

# Fish Schooling: A Possible Factor in Reducing Predation

By

Vernon E. Brock and Robert H. Riffenburgh\*

Bureau of Commercial Fisheries, Biological Laboratory, Honolulu, Hawaii

---

## Introduction

The schooling of fishes has long attracted attention, and a number of workers have studied fish schools and the behaviour pattern of the fish to gain some understanding of the nature of the factors responsible for schooling.

PARR (1927) described the schooling behaviour of chub mackerel and killifishes in aquaria and concludes that the behaviour observed is a visual response to other individuals of the same species. BREDER and HALPERN (1946) found that blinded goldfish do not school, and BREDER (1951) in his study of schooling in *Jenkinsia* states that schooling will not occur in darkness or with blinded fish for some ten species which have been tested by various authors. KEENLEYSIDE (1955) found that blinded fish did not school effectively but there was evidence that the blinded fish could detect others, possibly through smell. SPRINGER (1957) concluded that his observations of a school of *Jenkinsia* "make untenable the view that individual fish of this school maintained contact with one another solely by visual means". BREDER (1954) developed equations descriptive of the forces in schooling.

In general, the concern of the authors briefly reviewed above was with the internal factors responsible for schooling, and the school was considered largely as an isolated phenomenon. However, BREDER and HALPERN briefly discuss the possibility that schooling may confer some protection from predation and indicate some of the difficulties which must be considered, but the matter is not developed quantitatively. SPRINGER described a school which resembled an unknown large creature as an example of "collective mimicry" and was, in the authors' opinion, protected by its frightening appearance. WELTY (1934) experimented with the effects of grouping fishes on learning, and found that, except for mudminnows, grouped fishes learned faster, retained longer, and ate more than did isolated fishes of the same species. The grouped fishes tended to respond as a unit, a mixture of fishes with two different responses to the

---

\* Also on mathematics faculty, University of Hawaii, Honolulu.

same stimulus responded more slowly than did a group trained to give a single uniform response to the stimulus, an effect which WELTY labelled group cohesion.

Species of fish that ordinarily school and school strongly seem to have two characteristics in common: (1) they are open water species whose immediate environment offers little in the way of shelter and (2) they are not climax predators, at the end of a food chain, but are prey species at least for a substantial portion of their life history. Likewise, the predators at the end of a food chain are ordinarily non-schooling, solitary fish.

This aspect of the predator-prey relationship suggests that schooling may confer some protection against predation and that for perhaps similar reasons predators function more effectively if solitary.

The schooling of some predatory species such as the tunas does not necessarily constitute contrary evidence. There is evidence that for much of the life span of these species, they are prey species, and when they do attain sizes sufficient to render them largely immune from predation, the schools formed are smaller and less stable than is true for younger and smaller fish of the same species. SETTE (1950) suggests that schooling of predators may assist in the capture of prey. His discussion of the reasons for such an advantage would seem to apply after the prey was located. If the relationships suggested in this paper between predator and prey be true, it would seem that schooling by a predator may, under some conditions, reduce the efficiency of scouting for prey.

If schooling does provide some protection against predation, this may occur simply because scattered prey will be detected more frequently by a predator than would be true of the same number of prey bunched into a school. While the true measure of the validity of this concept must depend upon observations and measurements in the field, certain relationships which seem essentially reasonable, make it seem likely that schooling is, in one common aspect, a mechanism of protection against predation. This aspect of schooling will be discussed with the assumption that the means of detection employed by the predator is visual. Other means of detecting prey are, of course, possible; their use would not change the conclusions reached on the basis of a visual model unless detection is independent of distance.

Consider schooling as a protective device; there are two factors operating at cross purposes: if a single fish is regarded as a group of size one, schooling (a) reduces the number of groups and consequently the frequency of encounter with predators; we shall call this encounter advantage; (b) increases the size of groups, thus increasing the chance of detection; we shall call the advantage here lost a detection advantage. A third factor which may give an advantage from schooling is the limitation of capacity of the predator. If a predator sights a large school of prey, he will eat to capacity, possibly leaving alive most of the school, and will reduce his searching activity to a negligible amount for some time thereafter. We shall call this advantage due to the predator's limited capacity a capacity advantage.

### Development of Method

We shall develop probabilities for advantages of schooling on the basis of mathematical models relating to the above events. We shall consider in this paper only non-schooled predators; if predators school, they overlap each other's sight ranges, reducing the volume of ocean scouted and hence reducing

scouting efficiency. Schooling of predators would be advantageous to the predators only in the special case in which their prey are schooled and cannot be seen at full sight range; here a predator could see another predator engaging in feeding activity when he could not see the prey being consumed. A consideration of the optical peculiarities of water is pertinent in this connexion. The distance which an object of given size can be seen depends upon two factors: the intercept angle at the eye and the contrast difference between the object and the background. Due to backscatter and light absorption an object of the highest contrast will fade from sight regardless of size at a relatively small distance, say 200 feet or less, even in the clearest water. This means that for objects above a fairly modest size, large enough to give an intercept angle adequate for effective vision at the distance where light absorption and backscatter reduce contrast difference to the point of invisibility, taken at 2 per cent. for man (DUNTLEY, 1952), any increase in the size of the object will not effectively increase the distance which it may be seen. The critical intercept angle for the human eye is taken as one minute which would occur for an object 0.72 inches in diameter at 200 feet.

Consequently the observation of feeding behaviour of a predator by another as a means of locating food would be effective only for rather small prey; the greater the reduction of sight range by contrast loss, the smaller the prey.

In supposing that schooling is of advantage to prey, we shall give predators every advantage, hence the first two assumptions given below. But predation will be assumed effective only during daylight hours.

#### Definitions:

- (1)  $n_p$  represents the number of predators.
- (2)  $n_f$  represents the number of prey ( $f$  for food fish).
- (3)  $n_e$  represents the number of schooled prey a predator can hold at one eating.
- (4)  $r$  represents the distance at which a predator can see its prey.
- (5)  $r'$  represents the radius of a school of prey (assumed to be approximately spherical).
- (6)  $d_{ik}$  represents the distance between the  $i$ th prey and the  $k$ th predator,  $i = 1, 2, \dots, n_f$ ,  $k = 1, 2, \dots, n_p$ .
- (7)  $d_{k'}$  represents the smallest  $d_{ik}$  for any  $k$ , i. e.  $\min(d_{ik})$ ,  $k = 1, 2, \dots, n_p$ .

#### Assumptions:

- (8) If a predator is in sight of a prey, he will sight it.
- (9) If a predator sights a single prey, he will eat it.
- (10) The average distance between predators and between non-schooled prey is greater than  $r$ .
- (11) Predators and prey move randomly.
- (12) The concentrations of predators and prey are constant.
- (13) If schooling occurs, all members are schooled and schooled in a single school. (It will be seen later that this assumption may be relaxed.)

$d_{ik}$  are random continuous variables, and therefore so are  $d_{k'}$ . Whenever  $d_{ik} > r$ , the  $i$ th prey remains alive; thus whenever  $d_{ik} \leq r$ , the  $i$ th prey is eaten. Let us denote by  $P[d_{ik} \leq r]$  the probability that the  $i$ th prey is sighted (and therefore eaten) by the  $k$ th predator.

Since the  $d_{ik}$  are random for all  $i$  and all  $k$  and the initial positions of all fish at daybreak are random,

$$(14) \quad P[d_{ik} \leq r] = P[d_{jl} \leq r], \quad i, j = 1, 2, \dots, n_f; \quad k, l = 1, 2, \dots, n_p.$$

Hence the expected number of non-schooled forage fish which will be eaten is  $n_f n_p P[d_{ik} \leq r] \equiv E_1$ .

In the case of schooled fish, the probability that the  $k$ th predator will sight the school will be  $P[d_{k'} \leq r]$ ,  $k = 1, 2, \dots, n_p$ . Since  $d_{ik}$  are random for all  $k$  and initial positions of predators at daybreak are random,

$$(15) \quad P[d_{k'} \leq r] = P[d_{l'} \leq r], \quad k, l = 1, 2, \dots, n_p.$$

Hence the expected number of schooled prey which will be eaten is  $n_e n_p P[d_{k'} \leq r] \equiv E_2$ .

It follows that whenever schooling is advantageous to the prey,

$$(16) \quad E_2 < E_1,$$

or, upon substituting, rearranging, and cancelling,

$$(17) \quad \frac{n_e}{n_f} < \frac{P[d_{ik} \leq r]}{P[d_{k'} \leq r]}$$

since all components are non-negative.

At this point a few comments are in order. It should be clearly recognized that the primary variable ( $d_{ik}$ ) being considered is distance and is the distance between two particular, randomly placed fish; it does not involve a number of fish in any sense. It would be possible to consider the number of prey within sight of the predator at any time, which would be a discrete variable having a poisson distribution with parameter the expected number of prey in an ocean volume the size of the predator's sight sphere, viz.  $\mu \frac{4}{3} \pi r^3$ , where  $\mu$  is a density parameter. An inequality analogous to (16) could be set up for the probabilities that exactly zero prey are in sight and the resulting exponentials could be easily simplified. However, this approach is density dependent, is time dependent, and makes the assumption of uniform distribution of fish throughout the ocean.

The approach taken in this paper, by isolating in the expectations of (16) the components which deal with the distribution of distance between two particular fish, has definite advantages. From the definitions and (14) and (15) it can be seen that we are concerned with the probability distribution of a single  $d_{ik}$  or  $d_{k'}$ , where  $i, k$  may take on any admissible values, for a fixed point in time with fixed  $n_p, n_f$ . Thus the probability distributions for  $d_{ik}, d_{k'}$  are not dependent upon the density of predators or prey in the given ocean space. Also, the probability distribution of distance between two fish is the same for any one time as for any other, and so is independent of time as well as density. (This may be said more rigorously as the distance between two randomly placed fish is orthogonal to time so that the probability distribution of distance is the marginal distribution with respect to distance obtained from the joint distribution with respect to distance and time.) Furthermore, the unjustified assumption of uniform distribution of fish is not made.

The probability distribution for  $d_{ik}$  must now be considered. It is well known that even non-schooled fish are contagiously distributed, although the cause, perhaps oceanographic conditions, perhaps food concentrations, is unknown. Thus non-schooled fish may be thought of as uniformly distributed for only

small regions of ocean. Within such a region, the probability that there will be a second fish at some distance from a first fish increases as a power function. As the region considered exceeds the contagion region, however, the density of fish becomes less, so that the probability of a second fish at some distance from a first fish will decrease again as the distance becomes great. It is obvious that the derivative (rate of change of distance) must exist for all distances. Thus our curve is smooth in the vicinity of the maximum and must be some sort of bell-shaped curve. The functional form of this curve is unknown. However, we are dealing with a comparison of probabilities at the extreme left of the curve, i. e., from zero to at most  $r + r'$ , which may reasonably be restricted to the order of a few hundred feet or less. Now for any stable ecological system, the predator will not be very frequently in sight of prey, and thus  $E(d_{ik})$  is considerably larger than either or the sum of  $r, r'$ . If  $E(d_{ik})$  were not much larger than either or the sum of  $r, r'$ , the predator would encounter the prey often and would eat the prey rapidly and reproduce rapidly. The number of prey would soon reduce to a number implying fewer encounters, which in turn implies an  $E(d_{ik})$  much larger than either or the sum of  $r, r'$ .

We may now assume that the predator and prey relationship is stable or but slowly changing and thus that we are dealing with the extreme left tail of the distribution. For this tail and the small distances involved, we shall assume uniformly distributed predators and non-schooled prey.

The distribution of  $d_{k'}$  is complicated by  $r'$ . A predator sights the school if he comes within the distance of  $r + r'$  of the centre of the school. If we think of a single fish as a school of size one,  $d_{ik}$  is the distance from the  $k$ th predator to the centre of this school. The generalization to thinking of  $d_{ik}$  as the distance to the centre of any size school is obvious if we now speak of the  $i$ th school rather than the  $i$ th fish. Then  $d_{k'} = d_{ik} - r'$ . Let us denote  $E(d_{ik}) \equiv \mu$  and  $E(d_{ik}^2) - \mu^2 \equiv \sigma^2$  and assume finite means and variances throughout. If  $r'$  is taken as constant,

$E(d_{k'}) = E(d_{ik} - r') = E(d_{ik}) - r' = \mu - r'$ . Also  
 $E(d_{k'}^2) - E^2(d_{k'}) = E(d_{ik}^2) - 2r'E(d_{ik}) + r'^2 - (\mu - r')^2 = E(d_{ik}^2) - \mu^2 = \sigma^2$ .  
 If  $r'$  is taken to be a variable with mean  $\mu_{r'}$  and variance  $\sigma_{r'}^2$ ,  
 $E(d_{ik}r') - \mu\mu_{r'} \equiv \text{cov}(d_{ik}, r') = 0$ , and it is simple to show in a similar fashion that  $E(d_{k'}) = \mu - \mu_{r'}$  and  $E(d_{k'}^2) - E^2(d_{k'}) = \sigma^2 + \sigma_{r'}^2$ . We shall take  $r'$  as constant.

Now since  $d_{k'} = d_{ik} - r'$ , (17) may be written

$$(18) \quad \frac{n_e}{n_f} < \frac{P[d_{ik} \leq r]}{P[d_{ik} \leq r + r']}$$

In a stable predator and prey relationship, where  $\mu$  is much larger than either  $r$  or  $r'$ , and under the assumption of uniformity of distribution of fish for the small distances involved in the extreme left tail of the probability distribution, the right side of (18) reduces to the ratio of volumes of water about the  $i$ th prey, representing the predator's effective scouting sight range under non-schooled and schooled prey conditions, respectively. Such volumes reduce to three cases: (i) the prey is at a distance greater than  $r + r'$  from either the surface of the ocean or some depth below which the fish are unlikely to go, so that the volumes will be spheres. (ii) the prey is at a distance less than  $r + r'$  but greater than  $r$  from either the surface or this depth so that one volume will be a truncated sphere, i. e., it has lost its cap at one or the other pole. (iii)

the prey is at a distance less than  $r$  from either the surface and this depth so that both volumes will be spheres truncated on one pole. The last two cases will be discussed for truncation at the top of the sphere, i. e., by the surface of the ocean. If the sphere should be truncated at both poles by both the surface and maximum depth, then the solutions of either or both of cases (ii), (iii) may be used independently to truncate both poles.

Case (i): The volumes are spheres. We have immediately

$$(19) \quad \frac{n_e}{n_f} < \frac{r^3}{(r + r')^3}$$

Case (ii): The smaller volume is a sphere, but the larger volume intersects the surface. Let  $\Phi_1 (>0)$  denote the angle about the centre of the sphere from horizontal to the intersection of the sphere with the surface. Then (18) becomes

$$(20) \quad \frac{n_e}{n_f} < \frac{\frac{4}{3}\pi r^3}{\frac{2}{3}\pi(r+r')^3 + \frac{2}{3}\pi(r+r')^3(1 - \cos\Phi_1) + \frac{1}{3}\pi[(r+r')^3\sin\Phi_1 - (r+r')^3\sin^3\Phi_1]}$$

where the first term of the denominator is the lower half of the volume of the total sphere, the second term is the area of the sector of the great circle between

$$0 \text{ and } \Phi_1 \text{ rotated } 2\pi \left( \text{explicitly } \int_0^{2\pi} \int_0^{\Phi_1} \int_0^{r+r'} r^2 \sin\Phi_1 \, dr \, d\Phi_1 \, d\theta \right),$$

and the third term is the usual formula for the volume of a cone, which of course is the remaining volume of the figure where  $(r + r') \sin \Phi_1$  is the distance from the centre of the sphere to the surface.

(20) reduces easily to

$$(21) \quad \frac{n_e}{n_f} < \frac{r^3}{(r + r')^3 [1 - \frac{1}{2} \cos \Phi_1 (1 - \frac{1}{2} \sin \Phi_1)]}$$

If  $\Phi_1 = \pi/2$ , (21) reduces to (19), which is obvious since the sphere will not be truncated. For any  $\Phi_1 < \pi/2$ , the quantity in brackets in (21) is always positive and less than unity, so that the right side of (21) is always greater than the right side of (19), implying an advantage to prey if the centre of the school is less than  $r + r'$  but greater than  $r$  from the surface (or alternatively if the predator is in the equivalent position, which reduces his effective scouting volume).

Case (iii): Both the smaller volume and the larger volume intersect the surface. Let  $\Phi_1 (>0)$  denote the angle about the centre of the sphere from horizontal to the intersection of the larger sphere with the surface; let  $\Phi_2 (>0)$  denote the similar angle for the smaller sphere. Then (18) becomes

$$(22) \quad \frac{n_e}{n_f} < \frac{\frac{2}{3}\pi r^3 + \frac{2}{3}\pi r^3(1 - \cos\Phi_2) + \frac{1}{3}\pi[r^3\sin\Phi_2 - r^3\sin^3\Phi_2]}{\frac{2}{3}\pi(r+r')^3 + \frac{2}{3}\pi(r+r')^3(1 - \cos\Phi_1) + \frac{1}{3}\pi[(r+r')^3\sin\Phi_1 - (r+r')^3\sin^3\Phi_1]}$$

in which both numerator and denominator of the right side are obtained as the analogous expression in (20). (22) reduces easily to

$$(23) \quad \frac{n_e}{n_f} < \frac{r^3 [1 - \frac{1}{2} \cos \Phi_2 (1 - \frac{1}{2} \sin \Phi_2)]}{(r + r')^3 [1 - \frac{1}{2} \cos \Phi_1 (1 - \frac{1}{2} \sin \Phi_1)]}$$

If  $\Phi_1 = \Phi_2 = 0$ , (23) reduces to (19), which is obvious since the same proportion is truncated from each sphere. Note that for  $\Phi_1 > 0$ ,  $1 - \frac{1}{2} \cos \Phi_2 (1 - \frac{1}{2} \sin \Phi_2) > 1 - \frac{1}{2} \cos \Phi_1 (1 - \frac{1}{2} \sin \Phi_1)$  which may be written

$$(24) \quad \frac{\cos \Phi_2}{\cos \Phi_1} < \frac{1 - \frac{1}{2} \sin \Phi_1}{1 - \frac{1}{2} \sin \Phi_2}$$

which is always true since  $\Phi_2 > \Phi_1$ . Thus, the right side of (23) is greater than the right side of (19), implying an advantage to prey if the centre of the school is less than  $r$  from (but not actually on) the surface (or alternatively if the predator is in the equivalent position).

Since (21) and (23) imply an advantage to prey if a predator is too close to the surface or some limiting depth, which may be the bottom, we shall discuss the most conservative result, viz. (19). If (19) be written

$$(25) \quad n_e < \frac{r^3}{(r + r')^3} n_f,$$

we see that the number of schooled prey a predator must consume after locating a school of prey in order to nullify the advantage the prey gain by schooling is the fraction  $r^3/(r + r')^3$  of the total prey in the school.

If we think of a school of  $n_f$  prey as being spherical in shape and having all fish distributed uniformly therein,  $r'$  is the radius of this sphere and the prey will be some constant number of distance units, say  $c$ , apart along a radius.

Then there are  $\frac{r'}{c}$  prey along a radius, from which we immediately obtain

$$(26) \quad n_f = \frac{4\pi}{3} \left( \frac{r'}{c} \right)^3$$

or

$$(27) \quad r' = c \sqrt[3]{\frac{3n_f}{4\pi}}.$$

Thus  $r'$  is a function of  $c$ ,  $n_f$  and upon substituting (27) into (25) we obtain

$$(28) \quad n_e < \frac{r^3 n_f}{\left( r + c \sqrt[3]{\frac{3n_f}{4\pi}} \right)^3}$$

For fixed  $n_f$ , as  $c$  approaches zero, the right side of (28) approaches  $n_f$ , which implies that as the prey in a school draw closer together, a predator must be able to consume more and more nearly the entire school in order to nullify schooling advantage. Here the detection advantage increases as the prey draw close together while the frequency of encounter advantage and predator capacity advantage remain unchanged.

Now let us see what happens when  $c$  grows larger. The largest  $c$  can grow is  $r$ ; we are assuming only visual communication in our model so that when  $c > r$  the prey cannot see one another and thus cannot communicate so that the school ceases to exist by definition. Then since the most disadvantageous  $c$  admissible is  $c = r$ , let us investigate (28) for  $c = r$ .  $r$  cancels in (28) when  $c = r$ , leaving

$$(29) \quad n_e < \frac{n_f}{\left(1 + 0.6204 \sqrt[3]{n_f}\right)^3}$$

This inequality is violated for most reasonable sizes of  $n_f$ . For example, if the predator can eat only four prey, which is rather a small number, the schooling advantage is not gained until the school reaches 1,000,000 in size. It is obvious that fish do not school with distances apart approaching the sight range when visual distances are good, but this result shows that schooling in extremely turbid waters or at night may work to the disadvantage of the prey. There exists considerable observation to indicate that schools tend to break up at night and that there is little schooling in waters having poor visual properties. The exact sight range  $r$  at which schooling gives neither advantage nor disadvantage will depend upon  $n_f$ ,  $n_e$ , and  $c$ , and can be obtained from (28) for any desired values of these variables.

Some values of  $n_e$  from (28) for selected values of  $n_f$ ,  $r$ , and  $c$  are shown in Table 1.

**Table 1**

**Values of  $n_e$  (rounded to the whole fish), larger than which will violate (28), for various  $n_f$  and  $r$  with  $c$  fixed at 4 feet**

(Thus in a school of 1,000 prey distributed 4 feet apart, a predator must consume 514 prey to nullify schooling advantage if the sight range is 100 feet, but only 3 prey if the sight range is 4 feet, i. e., the distance apart.)

$n_f$	$r = 200$ ft.	$r = 100$ ft.	$r = 10$ ft.	$r = 4$ ft. (= $c$ )
1	1	1	1	0
10	9	9	3	1
100	85	72	10	2
1,000	704	514	24	3
10,000	4,913	2,767	39	3
1,000,000	88,877	23,695	57	4

If  $r$  and  $c$  are assumed to be constant and  $n_f$  be given various values, the ratio between schooled and scattered prey, viz. (28) will under conditions of uniform abundance of predators and prey, give the frequency of encounter of schooled prey by the predators. Once a school is sufficiently large so as not to be totally consumed during the period of encounter by a predator, further increases in school size would not increase the quantity of prey consumed under these assumptions.

As  $n_f$  is increased, the frequency of encounter is reduced, and assuming  $n_e$  constant for each encounter, the average amount of prey consumed per unit time is likewise reduced. Obviously there exists some minimal rate of consumption that will permit the survival of the predator, and some maximal rate that depends upon the digestive capacity of the predator.

Let us further illustrate the use of the inequality (28) with some reasonable values drawn in part from observation. From observations and photographs taken from an underwater observation port on the research vessel of the Honolulu Biological Laboratory, schooled skipjack are about 2 feet apart or about 4 feet between the centres of any two fish. The sight range,  $r$ , is conservatively,



100 feet. If a marlin, preying on skipjack, eats during an average encounter with a school, some 40 pounds, and skipjack are abundant enough to supply this amount of prey daily if not schooled, the daily consumption rate will vary with school size as shown in Table 2.

**Table 2**  
**Variation of consumption rate by a predator**  
**with prey school size based on model in text**

School size	Daily weight of fish eaten in pounds
1	40
10	4.68
100	0.55
1000	0.08

A school of 2,000 skipjack of 10 pounds average weight would occupy a sphere of about 31.3 feet in radius, and from (28) the marlin must eat  $\frac{(100)^3}{(131.3)^3} = \frac{1,000,000}{2,262,020} = 0.442$  of the school or 8,840 pounds during the period of encounter to nullify the schooling advantage.

To illustrate again, let us note that the average successful purse seine set about a pilchard school in British Columbia produced 35 tons while sets upwards of 100 tons were not unknown (HART, 1933). Schools of other marine pelagic fishes reach similar if not greater magnitude. For a large part of such schools to be consumed by a predator, even assuming that he remains with the school for a long period and that the school permits his presence without disintegrating, is quite impossible. If the prey should adopt the strategy (and there is some evidence that this occurs) of disintegrating the large school when sighted by a predator and later reforming, the predator could not physically remain with more than one segment of the school, which puts physical as well as physiological limits on  $n_e$ , and thus schooling could not be other than advantageous to the prey under optimum strategy.

Thus far we have discussed  $P[d_{ik} \leq r]$  and  $P[d_{k'} \leq r]$  only in ratio; this is satisfactory if we are strictly comparing advantages of schooling to non-schooling. However, if we should be interested in estimating one or both of these probabilities in order to describe what actually occurs in the pelagic ecology rather than to assess strategies, then we should have to deal with one of the probabilities alone. It is of interest to note that  $P[d_{ik} \leq r]$  and  $P[d_{k'} \leq r]$  are very nearly zero and approximately equal, since they both represent small areas under the extreme tail of a probability curve. Since we do not know the probability functions exactly, we cannot evaluate exactly these probabilities, but let us demonstrate what happens approximately by taking the bell-shaped curves discussed earlier to be approximately normal. Under this assumption,  $d_{ik}$  is a random variable distributed as a truncated  $n(\mu, \sigma^2)$ , since  $0 \leq d_{ik} < \infty$ . Using the notation of CRAMÉR (1946) in which

$$\varphi(y) = \int_{-\infty}^y n(0,1) dt,$$

we have

$$(30) \quad P[d_{ik} \leq r] = \frac{\varphi\left(\frac{r-\mu}{\sigma}\right) - \varphi\left(-\frac{\mu}{\sigma}\right)}{1 - \varphi\left(-\frac{\mu}{\sigma}\right)}$$

and

$$(31) \quad P[d_{k'} \leq r] = P[d_{ik} \leq r + r'] = \frac{\varphi\left(\frac{r+r'-\mu}{\sigma}\right) - \varphi\left(\frac{r'-\mu}{\sigma}\right)}{1 - \varphi\left(\frac{r'-\mu}{\sigma}\right)}$$

which are approximately equal.

To illustrate, let us find parameter values from a situation which may be taken as reasonable. The maxima of  $r$  and  $r'$  may reasonably be restricted to the order of magnitude of a few hundred feet or less, say 0.03 nautical miles. In the Marquesas Islands, it has been found that schools of skipjack are sighted about every four nautical miles along a transect of ocean surface. It is reasonable that schools average about 10 tons, and that marlin are in weight about 1/50 as abundant. If a marlin weights 200 pounds, then there will be about two marlin per school along the transect, yielding  $\mu \doteq 2$  miles. Let us note the similarity between the left-truncated normal and the poisson distribution and use the poisson property that  $\mu = \sigma^2$ , so that  $\sigma \doteq \sqrt{2}$  or about 1.4. Let us take 100 feet  $\doteq 0.012$  as reasonable values of both  $r$  and  $r'$ . Substituting these values in the probability values of both sides of (21), we obtain respectively

$$\frac{\varphi(1.42) - \varphi(1.41)}{\varphi(1.42)}, \quad \frac{\varphi(1.43) - \varphi(1.42)}{\varphi(1.43)}$$

or, upon evaluating,

$$\cdot 0015940, \quad \cdot 0015590,$$

which are approximately the same.

### Discussion

The assumptions made and conclusions reached herein are admittedly not related to the observed behaviour pattern of any particular species of fish, however, the relationships of school size of prey and encounter frequencies between prey and predators may, for a particular prey-predator combination, be a more complex situation elaborated from that described here. For example, predators may attempt to remain with a school of prey even though satiated, and it is not unlikely that a large school of prey may leave an easily detectable trail of odour behind for a predator to follow. While fish schools of some species do remain together during darkness as indicated for the California sardine by a night fishery (LINDNER, 1930) yet even here the dispersion of tagged fish through the stock as indicated by recovery patterns would argue that a substantial interchange of individuals among schools must occur at least which suggests the possibility of the dispersal and reforming of schools.

The general lack of field data concerning the behaviour pattern for a prey species and its predators renders either the confirmation or refutation of the

conclusions reached in this paper by the elaboration of some scheme of predator strategy rather futile. HIATT and BROCK (1948) described the herding of a small school of mackerel scad (*Decapterus*) by a few little tuna (*Euthynnus*) which would seem to constitute a more elaborate strategy than implied here. We do not conclude that complex strategies do not exist; we do suggest, however, that the relationships among predators, prey, and prey school sizes, described here, may be basic to such strategies.

### Summary

The schooling of fish is considered as a mechanism for protection against predation. It is shown that the frequency of detection of prey by a predator is an inverse function of the number of schooled or grouped prey. The quantity of fish that a predator can consume on any single encounter with a school of prey has some average limit, and once school size exceeds this quantity, further increases in school size reduce the frequency of predator-prey encounters without necessarily changing the quantity of prey consumed on the occasion of each encounter, which in turn may reduce the rate of consumption of a prey species by a predator.

### References

- BREDER, C. M., JR., 1951. "Studies on the structure of the fish school". Bull. Amer. Mus. nat. Hist., **98**: 1-27.
- BREDER, C. M., JR., & HALPERN, F., 1946. "Innate and acquired behavior affecting the aggregation of fishes". Physiol. Zool., **19**: 154-92.
- CRAMÉR, H., 1946. "Mathematical methods of statistics". Princeton, N. J., Princeton Univ. Press.
- DUNTLEY, S. Q., 1952. "The visibility of submerged objects". Final Report. Visibility Lab., Mass. Inst. Tech. 74 pp.
- HART, J. L., 1933. "The pilchard fishery of British Columbia". Bull. biol. Bd. Can., **36**: 1-27.
- HIATT, R. W., & BROCK, V. E., 1948. "On the herding of prey and the schooling of the black skipjack *Euthynnus yaito* Kishinouye". Pacif. Sci., **2**: 297-98.
- KEENLEYSIDE, M. H. A., 1955. "Some aspects of the schooling behavior of fish". Behaviour, **8**: 183-247.
- LINDNER, M. J., 1930. "Luminescent fishing". Calif. Fish Game, **16**: 237-40.
- PARR, A. E., 1927. "A contribution to the theoretical analysis of the schooling behavior of fishes". Occ. Pap. Bingham oceanogr. Coll., **1**: 1-32.
- SETTE, O. E., 1950. "Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part II, Migration and habits". Fish. Bull., U. S., **51**: 251-358.
- SPRINGER, S., 1957. "Some observations on the behavior of schools of fishes in the Gulf of Mexico and adjacent waters". Ecology, **33**: 166-71.
- WELTY, J. C., 1934. "Experiments in group behavior of fishes". Physiol. Zool., **7**: 85-128.