SENSORY FACTORS IN THE SIDE-TO-SIDE SPACING AND POSITIONAL ORIENTATION OF THE TUNA, *Euthynnus affinis,* DURING SCHOOLING

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ABSTRACT

This study was designed to demonstrate the role of the lateral line sensory system in fish schooling. Groups of 2, 3, 4, and 6 adult *Euthynnus affinis* were filmed during schooling orientation in the presence or absence of transparent partitions between them. When the hydrodynamic field between orienting fish was blocked by the partition, they significantly increased their side-to-side spacing, and changed their diagonal to abeam position ratios so that abeam orientation assumed increased importance. Apparently, hydrodynamic contact is essential for the typical spacing and positional orientation in schooling, and the lateral line, as the water turbulence detector, plays a prime regulatory role.

The primary role of vision for the initial approach and prolonged maintenance of parallel orientation of fish in a school has been well known for many years (Parr, 1927). The accessory role of other sensory systems, especially the acoustico-lateralis, for maintenance of fish-to-fish distance during schooling, has been implicated by numerous investigators (Breder, 1959, 1965; Cahn, Shaw, and Atz, 1968; and Moulton, 1960), but direct evidence has been difficult to obtain. Breder (1965) showed that the side-to-side spacing of danios in a school (*Brachydanio albolineatus*) is "usually just a little over twice the distance from the side of each fish to the outer edge of the trail of vortices" each generates while swimming. He considered that the fish space themselves so as to "respect these vortices or suffer a considerable reduction in locomotor efficiency". Thus, the sensory system primarily involved in hydrodynamic detection should play a key role in regulation of this spacing. Our work (Cahn, Siler, and Fujiya, in press), and that of Dijkgraaf (1963), strongly implicates the lateral line mechanoreceptors in this function.

In a preliminary report on tuna schooling (Cahn, 1967), it was found that a transparent partition that blocked hydrodynamic contact between orienting fish also resulted in somewhat diminished fish-to-fish attraction, and in changed spacing and positional relationships. Prior to this study, many other investigators of fish schooling tried to separate the sensory components involved, and used transparent plastic and glass boxes, tubes and plates, as well as mirrors (reviewed by Shaw, 1970). Variable results were obtained, with little quantification, except for Shaw's study on *Caranx hippos* (1969), which showed a reduced duration of schooling when the fish were separated by transparent partitions.

The present study quantifies the changes in spacing and positional orientation of the tuna, *Euthynnus affinis* (common name, kawakawa), observed in the earlier report, when transparent partitions blocked non-visual schooling cues. The results strengthen the role of hydrodynamic detectors in control of fish positional relationships and side-to-side distance between fish in a school.

MATERIALS AND METHODS

This work was carried out at the Honolulu Biological Laboratory of the National Marine Fisheries Service, where the facilities are available for experimental studies on scombroid fishes. Special transport containers (Nakamura,

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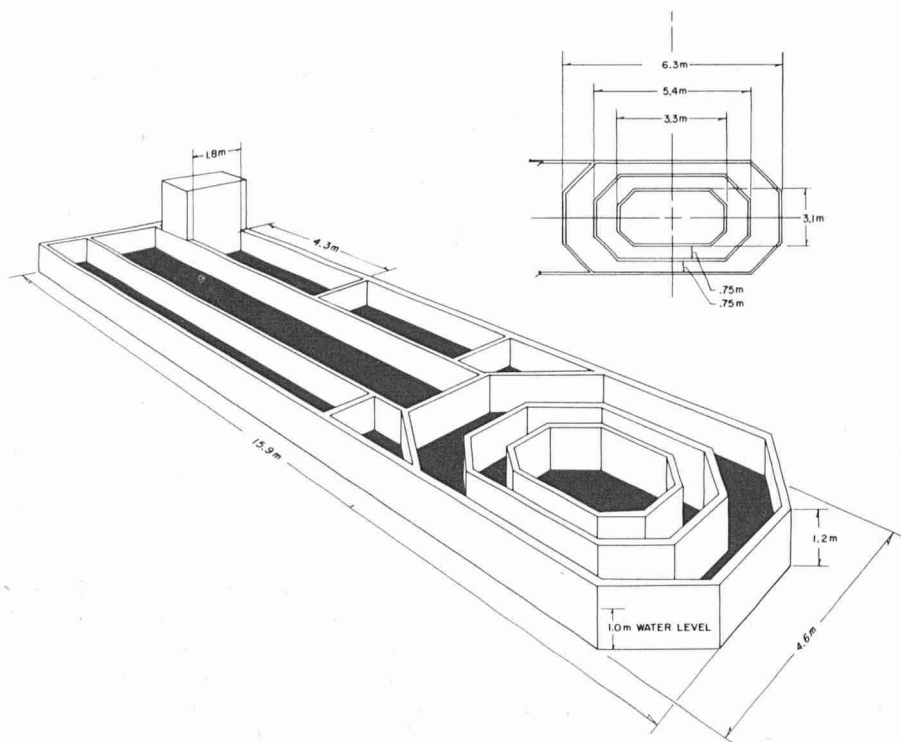
FIGURE 1.—Schematic diagram of cement tank used for tuna schooling studies. Insert shows true dimensions of octagonal channels formed by acetate partitions. Rectangular sidearms were divided in half lengthwise by the Plexiglas partitions, not shown here. Center rectangle was used as a catwalk.

1962) permit the fish to remain in the water from the time of capture until release into tanks on shore.

The experiments were done in a large cement tank that consisted of several differently shaped compartments (Figure 1). An octagonal area at one end was attached by moveable gates (not shown in figure) to rectangular sections at the other end. With the gates up the fish could be transferred to one or the other section without renetting for each experiment. Two concentric octagons of transparent acetate formed three separate swimming compartments for the experimental studies in the octagonal area; in the rectangular areas, rigid, 6.3 mm thick, transparent Plexiglas formed the partitions. The more flexible acetate permitted some hydrodynamic transfer, but the rigid Plexiglas did

not. In one series of tests with the Plexiglas partitions, circular holes, 1.25 cm in diameter, were evenly spaced about every 15 cm along the partition.

Films were taken from observation booths at the ends of the sidearms and above the ceiling, over the octagonal area. A 16 mm Bolex was operated at 16 frames per second; a 10 mm Kern-Paillard Switar or a 5.7 mm wide-angle Kinoptic Tegea lens was used. Single frame analysis of selected sequences provided data for quantitative study (L-W Inc. Photo Optical Data Analyzer, Model 224 A, Van Nuys, Calif.). At the film speeds used, it was satisfactory to measure every fifth frame, since positions changed minimally during this time interval. The number of frames given in the tables should

be multiplied by five to reflect the number of frames examined.

Eighteen fish out of 22 adapted to the test conditions; they were tested in groups of 2, 3, 4, and 6, and each fish was used in more than one test. To determine the side-to-side distance between fish that were in parallel orientation, the position of each fish and his body axis were drawn from the motion picture frames. The perpendicular distance between the axes of pairs of orienting fish was measured (Figure 2).
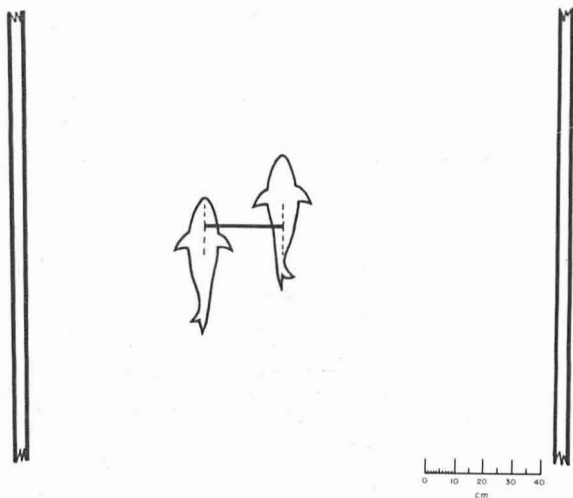

FIGURE 2.—Scale diagram showing tunas swimming without a partition in rectangular channel. The dimensions were taken from a fish of 43 cm fork length. Body axes are shown as dashed lines. The side-to-side distance of 25.9 cm (solid line) is the group mean for a school size of 2 fish.

When occasional non-parallel axes were encountered, the inter-fish spacing was measured from the snout of the leading fish perpendicular to the axis of the trailing fish, or from snout-to-snout if the fish were abeam. The slight body undulations produced while swimming and when each fish turned resulted in slight angular differences in the headings of two otherwise parallel fish. For our purposes it was not necessary to measure these angles, although we spot-checked the first frame of each sequence used to be sure that the angular headings from one another were approximately 26° or less. This

was the angular value which Hunter (1968) and Shaw (1969) considered small enough to be counted as parallel fish.

To determine how often two fish in parallel were in an abeam position (directly alongside each other, as in Figure 3), or in a diagonal relationship (alongside, but slightly in front or behind), we scored each frame of the measured sequences as abeam or diagonal, and counted the total number of frames the fish were in these positions. Initially, we measured the diagonal distances to get some idea of how far ahead or behind each other the fish were keeping. At the turns, however, these values became difficult to keep track of. For our purposes, we found it satisfactory to score as diagonal all frames where fish in parallel were more than 5° displaced from a strictly abeam position. We did
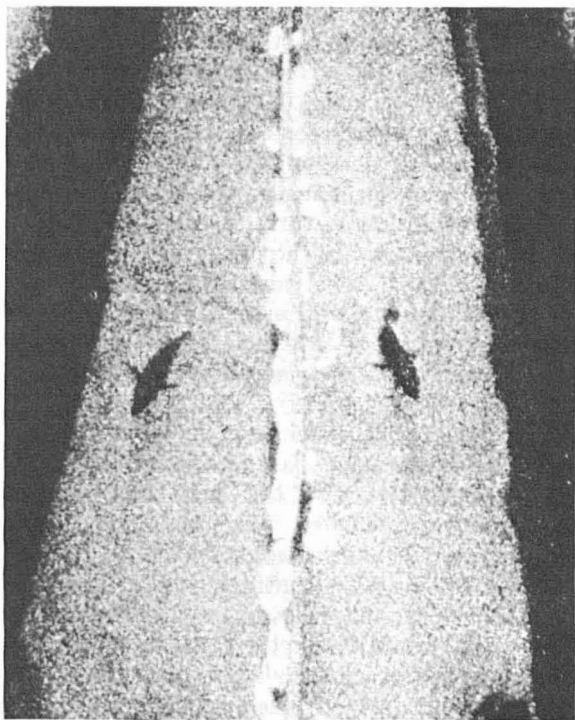

FIGURE 3.—Single frame from test on a pair of fish separated by a Plexiglas partition (top of column in Table 2). Upper edge of partition is obscured by reflection from overhead lights. In this frame the fish are about 93 cm apart, just about the mean distance for this test.

199

not include any frames where fish were in single file formation.

Kawakawa does especially well in captivity (Magnuson, 1965). Young adults were used, of about 37 cm fork length; they had been in holding tanks with running seawater for about 6 months, and appeared normal in all respects. Thawed marine smelts (California osmerids), were fed daily. The water temperature was 23 to 26° C, and was pumped into the tanks at 520 liters/min from a storage sump fed by a well 6 to 9 m deep. The salinity was 33 to 35‰. Dissolved oxygen levels averaged 6 mg/liter. A 1,000 watt and a 300 watt underwater incandescent light, at the bottom of the tank, were used, in addition to banks of overhead fluorescents, to simulate daylight.

RESULTS

In the absence of partitions the diagonal to abeam position ratios for fish orienting in parallel were 5.17/1 and 6.04/1 respectively in the rectangular and octagonal areas. It appeared that the abeam position was assumed for only brief periods when changing speeds in the course of altering direction, turning, or shifting position in the school. In the presence of partitions the ratios were 1.28/1 and 2.36/1 respectively in the rectangular and octagonal areas. Thus the abeam position assumed increased importance during parallel orientation with partitions (Table 1).

The side-to-side spacing is shown in Table 2 as the mean distance apart of either the two fish in a group of two, or of the two closest fish in a group of three or more. Each mean represents measurements made between a single pair of fish during a single continuous film sequence. Without partitions, this distance ranged from 14.0 to 29.8 cm in the rectangular area, and 13.4 to 23.0 cm in the octagonal area. Fish separated by a partition stayed much farther apart; the side-to-side spacing ranged from 64 to 134 cm in the rectangular area (Figure 3), and from 30 to 82 cm in the octagonal area. Fish-to-partition spacing varied from a minimum of about 7 to 8 cm to a maximum of about 75 cm, and appeared to depend on the location of the other fish (Fig-

TABLE 1.—Positional orientation of schooling *Euthynnus*.

Test area		School size	Total no. frames analyzed[1]	Positions of parallel fish		D/A ratio
				No. frames diagonal (D)	No. frames abeam (A)	
No partition	Rect.	2	132	110	22	
		3	118	99	19	
		6	96	81	15	
				290	56	5.17/1
	Oct.	2	49	46	3	
		3	44	32	12	
		6	69	61	8	
				139	23	6.04/1
Partition	Rect.	2	360	201	159	
		3	36	25	11	
		4	24	10	14	
				236	184	1.28/1
	Oct.	2	51	36	15	
		3	82	52	30	
		6	52	42	10	
				130	55	2.36/1

[1] These are equal to the number of frames measured for each category in Table 2.

TABLE 2.—Side-to-side spacing of *Euthynnus* in schooling orientation.

Test area	School size	Mean distance apart and standard error					
		No partition			Partition		
		Dist. (cm)	SE	No. frames	Dist. (cm)	SE	No. frames
Rect.	2	22.0	3.4	(25)	92.4	4.2	(121)
		29.8	2.6	(107)	94.0	2.4	(186)[1]
					134.0	5.3	(53)
				132			360
	3	14.0	0.8	(24)	64.0	6.0	(18)
		17.4	1.0	(94)	90.0	4.4	(18)
				118			36
	6	15.2	0.4	(66)	74.0	2.8	(24)[2]
		16.2	2.4	(30)			
				96			
Oct.	2	19.6	0.6	(22)	30.0	2.1	(21)
		23.0	0.4	(27)	82.0	6.0	(30)
				49			51
	3	20.0	3.0	(21)	48.0	2.8	(27)
		20.0	0.6	(23)	49.5	1.3	(55)
				44			82
	6	13.4	1.0	(27)	42.0	2.2	(30)
		14.8	1.0	(42)	56.0	2.6	(22)
				69			52

[1] This partition contained the series of holes.
[2] There were only 4 fish in this group.

ure 4). Circular holes in the Plexiglas did not change the spacing (Table 2). Water movement through the holes was very slow. Fifteen minutes after fluorescein dye was placed on one side
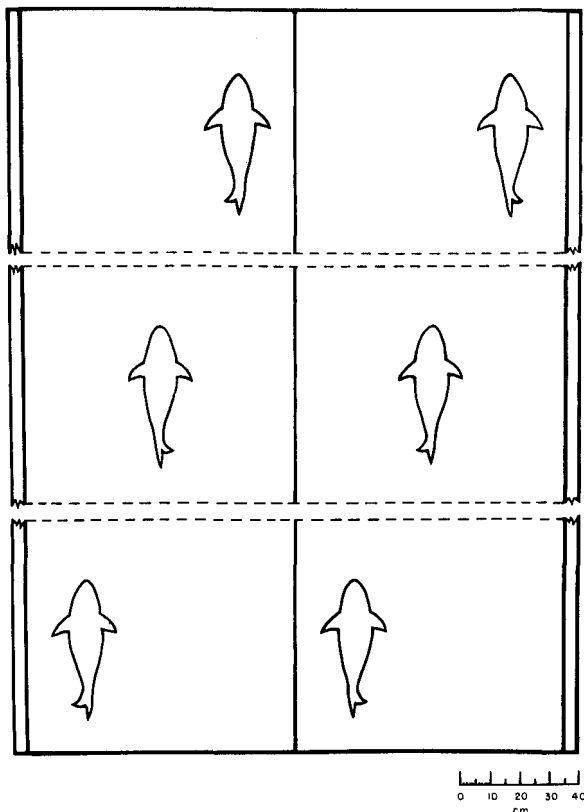
FIGURE 4.—Scale diagrams of tunas swimming with Plexiglas partition in rectangular channel. The 3 usual positions assumed relative to the partition are shown.

TABLE 3.—Summary of data on side-to-side spacing of *Euthynnus* in schooling orientation.

Test area	School size	Group means and standard errors (cm)			
		No partition		Partition	
Rect.	2	25.9	5.5	106.8	23.3
	3	15.7	2.3	77.0	18.2
	6	15.7	0.7	74.0	—[1]
Oct.	2	21.3	1.8	56.0	36.0
	3	20.0	—[2]	48.7	1.1
	6	14.1	0.9	49.0	9.9

[1] There was only one mean in this case; also only 4 fish in the school.
[2] The two means in this group were the same.

TABLE 4.—Three-way analysis of variance[1] of group means for side-to-side spacing of *Euthynnus*.

Source of variance	Sum of squares	Degrees of freedom	Mean squares	F Ratio	Significance level
Total	10,037.42	11			
P or no P	7,440.92	1	7,440.92	44.02	$F_{0.9995}(1,7)=37.0$ $P<0.0005$
Test area	936.94	1	936.94	5.54	$F_{.95}(1,7)=5.59$ not sig.
School size	476.45	2	238.23	1.41	not sig.
Residual	1,183.11	7	169.02		

[1] Fisher, 1970.

the amount that crossed to the other side was barely perceptible.

The data on the side-to-side spacing are summarized in Table 3, where the standard errors were calculated from the variance of the means of the runs in Table 2. It will be noted that in the presence of partitions the variability is much greater. A three-way analysis of variance on the group means (Table 4) showed that the increased spacing in the presence of partitions was highly significant. Although there was a tendency for the fish to remain slightly more compact in the larger groups, these differences were not statistically significant; the effects of shape of the test area was very close to but not quite significant.

Swimming speeds in the absence of partitions ranged from 50 to 64 cm/sec in both rectangular and octagonal areas. With partitions, in the rectangular channels the two orienting fish swam at about the same speed within the range of 50 to 64 cm/sec. During turns, usually made at the ends of the rectangles, they almost always maneuvered to begin the next lap together. Orientation persisted for periods as long as nine days for one pair. In the octagonal area the duration of fish-to-fish orientation was never longer than two days. The size differences between the octagonal channels necessitated differences in swimming speed to maintain fish-to-fish orientation. For example, the fish in the outermost octagon had to swim excessively fast (over 65 cm/sec) to maintain contact with the fish in the innermost section, swimming abnormally slowly (34 cm/sec). Therefore most of the data was obtained in the two larger octagonal channels, where the fish swam at close to normal speeds, at almost 50 to 64 cm/sec.

201

DISCUSSION

These results demonstrate that blockage of hydrodynamic contact between fish in a school resulted in a significant alteration in side-to-side spacing and a changed ratio of diagonal to abeam positional orientation. Of the various sensory factors of importance in the changes observed, it appears that the loss of acoustico-lateralis cues from neighboring fish played a key role. Some of the alternative explanations are discussed and dismissed below. We did not do any acoustic calibrations; the cement channels and plastic barriers may have caused some resonance of fish swimming sounds, and these may act as orientation cues. But this would assume that the sounds were above the auditory thresholds for these fish, and that the sound can be directionally localized; the latter supposition we can hardly make, as yet, even for other fish whose hearing ability has been extensively studied, with the exception perhaps of goldfish (Moulton and Dixon, 1967). We know nothing about hearing in kawakawa; the yellowfin, *Thunnus albacares*, has moderately good acoustic sensitivity, and also has a swimbladder, an organ that may be helpful for sound pressure to reach the ear (Iversen, 1967). Kawakawa lack a swimbladder; we therefore believe it unlikely that sonic pressure is as important in the lives of these fish as is hydrodynamic particle motion. The latter was blocked by our partitions, so that mate-generated cues to the lateral line mechanoreceptors were obstructed.

There are several hydrodynamic factors to be considered: while it is true that the partitions changed the hydrodynamic field around the fish, and that the solid Plexiglas could possibly cue him to move farther away and thus increase the fish-to-fish spacing, we do not believe this to represent the primary dynamics involved. The increased spacing appeared from our data to represent primarily the fish-to-fish orientation (Figure 4); this orientation resulted in fish moving close to the partition just as often as they moved away from it, while tracking their mates. At all times the fish keep a certain minimal distance of 7 to 8 cm from the barrier, so that we can say that there is some "orientation"

to the partition. Superimposed on this is the fish-to-fish orientation, and this exerts the major control of the side-to-side spacing.

Hydrodynamically, when two fish of about the same size are swimming side by side (abeam position) at about the same speed, there would be virtually no centrally located vortices between them. This is because the vortices generated by each fish trail slightly behind him (Rosen, 1959). The flow patterns at the center would, under these conditions, not be very useful as cues. For the fish to get maximal mate-generated hydrodynamic cues it therefore appears that the diagonal positional orientation is preferable. This preference for "diagonal position to each other over positions in front, behind, or directly abeam" was pointed out by Cullen, Shaw, and Baldwin (1965) in their three-dimensional analysis of fish school geometry. Van Olst and Hunter (1970) also called attention to the fact that "the minimum possible lateral space between neighbors to the side would be lower if fish consistently occupied diagonal positions than if they were perfectly aligned, because the areas of tail movement would not overlap." In relationship to our experimental results, the partitions blocked the mate-generated vortices so there was no longer any "advantage" to the diagonal position. The "advantage" factor, it should be emphasized, is not only for hydrodynamic cues from schoolmates, but also more importantly, to derive maximal locomotor efficiency while travelling in a school. The fish can best use the energy from mate-generated vortices if he is positioned within the influence of the vortex, and this is usually best at primarily right angles and a little behind the course of the fish (Breder, 1965), the diagonal position.

Since the fish, in the presence of the partitions, did not completely abandon the diagonal positioning while increasing the abeam orientation, the question comes up of whether or not vision is equally good from both positions? Tuna vision has been studied to a limited extent; for example Nakamura (1968) studied visual acuity in kawakawa by testing the fish's response to various targets. This involved the temporal region of the retina as the fish swam forward towards the target. A different region of the retina is no

doubt involved in lateral vision, with a perhaps different cone distribution. Nakamura did not study this for kawakawa, but others have demonstrated that schooling fish are nearsighted in forward vision but farsighted in lateral vision (Baylor and Shaw, 1962). This suggests that perhaps the kawakawa in our experiments with partitions shifted spacing and position to make more use of lateral vision. A possible reason may be that in the absence of mate-generated hydrodynamic cues, nearsighted vision is inadequate for efficient tracking of their schoolmates. To explain all of these visual factors, more information is needed on such problems as resolution and cone density in the different retinal regions of kawakawa.

One other question relative to vision requires some comment: did the partitions produce reflections sensed by the fish which led to the changes observed? As previously noted, fish in a school in the presence of a partition positioned themselves in different locations relative to the barrier, depending on the fish-to-fish distance across the partition, rather than on the distance from the partition (Figure 4). Thus if there were any reflections, they did not appear to be of any significance. The schooling tendency predominated: relative to this it should be pointed out that it is unlikely that the change in spacing could be attributed, to any major extent, to a waning of the stimulus to school. Fish-to-fish orientation sometimes persisted across the partition for as long as nine days.

We have considered the prime sensory factors, and omitted tactile and chemical contributions. Since these fish rarely touch each other when swimming except under special circumstances of school structure and size (Breder, 1967), there is no need for further concern with the tactile sense. Chemical cues, in our opinion, were probably not transmitted rapidly enough across or through the partitions to be of any consequence. Even with holes in the partitions, as in one series of tests, water-borne transfer was very slow. Also, the part played by chemoreception in fish schooling (McFarland and Moss, 1967; Moss and McFarland, 1970) appears unimportant for obligate schoolers such as tunas

and other scombroid forms (the use of obligate here is as in Breder, 1967).

The greater variability noted in the side-to-side spacing in the presence of a partition reflects, in our opinion, what happens when the normal hierarchy of sensory systems is interfered with. The dynamic stability of a fish school depends on feedback from all of the different senses. The partitions disrupted this balance, and although schooling persisted, certain limitations were imposed on the process.

In conclusion, this study suggests that the diagonal fish-to-fish positional orientation and the side-to-side spacing assumed during schooling may be more essential for hydrodynamic detection than for visual cues.

ACKNOWLEDGMENTS

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