

SCHOOL STRUCTURE OF THE SQUID *LOLIGO OPALESCENS*

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ABSTRACT

The squid *Loligo opalescens* forms schools which are similar in many respects to those of obligate schooling fishes. These schools are marked by parallel orientation of individuals and strong cohesiveness. Laboratory experiments indicate that the main sensory modality regulating schooling is vision. Squid on opposite sides of a clear rigid Plexiglas barrier readily schooled. The structure of schools of six squid depended on size of individuals and was modified by environmental disturbance. Parallel orientation was weaker in schools of smaller squid (ca. 7 cm dorsal mantle length) than it was in larger ones (ca. 12 cm). In the field, *L. opalescens* schools are composed of uniformly sized individuals. Laboratory experiments designed to determine whether this was due to actual size selection were inconclusive, but they did suggest mechanisms which might be important in determining squid position in the school.

Considerable effort has been spent in understanding the schooling behavior of fish in terms of physiological mechanisms and possible survival value and ecological consequences. (See reviews by Radakov 1973 and Shaw 1970, 1978.) Virtually no work has been done on schooling behavior of invertebrates which occur in the same environments as schooling fish. The most evident schooling invertebrates in the pelagic environment are the squid. Squid and fish play very similar ecological roles and the two groups of organisms possess a large number of similarities. (See Packard 1972, for a discussion of convergent evolution.)

Loligo opalescens is common off the west coast of North America with a reported range from Baja California to lat. 55°N (Fields 1965; Bernard 1970). Relatively little is known of the behavior or general ecology of *L. opalescens* in spite of the fact that there is a fishery for this species in California. The fishery is based primarily upon the tendency of squid to spawn in large aggregations in shallow water (McGowan 1954; Fields 1965). Very little is known about the distribution or location of newly hatched squid as well as squid in later stages of life. Attempts to catch the juveniles have often been unsuccessful (Okutani and McGowan 1969) and only recently have attempts been made to catch nonspawning adults. Even though field data are difficult to obtain, it is possible to keep both juvenile (Hurley 1976) and adult *L. opalescens* alive in the laboratory. Schooling in the

laboratory was examined to provide insights about the function of schooling in squid.

METHODS

The squid used in the behavioral studies were obtained either by dipnetting them after they had been attracted to an underwater light or by purchasing them from a local bait dealer. In the laboratory, the squid were maintained in a 3-m diameter circular tank with rapidly circulating seawater. They were fed irregularly on small fish (either mosquitofish, *Gambusia affinis*, or goldfish, *Carassius auratus*). Mosquitofish were taken much more readily than were the goldfish. Occasionally, the squid could be trained to take dead food. This was accomplished by first getting them to accept live fish and by then throwing dead fish in along with the live ones. In this manner, the squid could also be coaxed to accept pieces of frozen northern anchovy, *Engraulis mordax*. If the squid were undamaged when they arrived at the laboratory and there was an abundant supply of small fish available, it was relatively easy to keep them for over a month.

Experiments designed to examine various aspects of schooling behavior were run in a 2 × 3 m rectangular Plexiglas² tank which was filled to a depth of 0.4 m. The tank was painted flat white and the primary source of lighting (in addition to general room illumination) was provided by

¹Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, CA 95039.

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

fluorescent lights placed around the perimeter of the tank which shone through the walls. This provided even, diffuse light in the tank. The water in the tank was noncirculating.

Schooling behavior was recorded on Tri-X film using a 35 mm camera with motor drive and a variable setting automatic timer. A mirror was placed above the tank and pictures were taken of the squid by photographing the surface image reflected in the mirror. A black plastic barrier surrounded the experimental tank. A small hole in the barrier allowed observations to be made of the squid without disturbing them. Exact methods, timing of pictures, etc. varied with the experiment and will be described in the appropriate section.

After the films were developed, they were analyzed using a Scientific Data Products data tablet (Graf-Pen) coupled with a PDP 11-45 computer. The data tablet is a set of microphones placed at right angles which record the sound produced by an electrical spark made by a special marking pen. The x and y coordinates of a point were relayed to the computer by pressing the pen down on the tablet at that point. This device allowed the recording of large amounts of squid position data. In each frame, the tip of the tail, the tip of the outstretched arms, and a point midway between the two eyes were recorded for each squid. Other information, such as the position of barriers, was recorded in the same way. Measurements taken from the photographs were subsequently converted to real distances by multiplication by appropriate scale factors.

Students of schooling have examined school geometry both as a two-dimensional system on a horizontal plane (Breder 1959; Williams 1964; John 1964; Hunter 1966, 1968; Van Olst and Hunter 1970) and as a three-dimensional structure (Cullen et al 1965; Symons 1971a, b; Pitcher 1973). Since squid schools do have a three-dimensional structure in nature, a three-dimensional analysis will eventually be necessary to determine all of the structural details of the school. A three-dimensional analysis, however, is much more difficult than a two-dimensional analysis. It was felt that a two-dimensional analysis would suffice to examine certain aspects of squid schooling behavior. In these experiments, the squid were very nearly confined to a two-dimensional plane by the shallow water depth in the experimental tank. Observations of small schools (up to six squid) in a deeper tank (1 m

depth) indicated that the two-dimensional structure observed in the experimental tank was not uncommon.

Three indices were chosen to quantify the angular orientation of individuals in a school, the overall shape of the school, and the distance between neighboring individuals in a school. These indices were proposed by Hunter (1966) and he includes a detailed discussion of their properties. The three indices are:

1. Mean separation distance: An average of the horizontal distances separating each squid from every other squid in the school. It is influenced by school shape, distance between neighboring squid, and number of squid in the school. Distances between all possible pairs of squid are measured and these values are averaged. Distance is measured between the two closest points on the midline of the bodies (including outstretched arms) of the two squid.

2. Mean distance to nearest neighbor: An average of distances from each squid in the school to its nearest neighbor. The measurement is made between the two closest points on the midline of the bodies (including outstretched arms) of the two squid. The same measurement is used twice if two squid are closer to each other than to any other squid.

3. Mean angular deviation: This is a measure of the differences in orientation among squid within a school. The heading of each squid is determined and the resultant direction of the school is computed by assigning each squid a value of one and adding the headings vectorally. The mean number of degrees individual squid deviated from this resultant direction of the school was calculated as the index of orientation.

One difference between squid and most of the schooling fish which have been studied is that squid readily swim both forward and backward. Thus, a squid with an orientation that was 180° out of phase with the rest of the school might still be swimming with the rest of the school. For this reason, one orientation measure was calculated which regarded the squid as a line segment rather than as a directed vector and measured the smallest angular deviation between line segments. Such measurements were rarely different from measurements made considering the orientation of the squid and therefore will not be considered further in this paper.

Where measurements of squid length are given, they are of dorsal mantle length from tip of the pen to the tip of the tail. The total length of the squid (including arms but excluding tentacles) is about 1.3-1.5 times the dorsal mantle length (Fields 1965).

RESULTS

Response to Disturbance

One set of factors that caused changes in schooling can be grouped under "external disturbances." These included introducing objects (such as a net) into the water near the squid or tapping on the side of the tank. The typical response was for the squid to group more tightly and, in cases where it was not already marked, to increase the degree of parallel orientation. The amount of change in schooling behavior and the temporal characteristics of this change depended upon the nature and intensity of the disturbance and upon its duration.

One attempt at quantifying the stimulus involved placing an aquarium air stone in the tank. Pressurized air delivered to this air stone in differing amounts and duration produced a stream of bubbles which could be used as a disturbance stimulus of varied intensity and duration. A small stream of bubbles produced little squid reaction, while vigorous water action due to the bubble stream produced marked changes in behavior. Figure 1 shows the changes in three of the schooling indices in response to a moderate disturbance caused by turning on the air bubble stimulus. The degree of parallel orientation, which was already pronounced, did not change appreciably. But the squid did draw noticeably closer together.

Schooling Structure as a Function of Squid Size

Six squid of nearly equal size were haphazardly taken from the holding tank and placed in the experimental tank. The squid swam in this tank for an hour before measurements were made. With the exception of one experiment, a picture was taken of the squid every minute for approximately 1 h. During this other experiment, a picture was taken every 10 s for 10 min. This set of experiments was conducted during the daylight hours of two different days. All of the squid used in this set of experiments had been captured on the same night.

There was a decrease in the mean angular deviation as the size of the squid increased (Table 1). Since small values of the mean angular deviation index are associated with increased parallel orientation, the degree of parallel orientation is greatest in schools composed of large individuals. Even in the case of the small individuals, however, the value of the index does not approach what would be expected if the squid were each orienting in a random direction. In a simulation of 1 million values for six randomly oriented fish, Hunter (1966) found that the mode of the frequency distribution was 69°.

Although the average values for mean angular deviation do give a measure of average departure from parallel orientation for a whole experiment, they do not give an indication of how variable a particular group of squid is in its orientation over time. For example, an experiment of 30 pictures and an average value of the mean angular deviation index of 20° could have had all of the 30 values close to 20°. This would indicate a consistent moderate degree of parallel orientation over time. On the other hand, such an average value could also come from a situation where the squid had strong parallel orientation part of the time and were much more loosely oriented the rest of the time (e.g., the index value could have been 10° on 15 frames and 30° on 15). This kind of difference can be detected if a measure of the variability of the mean angular deviation index for each experiment is calculated. The variability (standard deviation, SD, Table 1) increased with decreasing squid size, indicating that not only do the smaller squid not orient on the average in as parallel a manner as larger squid, but they are also more temporally variable in their orientation. This difference can also be seen if individual experiments are examined. Figure 2 shows the values for mean separation distance and mean angular deviation

TABLE 1.—Relationship between average size of *Loligo opalescens* and parallel orientation and separation of individuals in the six-squid experiments. Each index was calculated for each frame.

Group number	Mean mantle length (cm)	No. frames examined	Mean angular deviation index (degrees)		Mean separation distance index (cm)	
			\bar{x}	SD	\bar{x}	SD
1	7.5	44	32.0	18.4	32.3	26.5
2	7.6	58	29.0	15.3	25.6	8.0
3	7.7	60	18.1	10.7	16.2	4.5
4	9.7	19	18.5	5.7	14.0	4.2
5	9.7	62	16.2	6.2	18.7	5.2
6	10.2	69	17.2	6.6	20.9	5.0
7	11.9	65	11.1	5.6	18.5	4.0
8	12.0	55	9.6	2.8	15.3	2.7
9	12.0	46	9.1	4.2	13.8	3.0

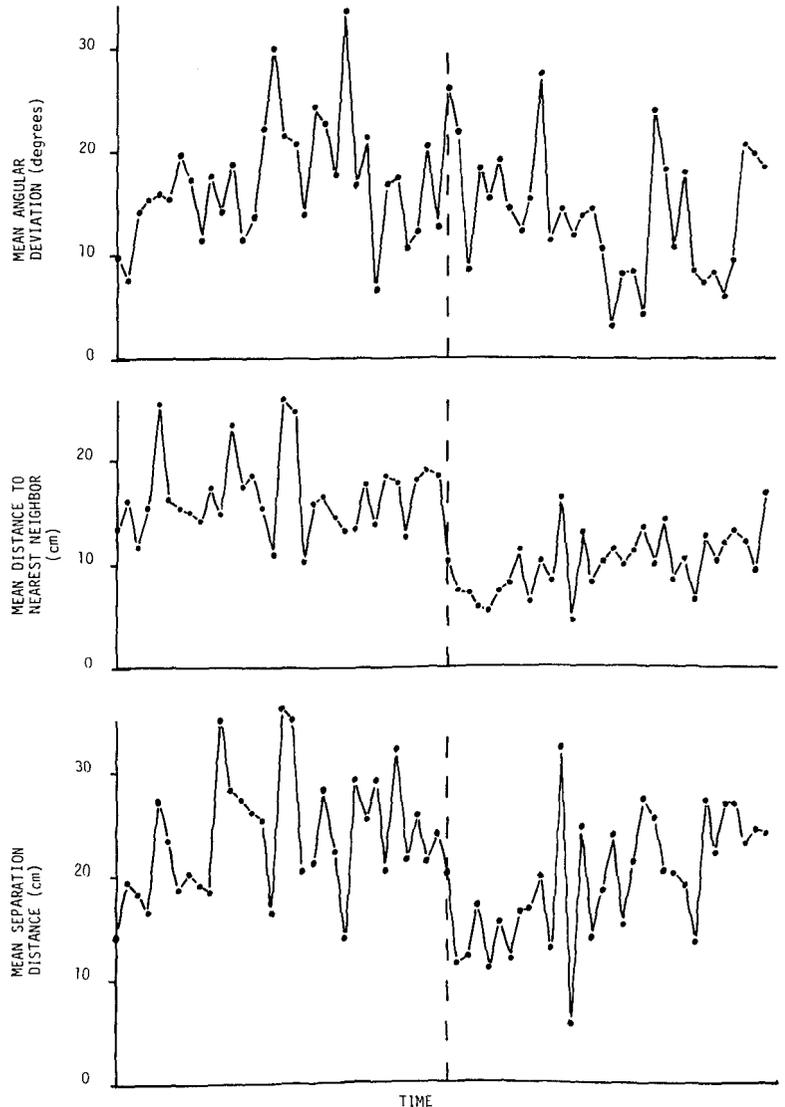


FIGURE 1.—Values of schooling indices for a school of six *Loligo opalescens* before and after disturbance (turning on bubbler). Dashed line indicates when air was turned on. Pictures were taken every minute for 64 min.

for two (Groups 3 and 7) of the experimental runs summarized in Table 1. The parallel orientation is stronger and the variability less in the larger squid (Figure 2C, D). The mean separation distance index is not as clear a function of size (Table 1; Figure 2A, B).

Schools in the Ocean

Very little is known of the natural behavior of *Loligo opalescens* when it is not in large mating schools. In many areas, there often is a large concentration of squid in the vicinity of the deep-scattering layer (C. Recksiek, Moss Landing Marine Laboratories, Moss Landing, CA 95039,

pers. commun., October 1976) and large layered concentrations of *L. opalescens* have been reported by those involved in submersible exploration (A. Flechsig, Sea Grant Marine Advisory Service, University of California at San Diego, La Jolla, CA 92093, 1973). There is evidence to indicate, however, that *L. opalescens* is often found in much smaller schools and that these schools contain a narrow size range of individuals. Fields (1965) presents data on the uniformity of size of young squid taken from the same fish catch (presumably the same squid school) and speculates that the size ranges in the schools he observed represent approximately one-half or less than one-half of a year's growth.

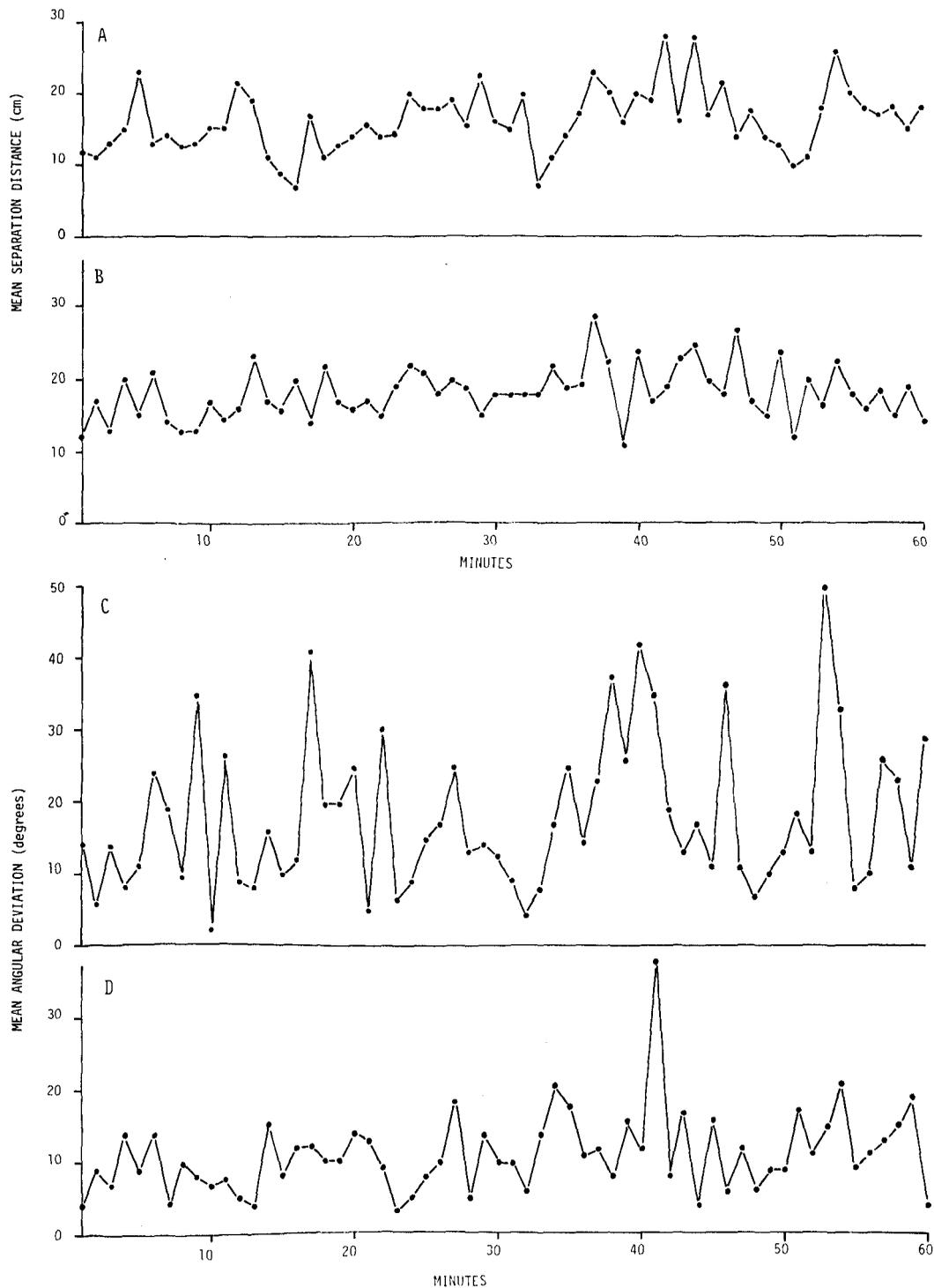


FIGURE 2.—Values of mean separation distance and mean angular deviation for two (Groups 3 and 7) of the experiments presented in Table 1. Mean size of *Loligo opalescens* in the experiment represented in A and C was 7.7 cm mantle length. Mean size of squid in the experiment represented in B and D was 11.9 cm mantle length.

I also obtained data on the uniformity of size in individuals of the same school. The squid were caught during a 1-wk period in August in locations ranging from San Diego to Santa Catalina Island, Calif. A night-light was placed off the stern of the ship in the center of an L-shaped 3-m long mesh net. Squid were attracted to the light and would rush into the net. The net was then raised and the squid could be removed with dip nets. The "schools" were all of the squid which swam into the net at the same time. Squid caught during this period ranged from 5.8 to 17.3 cm dorsal mantle length. But for a given school, they were much more uniform in length. The average size range for 29 schools of 2 to 32 individuals was 2.5 cm.

Maintenance of School Structure and Orientation

Experiments in the laboratory have indicated that vision is sufficient sensory input to mediate schooling behavior. Squid on different sides of a clear, rigid Plexiglas barrier will readily school with each other and they appear to maintain the same type of parallel orientation that is present in normal schooling behavior. Preliminary experiments using such Plexiglas barriers were run to try to elucidate the mechanisms by which spacing is maintained.

Two-Squid Experiments

Experiments were run to determine whether squid would school in the same manner with or without a clear Plexiglas barrier in place. Measurements were obtained for squid swimming together and for the same squid swimming on opposite sides of a Plexiglas barrier which divided the tank into two compartments. The order of the treatment was randomized for each pair of squid. Squid ranged in size from 7 to 13 cm mantle length. For a given experiment, the two squid were of similar length. Pictures were taken of the squid in each treatment every 10 s for 3 min after they first came together and again every 10 s for 3 min after the squid had been left undisturbed for 15 min. If the squid did not come together to within at least 0.5 m within 1 min, the experiment was terminated.

Table 2 shows the results of five such experiments. The first 3-min periods have been compared with each other, as have the later runs. This was to see if the pattern of schooling changed after the

TABLE 2.—Median nearest distances and median separation angles for two-squid (*Loligo opalescens*) experiments.

Item	With barrier	Without barrier	Difference ¹
Nearest distance (cm) first 3 min	20.6	16.2	$P = 0.05$ barrier greater
	11.3	6.6	$P < 0.01$ barrier greater
	38.6	11.65	$P < 0.01$ barrier greater
	14.9	7.9	$P < 0.01$ barrier greater
Nearest distance (cm) second 3 min	13.8	6.4	$P < 0.01$ barrier greater
	24.2	15.8	$P < 0.01$ barrier greater
	18.4	6.3	$P < 0.01$ barrier greater
	23.9	18.35	$P < 0.05$ barrier greater
Separation angles (degrees) first 3 min	14.35	13.1	$P < 0.05$ barrier greater
	12.5	8.2	$P < 0.01$ barrier greater
	16.4	52.7	$P < 0.01$ barrier less
	24.3	11.2	$P < 0.05$ barrier greater
Separation angles (degrees) second 3 min	75.1	21.0	$P < 0.01$ barrier greater
	21.2	12.2	NS ²
	17.0	30.9	$P < 0.05$ barrier less
	28.2	15.4	$P < 0.05$ barrier greater
Separation angles (degrees) second 3 min	15.4	13.6	NS
	19.1	18.0	NS
	25.4	18.3	NS
	11.1	24.9	$P < 0.05$ barrier less

¹Significance of difference in medians from Mann-Whitney *U*-test.

²NS = no significant difference, $P > 0.05$.

squid became more adapted to the experimental regime. This table presents results for the median nearest distance between the two squid for each run and for the median separation angle for these same runs. Separation angle for each frame is simply a measurement of the angle between the two squid and is a measure of orientation (0° separation angle indicating parallel alignment facing the same direction).

The barrier has an effect upon the separation distance between the two squid. In all cases, there was a significant difference between the distance between squid with and without the barrier. When the Plexiglas barrier was present, the squid tended to space themselves farther apart. There is not a clear relationship between angular separation and the presence of the barrier. Of the six runs showing significant differences, three had greater median separation angles with the barrier in place and three had greater median separation angles when the barrier was not present.

Three-Squid Experiments

The experimental tank was divided crosswise into three equal compartments (1×2 m each) by clear Plexiglas partitions. A squid was chosen from the holding tank and was placed in the central compartment. Then a squid for each of the outer compartments was selected. These squid were assigned at random to each of the outer compartments. The squid were allowed to adapt to the experimental situation for 15 min and then were filmed for 5 min (one picture every 10 s). The two

outer squid were then switched from one outer compartment to the other and the squid were again allowed to adapt for 15 min. They were then filmed for 5 min (once every 10 s). Squid in these experiments ranged from 9.2 to 15.3 cm mantle length.

It was hoped that this experimental design would indicate whether the center squid, if given a choice, would choose to school with a larger or smaller squid or one closer to its own size. One way to determine whether such a choice is being made would be to determine whether the center squid spends more of its time closer to one outer squid than to the other. Each 5-min run was considered as a unit and each frame was scored according to which outer squid the center squid was nearest. For each run, the data were compared with a binomial distribution which assumed that the center squid had an equal probability of being closest to either outer squid. Of the 17 runs, 16 showed a significant deviation from the expected binomial distribution ($P \leq 0.05$ for 1; $P \leq 0.01$ for 15). These 16 runs were now grouped according to whether the center squid was closest to the larger or smaller outer squid. In 8 of the 16 cases, the center squid was nearest the larger outer squid, while in the other 8 cases, it was nearest the smaller squid. There is no evident preference for large versus small squid. The data can also be arranged to determine whether the center squid spent most of its time near the squid closer to its own size. There were 14 runs for which it was possible to say that the center squid was closer in size to one of the outer squid. Of these 14 runs, the center squid was significantly nearer to the squid closer to its own size 9 times and nearer to the squid farther from its own size 5 times.

These experiments may be viewed in another way by looking at the absolute position of the squid in the tank. The nearest distances of the squid to the Plexiglas barriers were calculated for each frame. These data are summarized in Figure

3 for the 17 runs. The side squid usually are very near the barrier which separates them from the center compartment, while the center squid varies his position within the center compartment, but approaches the Plexiglas barriers much less often.

DISCUSSION

Pelagic fish and squid represent a striking case of convergent evolution, not only morphologically (Packard 1972), but behaviorally as well. One aspect of behavior where this is particularly apparent is schooling. Since many of the same ecological pressures exist for both pelagic groups, it is not surprising that some sort of schooling behavior would have developed in both fish and squid. What is surprising, given the very different physiology and mode of locomotion, is that so many aspects of this behavior are the same.

Loligo opalescens fits Breder's (1967) definition of obligate schoolers. Single *L. opalescens* are rarely caught in the field, and they immediately come together when placed in a tank in the laboratory. As has been reported for many species of fish (Radakov 1973), *L. opalescens* schools consist of individuals of approximately the same size. It has been suggested that the reason that fish school in such groups has to do with swimming speed. Small and large individuals would not swim at the same speed and thus would not normally stay together. This is possibly also true for squid, but data on the swimming speed of large and small *L. opalescens* are not available to substantiate the argument. For several reasons, the swimming speed hypothesis seems less plausible for squid than for fish. In schools of fish which show parallel orientation, the fish continually maintain forward motion and thus swimming speed is likely to be an important factor. But field and laboratory observations have indicated that individuals in squid schools spend much of their time hovering in the same position in the water column with only

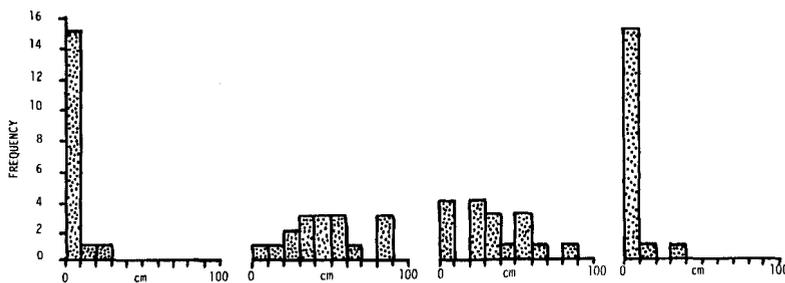


FIGURE 3.—Histograms of mean nearest distance between *Loligo opalescens* and barrier in the 17 three-squid experiments. Distances are broken up into 10-cm intervals. From left to right: left outer squid to left barrier, center squid to left barrier, center squid to right barrier, right outer squid to right barrier.

slight backward and forward motion caused by jets of water from the siphon. Even when disturbed, the squid do not make long extended swims which would tend to sort out those of differing swimming ability. In the field, the most common response of a squid school to a disturbance (the presence of a scuba diver or a shark) is to clump closer together and move off a slight distance. On one occasion when I was diving in a large spawning school (several thousand individuals), the squid executed the same type of maneuver that has been reported for fish schools. Instead of moving off, the school completely enclosed me, leaving a spherical space of approximately 3 m radius around the "predator."

One other piece of evidence suggests that it is not differences in swimming speed alone which cause the squid to school according to size. While diving in the Bahamas in the Hydrolab underwater habitat, we observed a school of squid which routinely visited the habitat. This school was composed of *Doryteuthis plei*, a species which quite closely resembles *L. opalescens* and presumably has similar swimming ability. This school consisted of seven squid and, in this case, was not composed of individuals of the same size, the largest individual being at least two times the length of the smallest individual. We chased this school several times but were never able to force them to separate. The smallest squid maintained the same swimming speed as the largest squid.

It is possible that squid maintain schools of individuals of a fairly narrow size range because of social factors. Generally, workers studying schooling have assumed that all of the fish in a school may be treated as equivalent individuals in the production of the behavior and that there is no social structure in the schools. In fact, some workers have suggested that schooling is really just a modified form of individual cover-seeking behavior (Williams 1964; Hamilton 1971). This assumption of equality of individuals may be an untenable one for squid schools. In the field, Hochberg and Couch (1971) observed signaling by some members of a school of *Sepioteuthis sepioidea* which they felt prevented other squid from joining the school. Furthermore, in the laboratory, I have observed complicated aggressive interactions in *L. opalescens* which certainly demonstrate that all squid cannot be considered behaviorally equivalent individuals at all times (Hurley 1977).

One aspect of schooling in fish which has been emphasized by many workers is that the structure

of schools may change as a function of the age or the physiological condition of the fish. Van Olst and Hunter (1970), for instance, found that in five species of marine fishes, schools of young fish were less compact and showed greater differences in angular headings than did schools of adult fish. In addition, Hunter (1966) showed that distances between jack mackerel tended to increase with food deprivation, while Keenleyside (1955) noticed that sticklebacks were more densely packed in a school when well fed than when starved.

I attempted to determine whether similar phenomena were observable in squid schools. Schools of small squid (7-9 cm mantle length) gave the impression of being less cohesive than schools of larger squid (13-15 cm mantle length). This was supported to some extent by the quantitative measurements, particularly those of angular orientation. The variability was also higher for all of the indices for the smaller squid. It has been suggested for fish (Van Olst and Hunter 1970) that the observed change with size could have been an adaptation to the higher food requirements of the juvenile fish. This speculation is supported by observations that a number of species school less cohesively under conditions of food deprivation. The same explanation may also hold for squid, but my existing data do not support it. I ran two experiments in which schools of six squid were filmed before and after feeding. In one experiment, there were no significant differences in the schooling indices before and after feeding, while in the other, there was significantly less school cohesion and parallel orientation after feeding. In any event, it is not possible to guess which factors are instrumental in this increased cohesiveness and consistent geometry.

As is the case for fish, vision seems to be the primary sensory system used in squid schooling. Squid will readily school across a clear, rigid Plexiglas barrier, although they tend to stay somewhat farther apart than they normally would. Investigators dealing with fish also found that the presence of a clear, rigid barrier caused abnormalities in the spacing between individuals, in some cases increasing the fish-to-fish distance (Cahn 1972) and in some cases decreasing it (Shaw 1969). These workers speculated that this change was due to lack of lateral line input and a resultant loss of information concerning the position of the adjacent fish. Squid do not have a similar extensive vibration-sensitive system, although they may be able to detect vibrations with their stato-

cysts. In the case of *L. opalescens*, the most likely explanation for this change in spacing is that the presence of the barrier physically limits the extent to which each squid can compensate for the other individual's movements. In the experimental tank, squid seemed to differ in their motivation to school. When the barrier was not present, a squid with a strong tendency to school could always maintain proximity to another squid. But if the barrier were present, that squid could only follow another squid as far as the barrier and had to remain there until the other squid returned.

I had hoped that the experiments with the three squid separated by Plexiglas barriers would give some clue as to whether the squid actively chose to school with individuals of the same size, but the results were inconclusive. The results did indicate, however, a possible mechanism for maintenance of spacing within a school. The center squid tended to stay toward the middle of the compartment, while the side squid maintained positions very near the Plexiglas barrier. It is possible that the center squid was attempting to equalize the visual angle subtended by the squid on each side, while the outer squid were attempting to get into positions with squid on each side. The measurements of visual angle which I can get from my photographs are not accurate enough to determine whether this is happening. If outer squid are continually trying to achieve a position where they have squid on either side of them, individuals in a school should be continually shifting positions. Casual observations have indicated that this does happen some of the time; but at other times, the individuals maintain the same positions relative to one another.

An area where a comparison of squid and fish schooling may be useful is in the speculation concerning the evolution of the schooling behavior and its possible advantages. Many recent papers have concentrated on the hydrodynamic advantages of fish schooling (e.g., Breder 1976) and base their explanations of many of the details of school structure on the fish mode of tail-flip locomotion and the vortices which are subsequently created. Van Olst and Hunter (1970) suggest that the typical nearest neighbor distance in fish schools is about one-half a body length and that this distance may be explained by considering the amplitude of the tail beat in swimming. It is interesting that in squid, with their very different mode of locomotion (jet propulsion as opposed to tail flips), the spacing between nearest neighbors is still maintained be-

tween one-half and one body length in undisturbed squid.

Other investigators have speculated that a primary function of schooling is as a defense against predation. (See reviews by Shaw 1970 and Radakov 1973.) Squid have many of the same reactions to disturbance that fish do. They both clump more closely together as a result of disturbance and both have been seen to surround their predators. Further evidence which suggests that predator defense may be an important function of squid schooling comes from the development of the behavior in juvenile squid. In the course of rearing *L. opalescens* (Hurley 1976), I made observations on schooling behavior. The newly hatched squid appeared to have no attraction to each other, but after 6 or 7 wk schooling was occasionally observed. This schooling was only evident in response to disturbance (tapping on the tank or putting a net into the water). When the squid were feeding undisturbed, there was no obvious schooling behavior.

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