played locally upon visual contact with the model, but depending upon their intensity they may disturb a larger part of the school.

These four types of behaviour are local responses of fish within the school. We distinguish them from packing, splitting, and shifts of the whole school, which we name global reactions because they affect the whole social group. For instance, packing of the whole school into a spherical shape seems to result from several successive local compressions arising from the influence

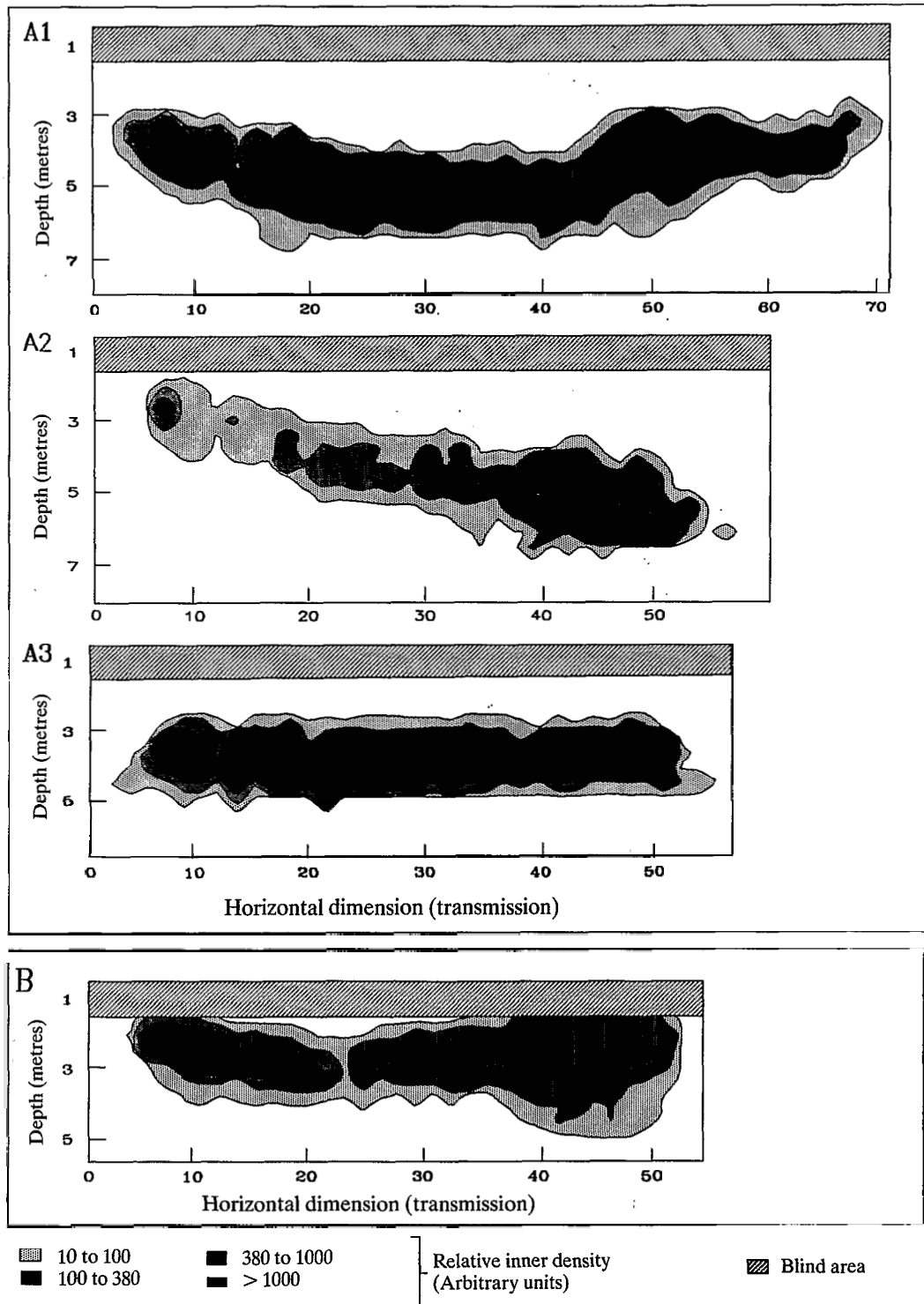


Figure 2. Internal density structure (acoustic vertical cross-sections) corresponding to Figure 1: (A) during three crosses of the dinghy towing a model predator above the school (5 June 1991); (B) during chases and attacks of predators (*Euthynnus* spp.) on a single school; drifting observations (6 June 1991).

Table 1. Data on school characteristics and reactions to different stresses (A) during crosses of the dinghy towing a model predator above the same school (5 June 1991), (B) during chase and attack of predators on a single school (6 June 1991).

A						
Crossing number	—	1	2	2	3	4
Figure 1, part	—	—	A.1	A.3	—	—
Time	7 h 07 min	7 h 10 min	7 h 13 min	7 h 13 min 30 s	7 h 16 min 50 s	7 h 22 min
Stress applied	None	Boat + model	Boat + model	Model	Boat + model	Boat + model
Density (a.u.)	—	—	1780	—	—	—
Height (m)	—	—	2–2.4	—	—	—
Depth (m)	—	—	4.5–5	—	—	—
Altitude (m)	—	—	1.8–2.2	—	—	—
Surface (m ²)	1300–1350	1160–1210	1100–1150	1100–1150	700–750	690–740
Circularity	2.3	3.3	1–1.1	1.1–1.3	2.2	6.3
Local reaction	None	Diving + Compressing	Diving + Compressing	Fountain	Wave agitation + Fountain Packing	Compressing
Global reaction	None	None	None	None	None	Aborted split
B						
Crossing number	5	5	5	6	6	6
Figure 1, part	A.4	A.5	A.6	A.7	A.8	A.9
Time	7 h 23 min	7 h 23 min 20 s	7 h 23 min 40 s	7 h 29 min	7 h 29 min 30 s	7 h 29 min 40 s
Stress applied	Boat approach	Boat	Boat + model	Boat approach	Boat	Boat + model
Density (a.u.)	—	710	—	—	5030	—
Height (m)	—	1.7–3.5	—	—	2.5	—
Depth (m)	—	2.0–7.0	—	—	3.5	—
Altitude (m)	—	6.0–1.0	—	—	0.5	—
Surface (m ²)	550–600	—	450–500	420–470	420–470	310–360
Circularity	5	—	3.6	10	2.6	2.0–2.1
Local reaction	Diving + Compressing	Compressing	Compressing	None	Diving + Compressing Packing	Compressing
Global reaction	None	Packing	Packing	None	Packing	Packing
B						
Figure 1, part	—	—	—	B.1	B.4 (top)	B.4 (bottom)
Time	7 h 23 min	7 h 24 min	7 h 24 min	7 h 29 min	7 h 29 min 25 s	7 h 29 min 25 s
Stress applied	Predators	Predators	Predators	Predators	Predators	Predators
Density (a.u.)	—	1560	—	2345	—	—
Height (m)	—	3.0–4.0	—	4.0–4.5	—	—
Depth (m)	—	4	—	1.0–1.5	—	—
Altitude (m)	—	0.5–1	—	1.0–1.5	—	—
Surface (m ²)	630	330	90–100	350–400	170–180	60–70
Circularity	12.2	3.2	3	11	3.3	1.3
Local reaction	Mills	—	—	Fountain	Compressing	—
Global reaction	Splitting + Packing	Drifting + Packing	Drifting + Packing	Splitting	Drifting + Packing	Drifting + Packing

a.u.: arbitrary units. Circularity: ratio of length to width in plan view. Height: thickness of the school. Depth: distance of school from the sea surface. Altitude: distance of school from the seabed.

of visual contacts with predators in different parts of the school. But it cannot be an instantaneous phenomenon as observed in aquaria. The detailed behavioural mechanisms allowing reversibility between compact and slack internal school structure have been proposed by Misund (1990) under the "moving mass dynamic hypothesis" and by Fréon *et al.* (1992) under the names of "compressing/stretching and stretching/tearing hypothesis".

It seems important to distinguish the diving behaviour in front of the hull from the other behaviours. This behaviour, unlike the others, was systematically displayed upon the approach of the boat. The intensity of stimulus applied did not change the behavioural pattern. Other results, from experiments with a sailboat alternately using sails and engine, support this idea (Fréon *et*

al., 1990). Actually, it seems that the fish react to a very simple stimulus which could be: something in the upper strata which moves rapidly. Nevertheless, changes in intensity of the behavioural response may appear: higher speed, different tilt angle, longer time and therefore longer flight distance (Olsen *et al.*, 1983).

Possible limitations to the interpretation of our results were studied in the acoustic and visual observations (e.g. representativeness of a couple of transmissions as an independent sample, acoustic limitations, influence of the observer or of the aircraft's shadow) but their effects cannot be considered as the only explanation of the large variability observed in school packing density (Fréon *et al.*, 1992). Variability in response of fish in front of a model or living predators has been described by several authors (Radakov, 1973; Helfman, 1984; Pitcher, 1986;

Magurran and Girling, 1986), but as Pitcher says, "we do not clearly know what factors influence fish in deciding to perform one manoeuvre or another." From the basic behavioural studies (Tinbergen, 1971; Lorenz, 1973) it seems that the rule of heterogeneous stimuli summation can be applied to our results: the intensity of the response fluctuates according to the intensity, number and duration of stimuli.

First, the local and instantaneous responses of the fish in front of the towed model seem to change with its threat level. For instance, the reactions of fish become stronger with increasing towing depth. Because real predators chase close to the bottom in order to maintain and gather the school from the bottom to the surface before launching their attacks, the intensity of the stimulus "model swimming close to the bottom" might be stronger because it includes characteristics of the chase behaviour of predators.

Secondly, concerning the number of stimuli and their duration, our results show that the "global" responses of the school (packing, splitting and shift) are flight reactions induced by the association of several stimuli applied (or repeated) during a given time. We observed these global reactions during two circumstances. The first occurs in front of active predators. By their form, speed, number, colour and behaviour (such as cooperative chase and lateral threats) they induce several strong stimuli. For this reason probably, the local and instantaneous responses of fish are more strongly displayed towards predators than the towed model, which presents some but not all of the required alarm releasers. In the same way, the packing of the school and its division into two subgroups were observed when the boat passed overhead towing the model but, as mentioned earlier, these reactions were partial. For instance in three passes splitting into two schools was just initiated. The neck which was being formed became resorbed and the two groups of fish coalesced again. In most cases, compression was observed only in the disturbed area of the school. The second circumstance is when we towed the model predator while encircling the school with the boat: the effect of the model seemed emphasized and the school became strongly packed. The reason may be the circling "behaviour" of the model and/or that meanwhile the sight and sound of the motorboat is perceived by the school to come from all directions. These observations may be compared with those obtained by Gerlotto and Fréon (1990) on avoidance reactions of tropical fish to a survey vessel. They proposed a schematic classification of gradual reactions of fishes (alarm, flight and panic) as a function of cumulative factors such as noise, noise + light, noise + light + boat's hull.

Evidently a dinghy does not present the same intensity of emitted stimuli as a big research or fishing vessel, but the rule of heterogeneous stimuli summation could explain the relatively low lateral avoidance reactions of fish observed during acoustic surveys in our areas: what-

ever the strength of one or several stimuli, if some of them are missing, avoidance reactions will not be successfully completed. As a result, plans for improving acoustic survey estimates by incorporating school characteristics may suffer more from natural variability (especially related to predation) than from research vessel stress.

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