

## Risk of predation, hydrodynamic efficiency and their influence on school structure

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### Synopsis

Laboratory studies were conducted on 15 schools of blackchin shiners, *Notropis heterodon*, to determine if they altered their structure in response to changing environmental demands. The hypothesis tested was that fish schools should sacrifice a flat, hydrodynamically efficient structure in favour of an unobstructed visual field in the presence of a predator by staggering in the vertical plane. Ten schools were exposed for two weeks to a simple environment with only a current. For the next two-week period a predator was added. Five control schools were exposed to the simple environment for both two-week periods. Six of the ten treated schools increased their staggering in the vertical dimension as predicted while none of the control schools changed. This result was suggestive that hydrodynamic advantages were sacrificed. Respirometer experiments indicated these fish were capable of achieving some hydrodynamic benefits from schooling but these benefits may be a function of fish size.

### Introduction

The shape of fish schools can confer specific benefits. This was noted by Belyayev & Zuyev (1969) and Weihs (1973, 1975) in the formation of the hydrodynamic hypothesis of fish schooling. Weihs (1975) predicted three different mechanisms whereby fish could gain hydrodynamic benefits. Fish could utilize vortices generated within the school to reduce their relative velocity for a given absolute fish velocity (vortex hypothesis), use other members of the school to improve thrust efficiency (channeling hypothesis), and use the wakes from neighbouring fish to provide lift (wing-tip uplift, useful only for negatively buoyant fish). For fish to gain these hydrodynamic advantages, members of the school would have to swim on the

same vertical plane as their neighbours (see Weihs 1975 for a more complete description).

The flat, compact structure necessary for hydrodynamic benefits would cause considerable blockage of the visual fields of fish in the school by their neighbours and would therefore be the least beneficial for the 'many eyes hypothesis' (Eggers 1976, Olson 1964). This hypothesis predicts that the sensory (visual) capabilities of individuals are pooled allowing a school to be more likely to detect environmental stimuli (e.g. predators and food) than individuals. This function could be maximized if neighbours tended to align themselves on different vertical planes (staggered structure) preventing visual fields from being blocked (see Fig. 1).

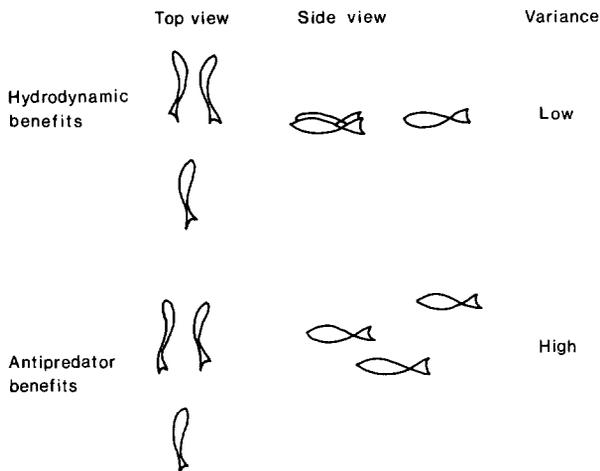


Fig. 1. The two differing school structures required to provide hydrodynamic benefits. The hydrodynamic structure is flat and therefore characterized by a low variance in the third dimension (height variance). The antipredator structure is staggered to prevent individuals in the school from blocking the visual fields of their neighbours. Consequently it will have a high variance in the third dimension.

This ability has been demonstrated by Pitcher et al. (1982). They examined the foraging success of goldfish, *Carassius auratus*, and minnows, *Phoxinus phoxinus*, in groups of different sizes and observed a decrease in time required to find food as group size increased. As of yet no studies have been able to demonstrate whether fish schools are capable of providing hydrodynamic benefits. Partridge & Pitcher (1979) examined the school structure of cod (*Gadus morhua*), saithe (*Pollachius virens*), and herring (*Clupea harengus*), for evidence of the vortex hypothesis. They observed only four of 659 frames which had the correct structure. However, recently Partridge et al. (1983) observed schools of giant bluefin tuna, *Thynnus thynnus*, and concluded that their structure supported the channeling hypothesis. The different observations were believed to be due to environmental constraints. Predatory schools are free from predation and therefore free to adopt an efficient structure, whereas prey schools were not.

The purpose of our study was to experimentally determine whether fish schools are capable of providing hydrodynamic benefits. Two experiments were performed to test this hypothesis. The first experiment examined the change in school

structure when schools were placed in a stream channel without and then with a predator. If fish schools provide hydrodynamic benefits the school structure should change from a flat to a staggered appearance after exposure to the predator. If the schools are unable to provide hydrodynamic benefits, no change in school structure should be observed. The second experiment used a respirometer to determine whether there is an energy saving from schooling. If fish schools are capable of providing hydrodynamic benefits then the respiratory rate for a swimming school should be less than the sum of the respiratory rates for the individuals swimming alone.

## Methods

### Pool experiment

Blackchin shiners, *Notropis heterodon*, were obtained in a series of seines during late August and September of 1981 from Lake Opinicon (40 km northeast of Kingston, Ontario). They were maintained at the Queen's Biology Department in well oxygenated flow tanks (86 cm by 47 cm by 31 cm) in groups of thirty with a 12 h photoperiod and fed a diet of fish flakes (Nutra Fin).

A circular channel was used to simulate different environments. The channel was created by placing a steel ring (102 cm by 76 cm) in the center of a wading pool (183 cm by 76 cm) and a 7 cm sec<sup>-1</sup> current was generated by a submersible pump (Fig. 2). The test area was restricted to a third of the circumference of the channel by pieces of fiberglass screening and coloured white allowing the fish and their shadows to be clearly visible on film. The apparatus now simulated an environment where the only function required by the school was to swim against a current.

To stimulate the school to provide an alternative function (and hence a different structure) the environment was altered so that the schools were subjected to a high predation risk when in the apparatus. This was achieved by placing a live predator (30 cm largemouth bass, *Micropterus salmoides*) in the test area with the school. To introduce

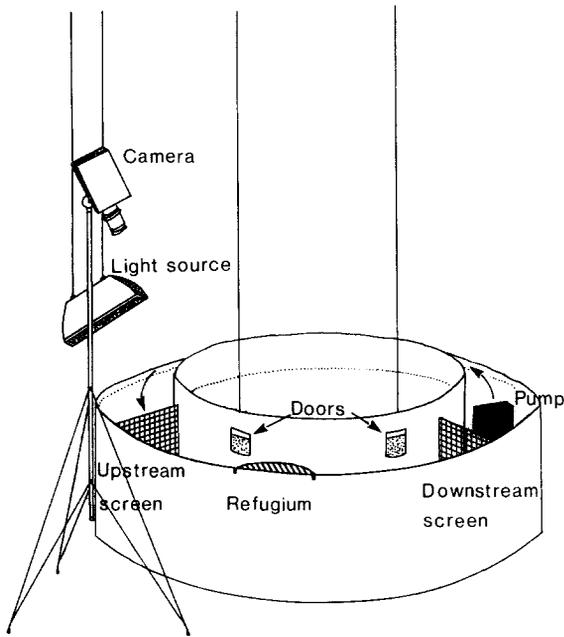


Fig. 2. Apparatus used to alter and record the structure of the fish schools.

the predator with as little outside disturbance as possible, the predator was trained to swim from the center of the pool to the test area through one of two small doors (5 cm by 7 cm) in the steel ring. Monofilament fishing line was attached to the doors so they could be opened or closed from behind a blind.

In order to protect the school of shiners from attack by the predators, a wire mesh semicircular refugium (15 cm by 10 cm) was placed in the outer edge of the test area. This refugium was used to encourage the school to develop avoidance behaviour to the predator: the sooner the school detected the predator and entered the refugium, the lower the probability of being captured by the predator.

A 16 mm Bolex cinecamera with a cable release was placed on a tripod 135 cm above the water surface by the upstream screen to record the school structure for both sets of experiments. A tungsten movie light situated at a  $72^\circ$  angle to the ground and  $80^\circ$  to the left of the camera allowed the vertical dimension to be calculated by the shadow technique (Cullen et al. 1965).

The schools for these experiments were formed

by removing three groups of six similarly sized individuals from one of the tanks and placing them in separate aquaria. These aquaria were maintained at the same temperature as the experimental chamber (between  $19$  and  $21^\circ\text{C}$ ). At 0900 h a group was netted and transferred to the experimental chamber where they remained in the current for two hours before being returned to their aquarium. At this point all the fish were fed and the motor turned off to prevent any heating of the pool. At 1200 h the second group was run for two hours. At the end of that time they were removed and the motor allowed to cool for another hour. Finally, the last group was tested between 1500 and 1700 h. In order to remove any time effects, the fish were tested in the next successive time slot each day. Schools were rotated through time slots, with the school run in the last time slot on one day run in the first time slot on the next day. The movie light was turned on during the second week to allow one week for acclimatization to the lighting necessary for filming.

Since time of day and time after feeding may influence school structure it was necessary to feed and film each school at exactly the same time. Consequently only one school a day could be filmed. When a school was filmed the fish were fed at 0900 h. In order to maintain acclimatization, one group would be run in the apparatus from 0930 to 1100 h. The school to be filmed was placed in the apparatus at 1200 h and allowed to swim for one hour. At 1300 h the fish were filmed and the fork length of each fish was recorded. Fifty feet of film was used for each school at 18 frames per second. After filming, another school was run in the apparatus from 1400 to 1600 h.

To expose the schools to a risk of predation the experimental protocol was the same as before except that after the school had been in the test area for 30 minutes one of the two doors was opened, releasing the predator. After the predator attacked the school it was removed and returned to the center arena. The predator was subsequently released on a random time basis so that typically the schools would be subjected to about four attacks per trial. If the predator killed a fish the run was continued until the two-hour trial had expired.

Similar sized individuals were placed in the holding tanks with the school to replace deceased individuals and used for the remainder of the acclimatization time. In addition, experiments were run for the rest of the day. However, at the end of the day the water in the pool was changed to remove any effect of alarm pheromone 'Schreckstoff' (Heczko & Seghers 1981). Again, the lights were turned on in the second week and at the end of two weeks the fish were filmed and measured as described above. To control for any effects other than exposure to the predator (e.g. residual Schreckstoff in the water, circannual effects, etc.), the third (control) of each triplet of schools was not exposed to the predator. It continued to swim against the current without being attacked. Consequently, changes in their school structure would represent nonexperiential effects.

This entire experiment was performed five times so that 15 schools of six individuals were examined. However, within each group of three, one school was always used as the control. Consequently, a total of 10 treated schools and five control schools were examined.

To analyze the films individual frames were projected on to an Apple Computer Graphics Tablet. A program was developed which read the coordinates of the positions of the nose of each fish and its shadow and calculated the height of each fish in the school (technique described by Cullen et al. 1965). This allowed the mean and variance of the school for all three dimensions to be determined. The mean values represented the positioning of the school in space and the variance values gave the distribution of the fish about this mean point (and hence data on the structure of the school). An autocorrelation was performed on each film sequence to determine the interval over which the measurements were statistically independent (Heiligenburg 1974). Dividing the total number of observations by this number yielded the number of independent observations in a film sequence. This sample size was used to determine weighted means for the school's structure based upon values for individual film sequences.

Comparisons of results between the school exposed only to the current (naive) and exposure to

both current and the predator (experienced) were made with Mann-Whitney U tests (Siegel 1956). In these tests, the result from a continuous sequence was considered as a single observation.

#### *Respirometer experiment*

Three schools of three fish each were used to test whether there was a measurable energy gain by solitary individuals swimming in a school when compared to their individual performance. Metabolic rates of swimming fish were measured in a fish respirometer similar in design to those used by Beamish (1966). The respirometer was submerged in a water bath which maintained the temperature at 22°C. The swimming chamber within the respirometer was a cylinder 5 cm in diameter by 25 cm with a current velocity of 7 cm sec<sup>-1</sup>. Oxygen readings were obtained from a Clark Type oxygen electrode connected to a Fisher Recordall chart recorder. This electrode was calibrated before every experiment using a sodium dithionite solution for the 0% measurement and air-bubbled water for the 100% reading.

A problem with this type of experiment is that individuals removed from a school will have artificially high respiratory rates due to stress. Schooling fish then have an automatically lower respiratory rate due to the calming effect of being with conspecifics.

To prevent calming from biasing our results we measured individual respiratory rates of fish in pairs. The fish were separated by a clear plexiglass partition preventing any physical contact but allowing the fish to sense each other both visually and through olfaction. Individual respiratory rates were then algebraically calculated based on the results of three paired observations. The respiratory rate for the school was determined by removing the partition and placing all three individuals in the respirometer. The respiratory rate was recorded and compared to the sum of the individual rates.

If the school rate was lower than the summed rate the result could be due either to hydrodynamic benefits or a calming effect. To distinguish between these two interpretations the individual respiratory rates were retested. The clear partition was re-

placed but only one individual was placed in the respirometer. If this individual rate was greater than that determined when paired, it was concluded that we had measured individual respiratory rates of calmed fish in pairs and that the difference in respiratory rates between the school and summed individual rates were due to hydrodynamic benefits.

## Results

From this experiment 4,399 frames of film were analyzed. Analysis of the school structure revealed that fish schools do respond to changes in their environment. When exposed only to a current the schools were flat in the vertical dimension; however when they were exposed to a high risk of predation the schools became staggered in appearance. In addition, the respirometer results indicated that the schools with individuals greater than 6 cm in length were capable of providing hydrodynamic benefits.

### School structure

All heights of fish in this experiment were determined indirectly by the shadow technique (Cullen et al. 1965). This technique relies on a precise measurement of the distance between the position of an object and its shadow. Since an artificial, non-parallel light source was used, the shadows became more diffuse as the object got farther from the bottom, potentially resulting in less precise measurements and an artificial variance component being introduced as the fish schools swam higher above the bottom.

To test whether the effect of increasing height was generating the changes in height variance observed, the mean height and the mean height variance for each school during both acclimation periods was plotted. The two points for each school were connected and the slope calculated. If changes in height were generating the increase in height variance, the rate of change should be constant, resulting in all the slopes being equal. However, as demonstrated in Figure 3, although the

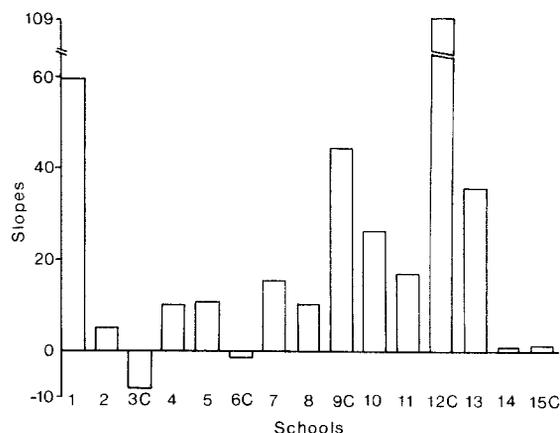


Fig. 3. A plot of the slopes for each school connecting the coordinate pair of mean height of the school (X) with the mean height variance observed (Y) for the first and second two week acclimation periods.

slopes for each school (both controls and treated) tended to be positive, they were different indicating that this effect appeared to have only a minor influence on the results obtained.

None of the five control schools demonstrated a significant change in their height variance ( $p > 0.05$ , Fig. 4). However, the 10 treated schools exhibited three different types of responses. Six schools increased their height variance significantly as predicted, two schools decreased their height variance, and the two other schools demonstrated

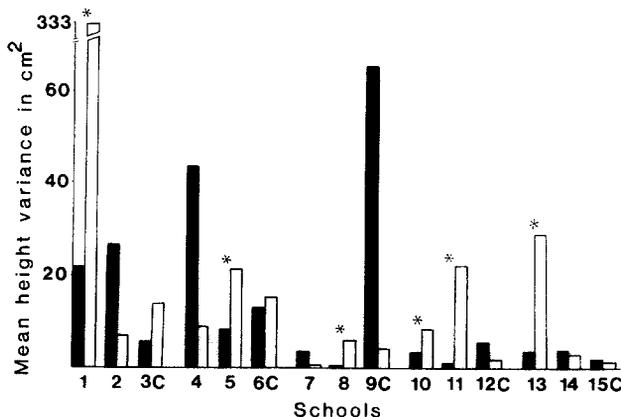


Fig. 4. Mean height variance of the school before (solid bars) and after (open bars) exposure to a predator. C after a school number indicates a control. An asterisk (\*) above a bar indicates a significant increase ( $p$  less than or equal to 0.05) in the height variance after exposure to a predator.

no significant change. This represented an overall increase in their height variance after exposure to a predator in comparison to the unexposed control group (Fisher exact probability test,  $p = 0.042$ ). No significant changes occurred in the other dimensions of the schools (Table 1).

### Size effects

The size of the fish which were in the school also appeared to influence the school structure. As individuals within the school got larger, the observed structure became flatter. This was noted both before schools were exposed to the predator (Fig. 5) and after (Fig. 6). The significance of this finding will be considered later.

### Respirometer results

The chart recordings of the decreasing oxygen content of the water in the respirometer were always linear demonstrating that the fish were consuming oxygen at the same rate throughout the experiment and therefore were not affected by the decreasing

Table 1. Comparison tables of the results obtained for the control group and those obtained for the treated group for all three dimensions. Probability levels of the distribution being random were obtained by Fisher Exact Probability tests.

Height variance		
	Change	No change
Control	0	5
Treated	8	2
		$p = 0.014$
Significant increase		
	Significant increase	No significant increase
Control	0	5
Treated	6	4
		$p = 0.042$
Length variance		
	Change	No change
Control	0	5
Treated	4	6
		$p = 0.154$
Breadth variance		
	Change	No change
Control	1	4
Treated	4	6
		$p = 0.350$

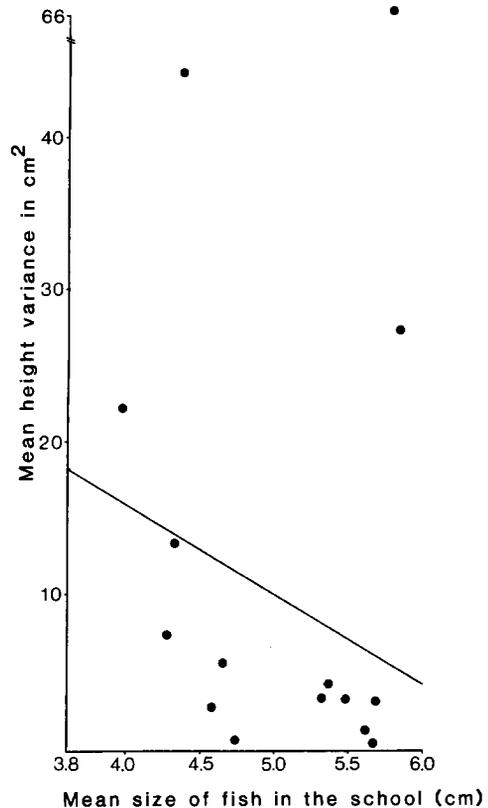


Fig. 5. Negative relation (Spearman correlation,  $p < 0.01$ ) between the mean size of fish in all the schools for the first two week acclimation period (current only) and their mean height variance (MHV). Line fitted by least-squares method excluding the outlier with a MHV of 66 (Dixon's test,  $p < 0.05$ )

amount of oxygen in the water. In addition, when groups of three were placed in the respirometer they formed a tight grouping on the same plane, usually with two individuals forming a lead row with the third fish located midway between and one half to one body length behind them.

When the small individuals (5 cm in length) were used, no detectable reduced oxygen consumption was found between the sum of the individual rates and the consumption rate for the entire school (Table 2). Hence, any energy savings through hydrodynamic benefits from schooling were either nonexistent or too small to be measured by this method. Therefore, fish of this size apparently do not receive any appreciable hydrodynamic benefits from schooling.

Fish of the larger size group (6 cm in length) did achieve substantial benefits from schooling (Table

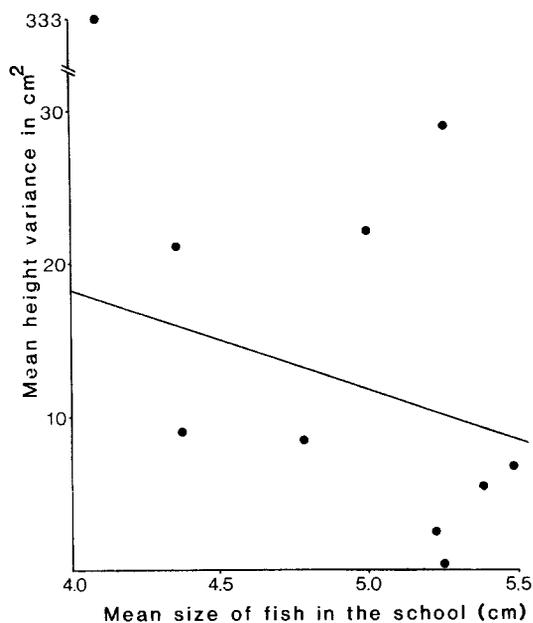


Fig. 6. Negative relation (Spearman correlation,  $p < 0.05$ ) between the mean size of fish in the treated schools for the second two week acclimation period (exposure to predator) and their mean height variance. Line fitted by least-squares method excluding the outlier with a MHV of 333 (Dixon's test,  $p < 0.01$ )

2). The respiratory rate for the school was approximately 13% lower than the sum for the individuals. When the respiratory rates of isolated individuals were measured they were much higher than that obtained when paired. Therefore, the lower value from the school is indicative of a hydrodynamic energy saving, not of calming from being in a school.

## Discussion

This experiment tested the hypothesis that fish schools are capable of providing hydrodynamic benefits. Two experiments were performed to test

this hypothesis. The first experiment examined the school structure when fish were placed first in a current and then with a current and a predator. This experiment was based on the inability of a single school structure to be both hydrodynamically efficient and best allow the school to detect and avoid predators. The inability to provide either function should result in an unchanged structure when the environment changed. However, if the schools are capable of providing both functions the schools should change from a flat, hydrodynamically efficient structure to a staggered structure which maximizes the sensory capabilities of the school. The second experiment directly tested the ability of fish schools to provide hydrodynamic benefits. If fish schools are capable of providing hydrodynamic benefits, then the respiratory rate for the schools should be less than the sum of the respiratory rates for individuals swimming alone.

The results of the first experiment found that six of the ten treated schools changed their school structure as predicted while none of the five control schools changed. The schools which did not conform to the hypothesis also exhibited behavioural differences when they encountered a predator. Typically the schools remained cohesive for initial attacks by the predator but after further attacks eventually broke up as individuals hid. However, in three of the four exceptions the schools always broke up upon initial contact. The fourth exception appeared to school regardless of any casualties. It is possible that the exceptional structural responses were a result of some underlying behavioural difference between these and the other schools.

The respirometer experiments provided evidence consistent with the hydrodynamic hypothesis. However, it is impossible to determine whether the reduced respiratory rate of the school represents hydrodynamic benefits or additional calming

Table 2. Summary of the respiratory rates ( $\text{mg h}^{-1}$ ) for fish swimming against a 7 cm per second current.

School	Summary rate (paired)	School rate	Percent decrease	Summary rate (individual)	Mean size (mm)
1	8.40	7.26	13.6	13.50	62
2	7.83	6.75	13.8	16.08	59
3	5.43	5.64	3.9	-	50

by being in a school. Evidence from the literature does not suggest that further calming is achieved by increasing group size from two to four individuals in goldfish (Shlaifer 1938). No similar studies have been performed on shiners but it is unlikely additional calming would be observed in this species. Therefore, since pairing fish in the respirometer did reduce metabolic rates when compared with the rates when isolated (Table 2), the data does provide support for the conclusion that metabolic rates of the school were reduced due to hydrodynamic benefits.

This experiment also noted that size of the fish in the school appeared to influence the observed structure. Schools of larger individuals tended to have flatter school structure. In addition, the school of smallest individuals in the respirometer did not have any measurable energy savings from schooling. This suggests that size of individuals may influence hydrodynamic benefits (a factor not predicted by Weihs 1975), however further study is necessary.

Many studies have been devoted to understanding why fish school, yet the ability of fish to use their school structure for hydrodynamic benefits is still theoretical. Partridge et al. (1983) provided the first evidence that tuna schools have the correct structure for achieving hydrodynamic benefits. However, it was believed that prey schools would be unlikely to adopt a hydrodynamically efficient structure because greater selective pressures were placed on other school functions such as antipredator benefits (Partridge & Pitcher 1979). This study has demonstrated that schools of blackchin shiners are able to assess their environment and alter their school structure to adopt the required function.

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### References cited

- Beamish, F.W.H. 1966. Swimming endurance of some north-west Atlantic fishes. *J. Fish. Res. Board Can.* 2: 341-347.
- Belyayev, V.V. & G.V. Zuyev. 1969. Hydrodynamic hypothesis of school formation in fishes. *J. Ichthyol.* 9: 578-584.
- Cullen, J.M., E. Shaw & H.A. Baldwin. 1965. Methods for measuring the three-dimensional structure of fish schools. *Anim. Behav.* 13: 534-543.
- Eggers, D.M. 1976. Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption. *J. Fish. Res. Board Can.* 33: 1964-1971.
- Heiligenberg, W. 1974. Processes governing behavioural states of readiness. pp. 173-200. *In: D.S. Lehrman, J.S. Rosenblatt, R.A. Hinde & E. Shaw (ed.) Advances in the Study of Behaviour*, Vol. 5. Academic Press, New York.
- Heczko, E.J. & B.H. Seghers. 1981. Effects of alarm substance on schooling in the common shiner (*Notropis cornutus*, Cyprinidae). *Env. Biol. Fish.* 6: 25-29.
- Olson, F.C.W. 1964. The survival value of fish schooling. *J. Cons. Perm. Int. Explor. Mer.* 29: 115-116.
- Partridge, B.L., J. Johansson & J. Kalish. 1983. The structure of schools of giant bluefin tuna in Cape Cod Bay. *Env. Biol. Fish.* 9: 253-262.
- Partridge, B.L. & T.J. Pitcher. 1979. Evidence against a hydrodynamic function for fish schools. *Nature* 279: 418-419.
- Pitcher, T.J., A.E. Magurran & I.J. Winfield. 1982. Fish in larger shoals find food faster. *Behav. Ecol. Sociobiol.* 10: 149-151.
- Shlaifer, A. 1938. Studies in mass physiology: effect of numbers upon the oxygen consumption and locomotor activity of *Carassius auratus*. *Physiol. Zool.* 11: 408-424.
- Siegel, S. 1956. *Nonparametric statistics for the behaviour sciences*. McGraw-Hill, London. 312 pp.
- Weihs, D. 1973. Hydromechanics of fish schooling. *Nature* 241: 290-291.
- Weihs, D. 1975. Some hydrodynamical aspects of fish schooling. pp. 703-718. *In: T. Wu, C.J. Brokaw & C. Brennen (ed.) Swimming and Flying in Nature*, Plenum Press, New York.

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