

SELECTIVITY OF TOWED-NET SAMPLERS

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ABSTRACT

The ideal sampler for plankton and nekton is one whose selective characteristics are known to be appropriate to any given problem, so that it catches the right organisms, and rejects others, with known efficiency. This paper presents a quantitative theoretical analysis of one aspect of selectivity, avoidance of towed-net samplers. The theory is evaluated against three sets of paired samples obtained by different nets at different speeds to provide absolute and relative tests of its validity. A single sample obtained by one net towed at one speed is then analyzed to illustrate the procedure. Final evaluation of the theory awaits studies of animal behavior when confronted by a sampler, but the theory provides informative and reasonable interpretations of plankton and nekton catch data, particularly estimates of population abundance and mesh losses, even when behavior of the animals is not known.

An ideal sampler for plankton and nekton must meet at least two requirements, one qualitative and the other quantitative: It must collect or detect certain components of these extremely diverse communities, while rejecting most others; and it must do this with known effectiveness. For some purposes the qualitative aspects of sampler selectivity are relatively more important than the quantitative ones, or vice versa, but neither can ever be completely ignored in the design and selection of sampling gear.

Sampler selectivity has usually been evaluated empirically, by comparing results obtained with one sampler under different conditions or by intercomparing various sampling methods. The plankton purse seine developed by Murphy and Clutter (1972) appears to be nearly ideal for the latter purpose. It is relatively nonselective for a wide spectrum of organism types and sizes, making it useful as a "primary standard" for calibrating more selective gear, as Murphy and Clutter demonstrate.

A sound theory of sampler selectivity would be of great value as a guide to the collection and analysis of empirical data, but relatively little effort has been devoted to the development of such theory (Tranter, 1968). What I propose

to discuss here is a special, rather basic, case of selectivity: the theoretical minimum probability of certain capture, for many individual encounters between similar organisms and a towed-net sampler.

The formulation of this problem was suggested by the work of Murphy and Clutter (1972). The results resemble those obtained by Gilfillan (reported by Clutter and Anraku, 1968) but are more general. This study is an extension of my earlier theoretical work on net avoidance (Barkley, 1964) and uses the same notation.

This paper is presented in recognition of the inspiration and leadership of Oscar Elton Sette. It is appropriate that it should appear just one century after the first worldwide use of the Müller net on the *Challenger* Expedition.

METHOD

Consider a towed-net sampler moving through the water toward an individual animal (Figure 1a); for simplicity assume that the net has a circular opening of radius R and moves at a constant speed U . The animal senses the oncoming net and begins to react to it at a distance x_0 , by swimming at some mean escape speed u_e . In the time available before the net catches up, the animal either can, or cannot, get out of the way, depending on its position, speed, and di-

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rection of movement relative to the net. There is, therefore, a cone-shaped space ahead of the net which, once it encloses the animal, results in certain capture. If the animal reacts before entering the (invisible) "lethal cone," it has enough time to get out of the way of the oncoming net. The base of this "lethal cone" is the opening of the net; its apex is at a distance X ahead of the net. This distance, X , is given by the equation:

$$X = R \sqrt{\frac{U^2}{u_e^2} - 1} \quad (1)$$

which is easily obtained from the following equation (Barkley, 1964) by setting $r_0 = 0$ and $x_0 = X$:

$$u_e = \frac{U}{\sqrt{1 + \frac{x_0^2}{(R - r_0)^2}}} \quad (2)$$

Figure 1 (panels a and b) gives examples of the "lethal cone" for several values of escape speed relative to net speed. For organisms which do not react to the net ($u_e = 0$) or have very low escape speeds the "lethal cone" is very large, occupying all or almost all of the volume of water in the path of the net; the probability of capture for such organisms approaches 1.0. On the other hand, for animals whose escape speed approaches the speed of the net ($u_e \simeq U$) the "lethal cone" is short; these animals can easily dodge the oncoming net, even if they wait

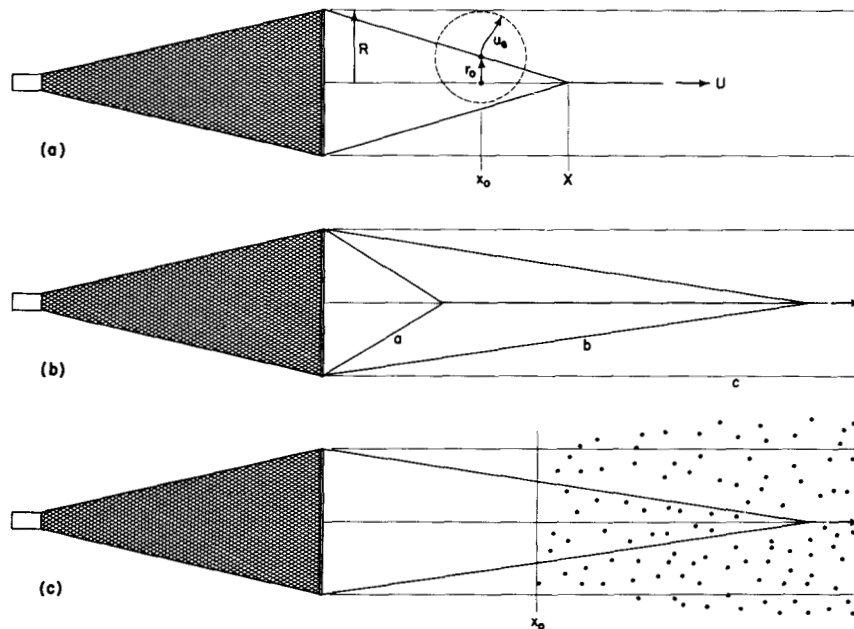


FIGURE 1.—(a) An animal at a point x_0 ahead of the net and r_0 from its axis of motion begins to react to the net. In the time available, it can go anywhere within the volume shown in dashed lines; if this volume is completely enclosed by the oncoming net, capture is certain. Animals which react before entering the cone-shaped space ahead of the net can escape; those which react after entering the "lethal cone" are caught. (b) For a given net, the length of the "lethal cone" depends only on the speed of the animal relative to the net. Cone a corresponds to animals which can move at 50% of the net's speed. Cone b represents a relative speed of 15%; cone c shows the case of no reaction. The "lethal cone" in panel a, above, corresponds to a relative speed of 30%. (c) If a school or cluster of animals reacts to the dodging movements of the animals nearest the oncoming net, only those animals already inside the "lethal cone" are certain to be captured.

until the net has almost caught up with them. We do not expect to catch any animals which can swim faster than the net; we wish to calculate minimum probabilities for certain capture, which implies that animals which could possibly escape do so. That is, the size of the "lethal cone" is minimized by assuming that animals are capable of optimum avoidance behavior.

However, probabilities of certain capture can only be calculated for animals which react individually. Animals which school or form clusters can "beat the odds" by reacting to each other's behavior instead of reacting only to the oncoming net. The effect of this is illustrated in Figure 1c, which represents a net approaching a group of animals whose reaction distances and escape velocities are assumed to be similar. If the animal shown nearest the net begins to react at the distance labeled x_0 , it can escape because it is outside of the "lethal cone." Those animals already within that cone will be captured in any case. If the other animals respond immediately to the actions of the one nearest the net, they can all escape. If, instead, they respond as individuals, as the net moves through the group, more will enter the "lethal cone" and then be captured.

Whether an organism, once captured (i.e., enclosed by the net) will be retained depends on the characteristics of the net's meshes and the size, shape, behavior, and fragility of the organism. Losses through the mesh have been reviewed by Heron, 1968; Tranter and Smith, 1968; and Vanucci, 1968. Lenarz (1972) presents results of more recent work. Losses can also occur due to faulty handling of the sampler, particularly sudden decreases in towing speed. Our primary interest here is in avoidance prior to capture, although the theory to be developed will throw some light on the problem of mesh losses.

The catch obtained from a towed-net sampler can be calculated, in principle, from equations such as the following:

$$\begin{aligned} \text{Catch} &= \text{Captures} - \text{losses} \\ &= (\text{volume sampled}) \times \left(\frac{\text{no. of organisms}}{\text{unit volume}} \right) \end{aligned}$$

$$\times (\text{probability of capture}) - (\text{losses}) \quad (2)$$

So that

$$\frac{\text{no. of organisms}}{\text{unit volume}} = \frac{(\text{catch} + \text{losses})}{(\text{volume sampled}) \times (\text{probability of capture})} \quad (3)$$

The central problem of selectivity theory is to evaluate the unknown factors in equations (2) and (3), so as to permit solution of these equations with a minimum of empirical work. The most important unknown factors are those governing probability of capture and losses after capture—primarily losses through the meshes.

Since both probability of capture and degree of mesh loss must vary widely with species, age, and condition, the above equations apply separately to each component of the plankton and nekton community.

For present purposes, a component must be defined as a set of organisms having the same probability of capture, and the same degree of mesh retention, under given circumstances. That is, they must be similar in their reaction distance, escape speed, shape, size, and condition.

The above operational definition of a component of the plankton or nekton may often coincide with the more usual biological definitions. For single species, one can reasonably expect that fish of similar size or crustaceans at the same stage of development should have similar reaction distances and escape speeds and the same percentage mesh retention. However, the distinction between the two ways of defining a component must be carefully borne in mind. The operational definition may lump several biologically defined components; to take a trivial example, bacteria, phytoplankton, and fish eggs small enough to pass through the mesh all have the same probability of capture, 1.0, and all have 0% retention. On the other hand, the operational definition may split one biological component into two or more parts; e.g., healthy and moribund animals of the same size and species should differ in their ability to avoid capture. In principle, empirical data on reaction distance,

escape speed, shape, size, and condition are needed to assign animals to different components when analyzing towed-net samples by means of the present theory. Such data could perhaps best be obtained by taking stereoscopic photographs of animals' reactions to the approach of a sampler. In practice, however, it may be possible to assign animals to operationally defined components *post facto*, based on analyses of catch data with the present theory. An example of this is to be found in Table 1, where *Bathylagus stibius* ranging from 52 to 92 mm in length were found to have essentially identical probabilities of capture and were apparently all retained by the meshes, thus meeting the criteria for a single component.

In equations (2) and (3) the major unknowns are the losses and the probability of capture. Neither can be formulated precisely until behavior of many animals, before and after entering nets of varied designs, has been studied. However, losses can be estimated to some degree from the difference between observed and theoretical catches; and probability of capture can be calculated for a limiting case, minimum probability of certain capture for individual encounters. This approach makes use of the geometry of the "lethal cone" (Figure 2). The minimum probability of capture, P_c , is:

$$P_c = \frac{\text{Area of "lethal cone" cross section at distance } x_0}{\text{Area of the sampler mouth opening}} \\ = (r/R)^2.$$

From Figure 2,

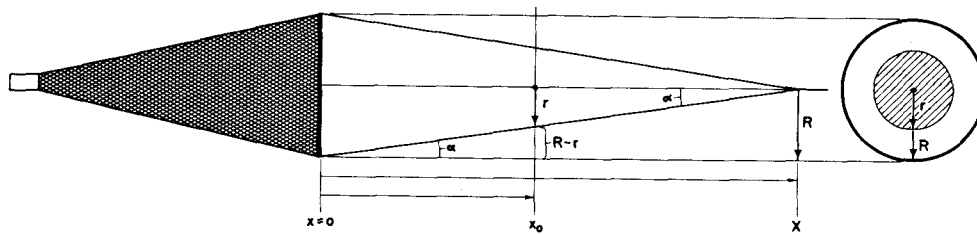


FIGURE 2.—Definition sketch for calculating P_c , the minimum probability of capture. P_c is the ratio of the area of the "lethal cone" (shaded) to the area of the net's mouth opening, at the mean reaction distance x_0 for one component of the catch.

$$\frac{R - r}{x_0} = \tan \alpha = \frac{R}{X}$$

so that

$$r = R(1 - \frac{x_0}{X})$$

and

$$P_c = (1 - \frac{x_0}{X})^2. \quad (4)$$

Substituting X from equation (1) into (4) gives

$$P_c = \left(1 - \frac{x_0}{R\sqrt{\frac{U^2}{u_e^2} - 1}}\right)^2 \quad (5)$$

which may also be written

$$P_c = \left(1 - \frac{x_0 u_e}{R\sqrt{U^2 - u_e^2}}\right)^2 \quad (6)$$

Where P_c is probability of capture, x_0 is the mean reaction distance, R is the radius of the net's opening, U is the net's speed, and u_e is the animals' mean escape speed. These results can also be derived from equations (4), (5), and (7) of my earlier analysis (Barkley, 1964).

DISCUSSION

To examine avoidance as a function of towing speed, Gilfillan (reported by Clutter and Anraku, 1968) assumed that the product $x_0 u_e$ is a constant, K . Starting with an apparent "effective"

net radius R' (identical with r in Figure 2), Gilfillan arrived at the following equation:

$$P_c = \left(1 - \frac{K}{RU}\right)^2, \quad K = x_0 u_e \quad (7)$$

where present notation has been substituted for the original and the equation slightly simplified. Clearly Gilfillan's equation is an approximate form of equation (6) for the case where u_e can be neglected compared to U ; which is to say, for animals which move much slower than the net. This approximation is good to within 5% as long as u_e is less than 30% of U .

It is not obvious that $x_0 u_e$ should in general be a constant, even for a single component of the plankton or nekton. Constancy of the product $x_0 u_e$ implies that either (1) reaction distance and escape speed individually are constant, (2) animals deficient in one of these survival traits can compensate for this by excelling in the other, or (3) animals given an unusually long time to react by faulty net design—such as a bridle or other conspicuous obstruction some distance ahead of the mouth—fail to take advantage of this warning. The first alternative is perhaps too much to expect; the second and third seem unlikely. Nevertheless, Gilfillan obtained nearly constant values for K in a series of field trials with different nets towed at various speeds, where catches of *Calanus* spp., *Euchaeta japonica*, and euphausiids were enumerated (Clutter and Anraku, 1968).

There is great practical value to knowing that K is a constant for any particular component of a sample, because this constant fully specifies the avoidance behavior of that component. If K is constant, it is possible to calculate probabilities of capture without making measurements of either x_0 or u_e , as long as U is known to exceed u_e by a factor of three or more.

Numerical values of K can be estimated, as Gilfillan suggested, from tows made at two different speeds, U_1 and U_2 , or by using two otherwise similar nets with openings of radii R_1 and R_2 , while holding other factors constant:

$$K = \frac{1 - \left(\frac{C_1}{C_2}\right)^{1/2}}{\frac{1}{R_1 U_1} - \frac{1}{R_2 U_2} \left(\frac{C_1}{C_2}\right)^{1/2}} \quad (8)$$

where C_1/C_2 is the ratio of catches of individual components in the samples taken under each of the two different conditions. Equation (8) is approximate; the exact form can be obtained

by substituting $\sqrt{U_n^2 - u_e^2}$ for U_n .

Holding "other factors" constant is obviously a problem, since the same net towed at different speeds, or different size nets towed at the same speed, may have widely different noise levels, mesh losses, hydrodynamic behavior, etc., which would tend to invalidate the comparison.

RESULTS

Although definitive tests of the theory developed above must await knowledge of avoidance and mesh escape behavior of at least some components of the plankton and nekton, a few informative comparisons can be made now between theory and catches obtained with various towed nets.

Equation (5) is presented graphically in Figure 3, where P_c , the minimum probability of capture (ordinate) is plotted as a function of the ratio u_e/U , the escape speed relative to the net's speed, for various values of the ratio x_0/R , the reaction distance relative to the net's radius. The linear graph shows the complete theoretical solution; it is used to provide a check on results obtained using the semilog format. In practice the semilogarithmic graph is more useful for analyzing catch data because it simplifies graphical calculations. Either of these graphs, as well as equations (5), (6), and (7), can of course be used to determine P_c , u_e , or x_0 if any two of these variables are known, along with R and U . For example, a 1-m net ($R = 0.5$ m) towed at 100 cm/sec should catch at least one-third ($P_c = 0.33$) of all those organisms in its path which react at a distance of 1 m and can swim 20 cm/sec ($u_e/U = 0.2$, $x_0/R = 2$).

A more interesting application is the use of Figure 3 to analyze size-frequency data from a tow, or set of tows, made with one sampler at one speed. To illustrate this application, suppose that the population in question is a species for which mesh losses are negligible beyond some

minimum size or stage of development and that the species' abundance does not change appreciably with size, or that corrections can be made for these two factors. Assume that the species' swimming ability is known, and proportional to size, while its reaction distance remains constant, or nearly constant, for all sizes sampled. Then if the catch were sorted into size class intervals (ideally, into components, in the operational sense) and counted, the size classes could each be assigned a corresponding escape speed, increasing with size; plotting these speed-frequency values as points on either graph of Figure 3 would produce a curve which resembles one of the family of curves shown on those graphs. Proper matching of observed data to the theoretical curves would yield unique values of both P_c and x_0/R (and therefore x_0 , since R is known) for each component or class interval of that species. Once P_c is known, the absolute population density can be calculated from equation (3). Finally, values of x_0 , or x_0/R , provide valuable information as to the relative merits of different sampler designs.

The following examples illustrate this use of avoidance theory. In the first example, the population density structure is known, so that P_c can be calculated directly and only x_0 remains to be determined from avoidance theory. In the second example, two different samplers are compared to obtain estimates of P_c and x_0 for both, from the theory, even though the population structure is not known. The third example illustrates information which can be obtained when one sampler is towed at two different ranges of speed. Finally, catch data from a single net, towed at one speed, are considered.

Murphy and Clutter (1972) present length-frequency data for Hawaiian anchovy, the engraulid, *Stolephorus purpureus*, caught with their plankton purse seine and a 1-m net. Their data for paired daylight tows are reproduced on Figure 4. The uppermost curve on this figure shows length-frequency data from the purse seine, assumed to represent the population structure as a function of size. I approximate these data by means of the straight line shown on this figure, in effect assuming that the population

declines exponentially as the fish grow to larger sizes. That is, $N_L = N_0 \exp(-kL)$, where N_L is the population density at length L , N_0 is a fictitious population density at zero length obtained by extrapolation, and k is a constant. The lowest curve on Figure 4, marked C_L , shows the catch (C) in each 1-mm length class (L).

To remove the effects of changes in population density, set $N_0 = 1.0$ by dividing all values of N_L by the population density at N_0 . On semilog graph paper this can easily be accomplished simply by aligning N_0 with 1.0 on the ordinate scale, after the length-frequency values have been plotted on tracing paper using the three-cycle semilog scale of Figure 3. Next, divide each value of C_L by the corresponding value of N_L to obtain the middle curve of Figure 4, labeled C_L/N_L . This division can be performed graphically by moving each value of C_L vertically upward a distance equal to the vertical distance between N_L at the corresponding length, L , and the horizontal line $P_c = 1.0$. This procedure yields the length-frequency curve which would have been obtained if the population density in each class interval had been the same, i.e., $N_L = N_0$.

The above procedure amounts to dividing catch per unit volume by the population per unit volume, which according to equation (2) yields

$$\frac{\text{Catch/unit volume}}{\text{No. of organisms/unit volume}} =$$

Probability of capture (if losses = 0).

Thus the curve labeled C_L/N_L on Figure 4 is also a curve showing P_c for each class interval, providing that catch per unit volume has been correctly related to the population per unit volume in each class interval and that mesh losses are negligible.

Mesh losses appear to be negligible for animals larger than the two smallest class intervals, which will not be used in the analysis. Since u_e is not known, length for each class interval is converted to escape velocity by assuming that $u_e = 10L$ where u_e is in cm/sec and L is in cm. Each value thus obtained is divided by U , nominally 76 cm/sec. Resulting values of u_e/U are shown in the upper abscissa of Figure 4. The

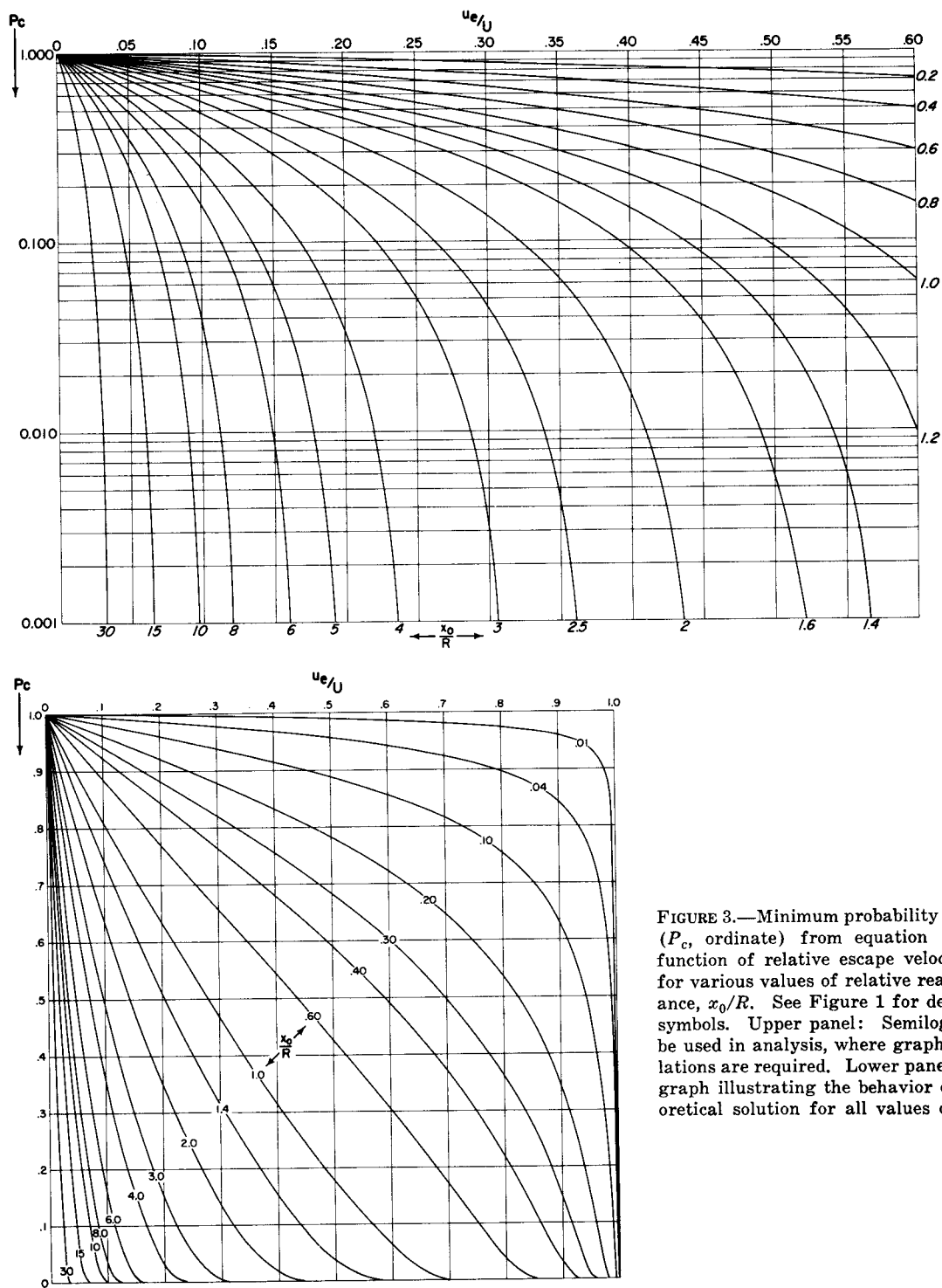


FIGURE 3.—Minimum probability of capture (P_c , ordinate) from equation (5), as a function of relative escape velocity, u_e/U , for various values of relative reaction distance, x_0/R . See Figure 1 for definition of symbols. Upper panel: Semilog graph to be used in analysis, where graphical calculations are required. Lower panel: Linear graph illustrating the behavior of the theoretical solution for all values of u_e/U .

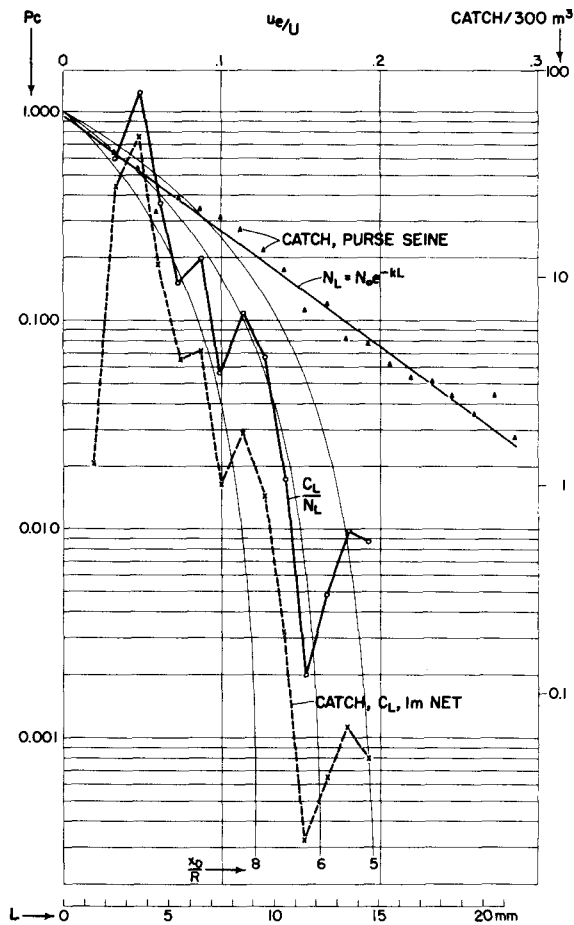


FIGURE 4.—Analysis of length-frequency data for day-light catches of *Stolephorus* from 44 paired samples. Purse seine data (triangles), a measure of absolute abundance, are approximated by the straight line, N_L . Catch with the 1-m net, C_L , has been corrected for changes in population (N) with length (L), to obtain the middle curve, C_L/N_L , which shows the minimum probability of capture, P_c , as a function of length for the 1-m net. Three theoretical curves for P_c at constant relative reaction distance (x_0/R) are reproduced from Figure 3, to show degree of fit between data and theory. Data from Murphy and Clutter (1972).

converted data can now be directly compared with the theoretical curves of Figure 3, three of which are shown on Figure 4 (the curves for P_c at $x_0/R = 5, 6$, and 8).

The adjusted 1-m net catch data fall near the theoretical curves for P_c at relative reaction

distances, x_0/R , of 6 and 8; since $R = 0.5$ m for this net, the reaction distance of *Stolephorus* apparently ranges between 3 and 4 m. Murphy and Clutter (1972) obtain comparable results from an equation they derive for calculating x_0 directly. They used similar assumptions—in particular, an escape speed of $10L$ per second—but set $P_c = 1.0$ for the third class interval (3.5 mm). Here P_c was set at 1.0 at the intercept of the purse-seine catch curve with the ordinate axis, i.e., $P_c = 1.0$ at N_0 , the fictitious population density at zero length, because only at this length does the assumed relationship between speed and length yield zero velocity. Since N_L , the population density at any given length L , is equal to N_0 for the adjusted data, the above procedure is internally consistent.

There are two exceptions to the otherwise fairly good fit between the adjusted data and the theoretical curves. The first, catch with P_c exceeding 1.0 for the third class interval (3.5 mm), may be due to sampling variability, overestimates of the water sampled by the purse seine, or underestimates of the water sampled by the 1-m net. It could also be due to less than optimum avoidance behavior by these small fish. The second exception, unexpectedly large catches in the three largest class intervals (12.5-14.5 mm) could be due to variability, or to a decrease in mean reaction distance for these animals, from a "normal" value of 3-4 m down to about 2.5 m ($x_0/R = 5$). Isaacs (1965) suggested that daytime tows should catch more than proportionate numbers of the sick, lame, or lazy; this effect should be most pronounced for the largest animals, which normally are the ones best able to dodge the net.

Minor fluctuations in the fit of the adjusted 1-m net data on Figure 4 are probably due to sampling variability, but to illustrate use of avoidance theory, suppose that the minor peaks and valleys for fish of intermediate sizes were significant. Note that these points tend to fall into two groups: those near the curve for P_c at $x_0/R = 6$, and others, $x_0/R = 8$. This could be an artifact due to schooling behavior, since group reaction should reduce the probability of capture below the theoretical minimum value for individual reaction. One measure of this effect

is an increase in the apparent reaction distance. Instead of the true value, x_0 , we would expect to obtain an apparent value which approaches ($x_0 +$ radius of the school) for large schools. If *Stolephorus* schools at all sizes represented on Figure 4, the different values of x_0/R , 6 versus 8, may reflect the presence of smaller and larger schools, differing in radius by about $2R$ or 1 m.

Some support for this apparently fanciful argument can be found in the *Stolephorus* catches obtained at night by Murphy and Clutter (1972). Night purse-seine catches showed marked peaks in abundance of fish in the 7-8 mm and 11-12 mm size classes and relatively low abundances in the 4-, 9-, and 14-mm class intervals. Simultaneous tows with the 1-m net, on the other hand, yielded precisely opposite results. The 1-m net apparently undersampled abundant size classes and was more effective with the less abundant size classes. This is precisely what is expected if the purse seine catches schools of various sizes equally well, whereas the 1-m net underestimates the abundance of schooled fish, more or less in proportion to school diameter, provided only that the fish school by size and that changes in abundance are associated with changes in school size, rather than changes in the number of schools.

This detailed treatment of a single set of length-frequency data is intended only as a demonstration of the amount of information which can be extracted from such observations in the light of theory, when and if measurements of typical reaction distances and escape velocities have been made. Results of this as-yet-tentative analysis may be summarized by saying that *Stolephorus* in the 1-m net sample apparently consist of:

- A. Animals in the 1.5- and 2.5-mm class intervals, which are partially lost through the meshes and probably are unable to avoid the net.
- B. Animals 3.5 mm long, which seem to be adequately retained by the meshes and apparently are too small to effectively avoid the net.
- C. Animals 4.5 to 11.5 mm long, which react at about 3-4 m distance (proportionately more, or less, if their swimming speed is

less, or more, than 10 body lengths per second). Maximum P_c for this group is about 0.35 for the 4.5 mm fish, dropping to 0.002 for the 11.5 mm fish.

- D. Animals 12.5 to 14.5 mm long, which have anomalously large values of P_c when compared to group C, above. If these differences are significant, this implies that their reaction distances or swimming speeds, or both, may be abnormally low.

In the following examples there are no measurements of absolute abundance to compare with towed-net catch data, so assumptions will have to be made as to the relative contributions of population structure and avoidance to the outcome of sampling. Before making such assumptions it will be useful to consider the relative effects of these two factors in the case of *Stolephorus*.

On Figure 4 it can be seen that population abundance of *Stolephorus*, N_L , changed by a factor of 10 over the length interval sampled by the 1-m net. Over this same size interval the catch per class interval (C_L) changed by a factor of 1,000 or more. Thus N_L accounts for no more than 1% or 2% of the observed changes in catch length frequency, the remaining 98% to 99% being attributable to avoidance, at least for animals large enough to be fully retained by the mesh. In this strictly relative sense a 10-fold change in population density with size is in fact negligible, however important it may be in another context.

The problem of relative significance can be placed in perspective by considering whether data such as the 1-m net *Stolephorus* catches might be used to estimate population structure. Daylight 1-m net catches appear to be so overwhelmingly influenced by avoidance that even a 100-fold change in N_L might not be measurable since it could be obscured by a mere 10% error in estimating the effects of avoidance. In this sense it would be fair to assume that a population's structure is uniform, constant for all class intervals sampled by a given net if changes in N_L could not have been measured by that net. This can reasonably be taken to be true whenever the right-hand slope of the catch curves (C_L) exceeds the slope of the population curve

(N_L) by a factor of 10 or more, as it does in Figure 4.

When this assumption is made, however, it must be recognized that the results of any subsequent analysis are contaminated by whatever population structure effects are present and erroneously attributed to avoidance.

Anchovy (*Engraulis mordax*) larvae were also collected off southern California by Murphy and Clutter (1972) with a 1-m net and an Isaacs-Kidd midwater trawl (IKMT). Both nets had similar mesh size and were towed in daylight and at night at comparable speeds, nominally 75 cm/sec (although the IKMT may have been towed somewhat faster). Figure 5 shows data from these tows, converted to speed frequency by assuming that $u_e = 10L$. No estimates of absolute abundance were made for anchovy by Murphy and Clutter; the plankton purse seine was not used in these trials. However, Figure 4 shows that even 10-fold changes in N_L , abundance as a function of length, do not materially alter the shape of the *Stolephorus* speed-frequency curve. Essentially identical results could have been obtained by fitting the catch data to the theoretical curves without correction for changes in population density. Since anchovy are in many ways similar to *Stolephorus*, it may be tentatively assumed that avoidance is the major determinant of size-frequency curves for anchovy, as it clearly was for *Stolephorus* (Figure 4).

Without an independent estimate of absolute abundance, there is no priori relationship between catch and P_c . This relationship must therefore be established by seeking the best possible fit between theory and observations. Speed-frequency values were plotted on tracing paper, using the semilog coordinate system of Figure 3. The resulting graph was placed over the upper panel of Figure 3 and moved up and down until a good fit resulted (right-left motion is not allowed, since the position of points along this axis is determined by size, the size-speed relationship, and net speed). This procedure is equivalent to making various assumptions about N_0 , the fictitious population density at zero length, for which $P_c = 1$ by definition since $u_e = 0$. When this is done, the speed-frequency curves

become speed - P_c curves, showing probability of capture for each class interval. Best fits were obtained for the 1-m net anchovy catches with $N_0 = 75$ anchovy per 100 ml wet plankton (left panel, Figure 5). For the IKMT, the best fit yielded $N_0 = 60$ anchovy per 100 ml wet plankton (right panel, Figure 5). It might have been worthwhile to treat day and night catches separately, as was done for the two types of gear, but the resulting differences in N_0 between day and night tows are small, change sign for the two different nets, and probably are not significant.

Figure 5 shows that the variance for anchovy data was smaller than that for *Stolephorus* catches (Figure 4), so that the anchovy data fit the theoretical curves somewhat better. There is no way to tell whether this difference in variance is due to differences in sampling or population structure. For both nets, day-night differences in x_0/R are small, but reaction distances tend to be slightly greater for tows taken during the day, as might be expected. A surprising result is the similarity in values of x_0/R obtained for the two nets: about 6.6 for the 1-m net and 5.4 for the IKMT (if slightly lower values for the largest size classes are ignored). This yields reaction distances, x_0 , of 3.3 m for the 1-m net and 8.2 m for the IKMT. Clearly anchovy reacted to the IKMT at considerably greater distances. A light dashed line on Figure 5 (right panel) shows the dramatically increased catches which would be expected if anchovy had reacted to the IKMT at 3.3 m ($x_0/R \simeq 2$), as they apparently did in the case of the 1-m net.

The analysis shows that maximum values of P_c for the IKMT amounted to only 0.25, as compared to maximum values of P_c for the 1-m net of 0.40 or more.

Mesh retention appeared to differ for the two nets, despite similarity in mesh size (according to Murphy and Clutter, 1972, the IKMT was meshed with Nitex,² and the 1-m net with gauze silk, 56xxx grit, having openings of 0.505 and 0.55 mm, respectively). Retention dropped below 100%, based on deviations from the the-

² Reference to commercial products does not imply endorsement by the National Marine Fisheries Service.

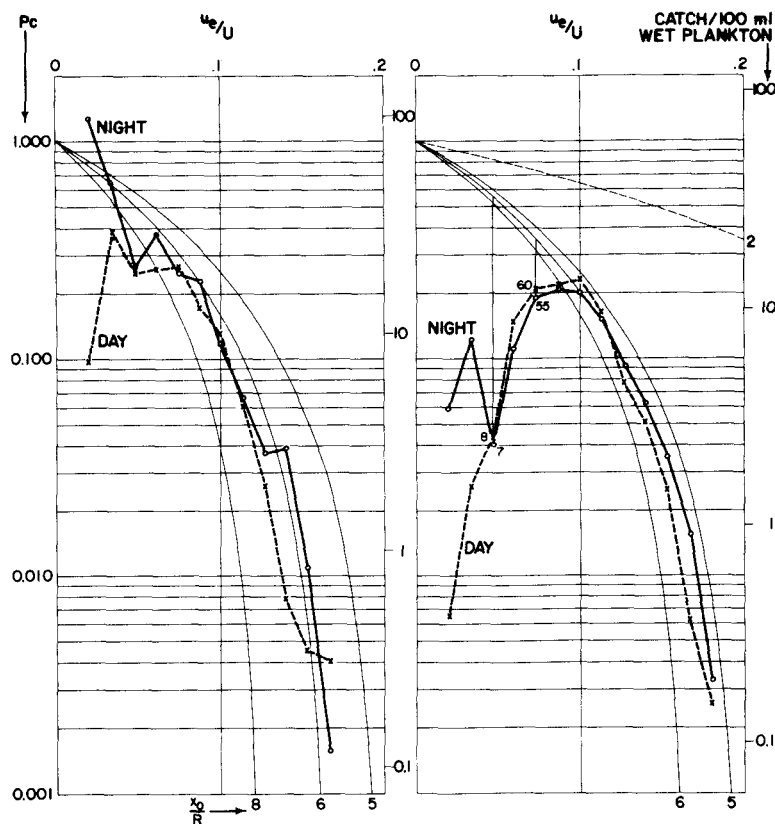


FIGURE 5.—Day and night catches of larval anchovy by a 1-m net (left) and an Isaacs-Kidd midwater trawl (right). Length-frequency data have been converted to relative escape speed (abscissa) versus frequency (ordinate, right hand scales), and compared with theoretical curves. Catch values at $P_c = 1.0$ provide estimates of abundance for all class intervals sampled. Dashed line for P_c at $x_0/R = 2$ on Isaacs-Kidd graph shows catches which could have been expected if the anchovy's reaction distance had been equal to that for the 1-m net. Net retention, based on differences between theoretical and actual catch, is shown for two class intervals on right panel: 7% to 8% for 3.75 mm fish and 55% to 60% for 5.75 mm fish. (Class sizes ranged from 1.75 mm to 12.75 and 13.75 mm by 1 mm increments.) Data from Murphy and Clutter (1972).

oretical lines of constant x_0/R , for anchovy shorter than 7.75 mm with the IKMT and 4.75 or 5.75 mm for the 1-m net. If x_0/R for a given species remains constant for any one net towed at a single speed, extrapolation of the theoretical curve toward the origin gives an indication of expected catch for smaller size classes (assuming, of course, that changes in population density

with length are negligible). This use of avoidance theory is illustrated in Figure 5, right panel, where retention is calculated at 7% to 8% for 3.75-mm fish and 55% to 60% for 5.75-mm fish. These values can be easily measured on the semilog graph; the vertical distance between the "theoretical" and the observed values is transferred to the vertical coordinate scale (e.g.,

with dividers), setting the upper point at 1.0 (100%) and reading the fraction or percentage retained at the lower point.

Let us now consider catches obtained with one type of gear at two different speeds.

Aron and Collard (1969) made carefully controlled IKMT tows at two different speed ranges, at night, using telemetering flow and depth meters to insure that the amount of water sampled was the same for all tows and that sampling was done at the desired depths. The speed of their net varied between about 1.0 and 1.7 m/sec and about 1.6 and 2.3 m/sec during the two sets of tows; I have assigned values, corresponding to modal speeds, of 1.2 and 2.0 m/sec to these tows for calculating values of u_e/U .

The assumption made thus far that $u_e = 10L$, cannot be used for the species enumerated by Aron and Collard because of their large size (up to 102 mm); escape speeds of 10 body lengths per second yield values in excess of the net's speed. Either fish that big should not have been captured, or their escape speed must be considerably less than 10 lengths per second. Accordingly, it was assumed that $u_e = 5L$ (with units of cm/sec and cm).

As was noted earlier, the effect of different choices of escape velocity to length ratios is to shift the observed points along the u_e/U axis of Figure 3, with proportional changes in resulting values of x_0/R . If a set of observed points fall precisely on the theoretical curve $x_0/R = 4$, for example, a twofold change in the assumed escape velocity results in points falling equally precisely on the curves for $x_0/R = 8$ or 2, depending on whether the escape velocities are halved or doubled. Values of P_c are not affected by the choice of velocity to length ratios.

Obviously, relative values of reaction distance, x_0 , can be estimated from the present theory, but absolute values can only be determined if in addition the animal's actual escape velocities are known, preferably as a function of size. Thus, from Figure 5 we can conclude with some assurance that anchovy react to the IKMT at distances some 2.5 times as great as they do to the 1-m net. But the reaction distances themselves, 8.3 m for the IKMT and 3.3 m for the 1-m net,

can only be correct if anchovy do in fact swim at an average speed of 10 body lengths per second when trying to avoid the net.

Of the species enumerated by Aron and Collard, *Bathylagus stilbius* seemed most amenable to analysis with avoidance theory, because the length-frequency curves for this species were somewhat smoother, and differed more with speed of tow, than was the case for other species. Figure 6 shows the speed-frequency curves for this species, assuming that $u_e = 5L$ and that $U = 120$ and 200 cm/sec, respectively. A fairly good fit could be obtained for P_c at $x_0/R \approx 3.8$ for the faster tow and for part of the slower tow. For the fit shown in Figure 6, N_0 , the abundance at zero length, is 1,400 animals per class interval (Aron and Collard, 1969, give catches as total numbers caught during all 34 tows made in January 1966). An alternative choice of N_0 , 340 animals per class interval, produces a good fit with $x_0/R = 2.4$ for the larger animals caught by the slower tows but does not fit any of the other data. In short, there is no way to fit the length-frequency data for *B. stilbius* to the theory under the assumptions used up to now.

The assumption most likely to be violated is that population size at different lengths has negligible influence on the size-frequency curve ($N_L \approx N_0$). This assumption when valid makes it possible to fit data from a series of length classes using a single value for N_0 , as was done for anchovy (Figure 5). If N_L varied significantly with length for *B. stilbius*, only identical length classes can be compared between the two sets of tows at different speeds. Figure 7 illustrates this procedure for the 62- and 97-mm length classes, where theoretical curves for P_c at $x_0/R = 2.8$ and 1.8, respectively, fit the data for these two size classes. Values of N_0 thus obtained were 900 individuals per class interval for 62-mm fish and 26 individuals per class interval for 97-mm fish. This 35-fold difference in apparent abundance is comparable in magnitude to differences in catch rates, 285 to 8 (48-fold) for the faster tows and 57 to 1 for the slower tows. It therefore seems likely that the shape of the length-frequency curves for *B. stilbius* was determined in large part by the population structure; avoidance apparently played

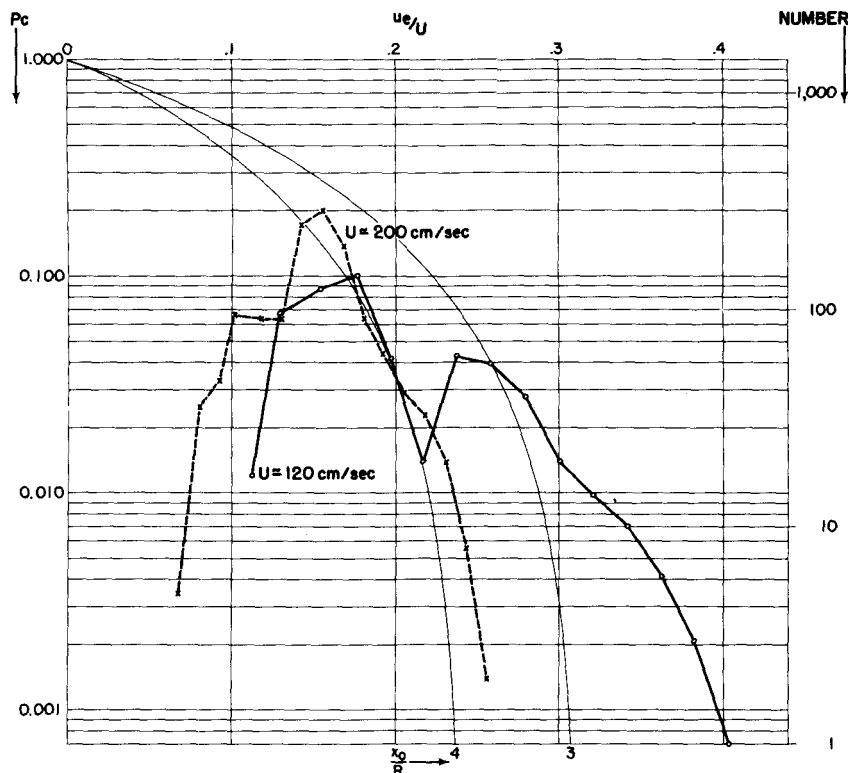


FIGURE 6.—Catches of *Bathylagus stilbius* with an Isaacs-Kidd midwater trawl at two speeds. Length frequencies converted to speed frequencies are compared with theoretical curves for P_c , showing fairly good fit at $x_0/R \approx 3.8$ for part of data. No overall fit is possible for these observations, indicating that length-frequency curves for this species were not determined primarily by avoidance. Data from Aron and Collard (1969).

a minor role, accounting only for the difference between the 35-fold range in apparent abundance and the observed 48- to 57-fold differences in catch rates for the 62- and 97-mm size classes. The most important effect of avoidance in the *B. stilbius* catch data is the nearly constant 5-fold difference in catch rates at the two different speeds, for all animals larger than 62 mm.

Figure 7 shows sample results for only two class intervals. Table 1 shows results for all class intervals of Aron and Collard's *B. stilbius* catch data: Catches (as read from length-frequency curves), ratios of catches at two speeds, and values of x_0/R , N_0 , and P_c obtained by fitting the catch data to the theoretical curves of Figure 3. Obviously, "fitting" two points to a

curve is a trivial exercise, which is only justified by the apparently consistent results obtained for larger fish in Table 1. Data from three or more sets of tows, at as many different speeds, should be used for such analyses.

Figure 7 also shows the ranges of values of u_e/U , and the extreme values for x_0/R and N_0 , which result when the full range of net speeds reported by Aron and Collard (1969) is used instead of the modal speeds. The numerical results, like the net speeds, vary by factors of about two—an indication of the uncertainty inherent not only in the *B. stilbius* data but also in the data for other species considered here, since variations in net speed comparable to those measured by Aron and Collard are doubtless present

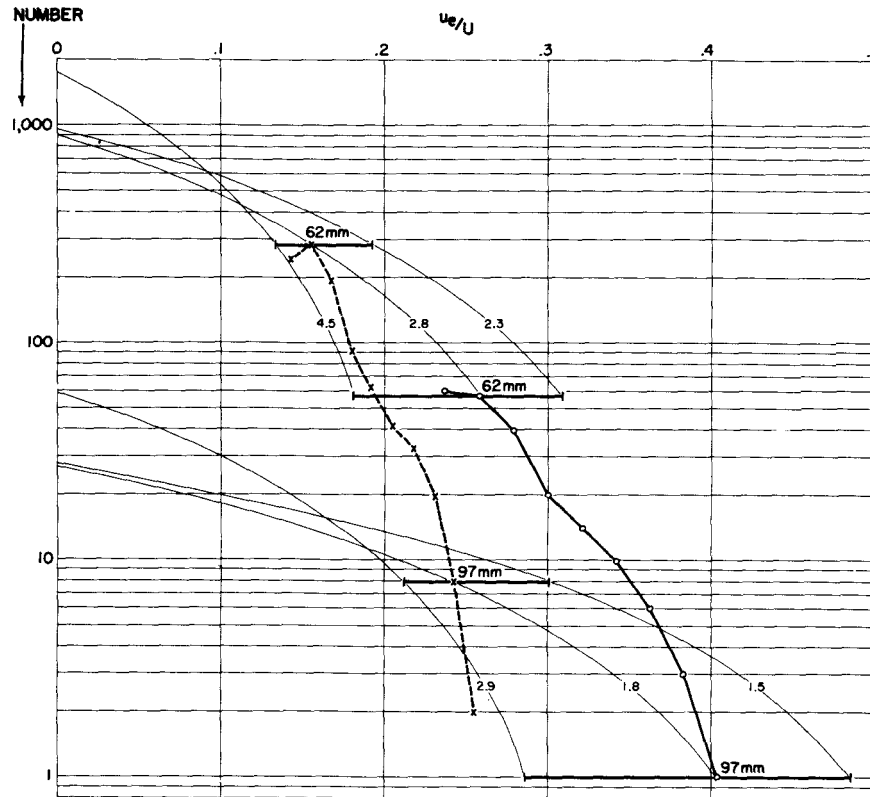


FIGURE 7.—Alternative analysis of *Bathylagus stilbius* data from Figure 6. Estimates of population (intercept of x_0/R curves for 1.8 and 2.8 with ordinate) by class interval show wide variations: from 900 animals at 62 mm to 26 animals at 97 mm. This range is comparable to the observed range in catch for these class intervals (57 to 1), showing that the length-frequency curves are primarily determined by population structure. Horizontal bars show measured ranges of towing speeds, and the effect of different speeds on the analysis. Data from Aron and Collard (1969).

during any normal towing procedure. This uncertainty does not affect the qualitative conclusions obtained from theoretical analyses; it is quite clear, for example, that anchovy react earlier to the IKMT than they do to the 1-m net. It is also quite clear that the population structure of *B. stilbius* determines the shape of the catch size-frequency curve, whereas differences in overall levels of catch for this species at two ranges of towing speed are due to avoidance, at least for those animals effectively retained by the meshes. In any case, numerical estimates of parameters such as P_c and population density which are correct to within a factor of two or

less are entirely adequate for many purposes.

Simultaneous solutions for P_c as a function of length have been obtained from the theoretical equations for three pairs of samples from as many populations. The results, while not definitive, appear encouraging.

It should therefore be possible to apply the theory to a more typical set of data, a single composite sample of larval and juvenile stages of *Katsuwonus pelamis*, the skipjack tuna. These animals were sampled with a large midwater trawl, the Cobb pelagic trawl (Higgins, 1970), during a series of five equatorial cruises made by the RV *Townsend Cromwell* in 1969-70. Repli-

TABLE 1.—Analysis of catches of *Bathylagus stibius* with an Isaacs-Kidd midwater trawl towed at two speeds, based on avoidance theory as illustrated in Figure 7. Data from Aron and Collard (1969).

Standard length (mm)	Catches		Catch ratio		Relative reaction distance x_0/R	Population abundance number per class interval	Probability of capture		Notes
	Low speed	High speed	High speed				Low speed	High speed	
			Low speed	High speed					
27	17	5	0.29	--	--	--	--	1	
32	93	36	0.39	--	--	--	--	1	
37	127	46	0.36	--	--	--	--	1	
42	143	94	0.65	--	--	--	--	1	
47	60	90	1.5	1.8	150	0.41	0.61	2	
52	20	90	4.5	3.3	300	0.068	0.31	2	
57	61	248	4.1	2.9	720	0.085	0.34	2	
62	57	285	5.0	2.8	900	0.063	0.31	--	
67	40	195	4.9	2.6	660	0.061	0.31	--	
72	20	92	4.6	2.3	280	0.073	0.33	--	
77	14	63	4.5	2.1	200	0.071	0.32	--	
82	10	42	4.2	1.9	120	0.084	0.25	--	
87	6	33	5.5	1.9	100	0.060	0.33	2	
92	3	20	6.7	1.9	62	0.050	0.33	2	
97	1	8	8.0	1.8	26	0.036	0.29	2	
102	0	2	--	--	--	--	--	--	

¹ Mesh losses probably significant, analysis with avoidance theory inappropriate.
² Mesh losses may be significant, analysis with avoidance theory questionable.
³ Sample size inadequate, results of analysis may be seriously in error.

cate 6-hr tows were taken every night for (usually) five successive nights at each of five locations (lat 12°N, 7.5°N, 3.5°N, 0°, and 3.5°S at long 145°W) during these cruises. Catches of skipjack larvae and juveniles during each of these cruises are summarized in Table 2.

Length-frequency data from three cruises, numbers 43, 44, and 48, were kindly made available to me by Walter M. Matsumoto. These data were similar for all three cruises and were therefore pooled to obtain a smoother curve (Figure 8, right panel). Of the 510 animals in this sample, 6 could not be measured. Another 5, the largest (see Figure 8, right panel) were suspected of being atypical, possibly moribund and unable to properly avoid the trawl. Figure 8 (left panel) shows the data for the remaining animals, converted to speed frequency using $u_e = 10L$ and $U = 150$ cm/sec.

Since the skipjack population structure as a function of length, N_L , is completely unknown, two extreme assumptions are considered: First, that avoidance has no effect, so that virtually all of the drop in catch with increasing length (Figure 8) is due to changes in the population. Second, that population structure has no effect, so that the length-frequency curve is determined only by avoidance and mesh losses.

The first assumption is illustrated in Figure 9, left panel, where the lowest curve shows speed-

frequency values. The straight line represents N_L , assuming the largest possible exponential decrease in population with size, consistent with the catch data. The upper curve shows P_c , obtained by dividing the catch data by N_L after setting $N_0 = 1.0$, exactly as was done on Figure 4. This analysis results in a wide range of values for P_c and x_0/R . N_0 in this case becomes 100%, equivalent to 500 individuals per class interval. Figure 9, right panel, shows P_c plotted on the linear theoretical graph of Figure 3.

The alternative extreme, assuming that $N_L = N_0$ so that population has no influence on catch length frequencies, is illustrated in Figure 10. There is no single apparent "best fit," between observation and theory, so three alternatives are considered. The upper curves, marked A, show

TABLE 2.—Skipjack larvae and juveniles caught with the Cobb pelagic trawl during RV *Townsend Cromwell* equatorial cruise series. Samples were taken along long 145°W, at lat 12°N, 7.5°N, 3.5°N, 0°, and 3.5°S.

Cruise no.	Dates	Number of tows	Number of successful tows	Skipjack caught
43	May 7- June 2, 1969	24	16	197
44	July 6- Aug. 3, 1969	25	10	154
46	Oct. 14- Nov. 13, 1969	27	11	297
47	Jan. 20- Feb. 25, 1970	21	1	1
48	Mar. 30- Apr. 30, 1970	25	15	158

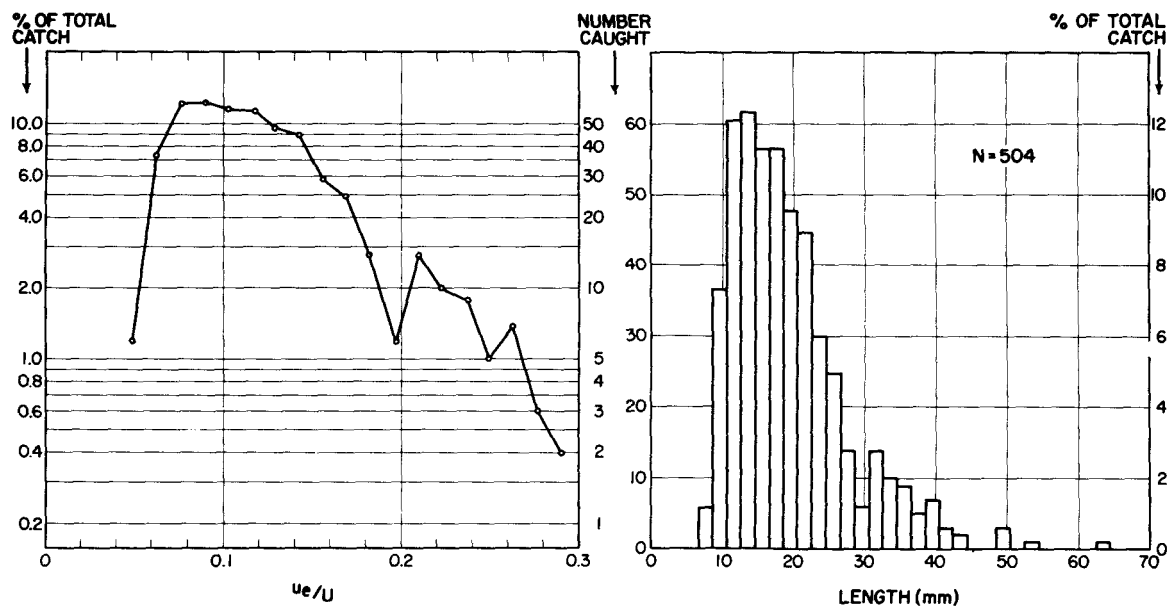


FIGURE 8.—Speed-frequency curve for skipjack larvae caught by a Cobb pelagic trawl (left panel) obtained from a length-frequency curve (right panel). Data courtesy of W. M. Matsumoto, NMFS, Southwest Fisheries Center, Honolulu Laboratory.

the data aligned to yield a fit for the best sampled class intervals. The lower curve, C, is aligned so as to fit the theoretical curves in regions of maximum slope, where sampling is most sensitive to avoidance. The middle curve, B, is a compromise which yields a reasonable fit at intermediate class intervals. Although all three analyses look plausible in the left panel of Figure 10, the linear graph shown on the right of Figure 10 clearly demonstrates that curve B yields the best match between theory and observation.

In principle there is no reason to prefer the analyses shown on Figure 10 to their alternative, Figure 9. However, I personally regard curve B on Figure 10 as the best solution because it provides the simplest and most informative explanation for the observations.

Note that all three sets of curves on Figure 10 fit two separate theoretical curves, in two distinct and well-separated groups of class intervals. As in previous examples, P_c for the largest animals markedly exceeds the values which would be expected if the theoretical x_0/R curve for smaller animals were simply extrapolated toward the right (except for curve A). In the

cases of *Stolephorus* and anchovy, these anomalies were relatively minor and could reasonably be attributed to selective sampling of animals with subnormal avoidance ability. In the case of skipjack, however, this anomaly is more pronounced.

A more likely explanation for the two-part curves of Figure 10 is the construction of the Cobb trawl, which is lined with netting of two different mesh sizes: 19 mm stretched mesh of 9-thread (210 denier) nylon netting in the forward sections, with 6.4 mm stretched mesh 6-thread (210 denier) nylon netting at the cod end (Higgins, 1970). This 3-fold difference in mesh size corresponds with a nearly 3-fold difference in the size of skipjack which makes up the two components of the catch (100% apparent mesh retention at lengths greater than 15.5 mm and 37.5 mm, respectively, from curve B of Figure 10). The Cobb trawl is, in effect, two distinct nets which happen to be rigged in tandem. The openings of the trawl and its cod end during a tow are estimated to have radii of about 4 m and 1.5 m, respectively, so that their mouth areas differ by a factor of seven. The volume of water filtered by the cod end should thus

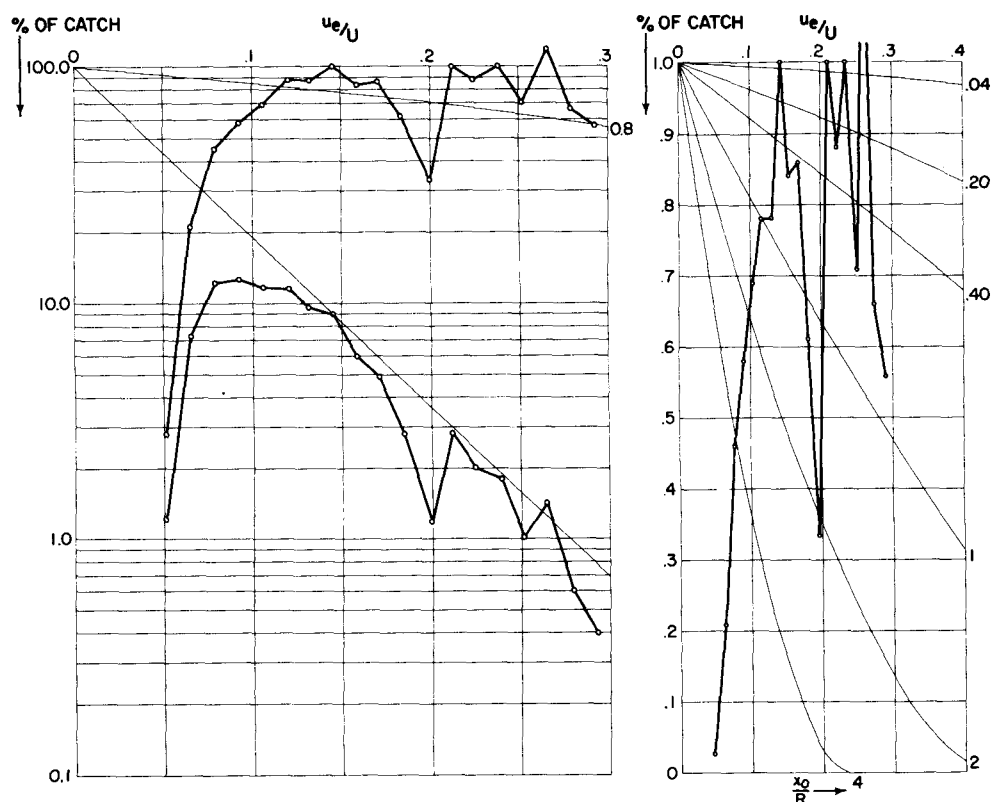


FIGURE 9.—One possible analysis of skipjack catch data, Figure 8, assuming that the length-frequency curve is determined by population density. Left panel: Lower curve, speed-frequency data, Figure 8. The straight line represents a hypothetical population density curve. Upper line shows P_c obtained by correcting catches for population changes. Right panel: Values of P_c from left panel, plotted on linear coordinates.

be somewhat less than one-seventh of the volume sampled by the trawl, because of the increased resistance to flow of the finer mesh. Catches of the six largest class intervals of skipjack all exceed the "expected" catch (theoretical curve for $x_0/R = 4$) by factors of seven or more, as would be expected if in fact these larger fish were captured by the main body of the trawl, rather than by the cod end.

The evidence suggests that curve B on Figure 10 represents a reasonable analysis of skipjack catches with the Cobb trawl. This implies that avoidance and mesh losses are dominant factors determining the size-frequency curves (Figure 8). The largest skipjack, 31.5 to 43.5 mm in length, were captured by the main body of the Cobb trawl, with P_c values between 0.05

and 0.009. Their reaction distance, x_0 , was $3R$, or some 12 m. Some losses through the coarse mesh are apparent for animals smaller than 39.5 mm in length. Skipjack smaller than 31.5 mm in length were captured by the cod end of the trawl, at P_c values ranging from about 0.3 to 0.03, corresponding to reaction distances of $4R$, or 6 m. Some losses through the finer mesh are apparent for animals smaller than 17.5 mm; estimated mesh losses reach 96% for animals 7.5 mm in length. As was pointed out earlier, the above estimates of reaction distances are dependent on the assumed escape speeds, 10 body lengths per second. If the animals move faster than this, x_0 values will diminish proportionately, and vice versa.

Estimates of P_c are not affected by escape

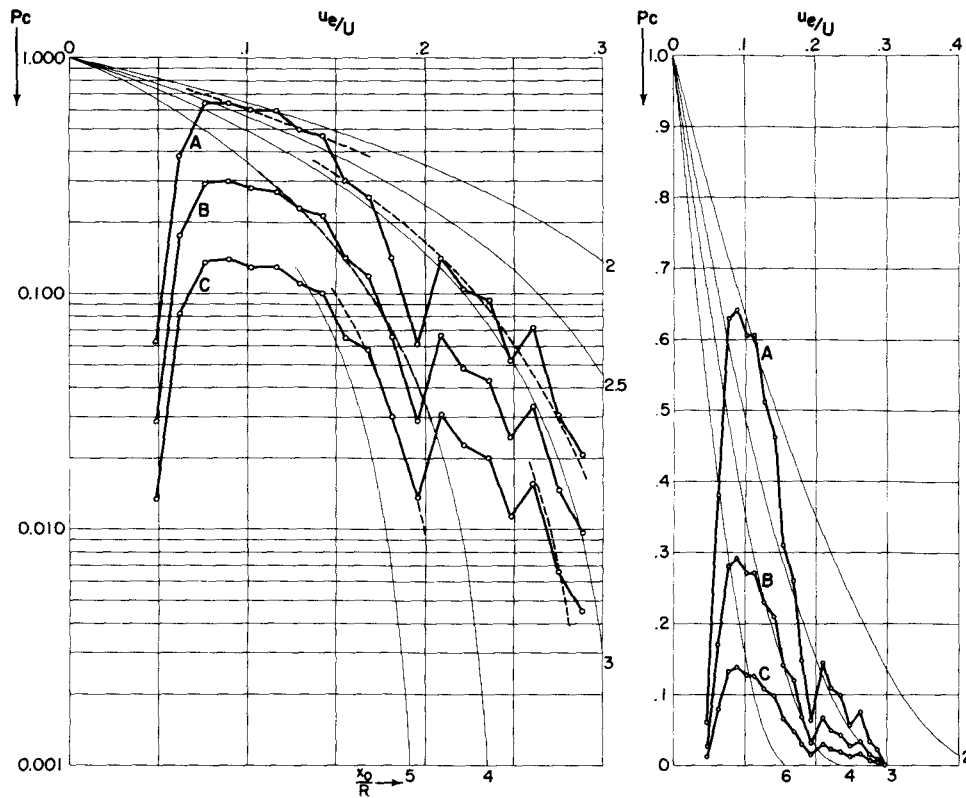


FIGURE 10.—Alternative analysis of skipjack data from Figure 8, assuming constant population density. Left panel: Three possible choices of fit between catch data and theoretical curves of P_c at constant x_0/R . Curve A shows fit for best sampled class intervals. Curve B shows fit for midrange class intervals. Curve C shows fit for regions of maximum slope. Right panel: P_c curves from left panel, plotted on linear coordinates.

speed assumptions, so the analysis yields usable estimates of population abundance of skipjack larvae and juveniles between 17.5 and 43.5 mm in length, if population structure is not important. From curve B of Figure 10, N_0 is 40% (of 499) or 200 individuals per class interval, as can be seen by placing the “% of catch” scale of Figure 9 in the proper position on Figure 10. Since abundance apparently does not seriously affect the length-frequency curve, each of the 19 class intervals sampled must also represent a population of about 200 individuals. Thus the sample of 510 skipjack was taken from a population of about 3,800, an overall catch efficiency of 13%. The total catch resulted from 41 effective tows (out of 74), an average catch per effective tow of 12.3. Accordingly, the popula-

tion sampled by the Cobb trawl must have numbered roughly 94 skipjack per effective tow, to yield the observed catches at 13% efficiency. By far the greatest number of skipjack were caught by the cod end of the trawl, so the volume effectively sampled was not more than 230,000 m³ (100% filtering efficiency). This leads to an estimated mean population density for larval and juvenile skipjack of one fish per 2,500 m³, in areas where skipjack were present during the three *Townsend Cromwell* equatorial cruises.

Since P_c is by definition a minimum probability of capture, reference to equation (3) shows that the above estimate of mean population density (during a tow) represents a maximum value. On the other hand, of course, the skipjack probably were not randomly distributed, so that

a 6-hr tow doubtless underestimates their actual (as opposed to mean) population density by integrating over a 33-km distance.

Finally, two of the four species discussed here were sampled in a manner which permits use of equation (8) to estimate values of K (the product x_0u_e). Anchovy were sampled with two different nets at one speed of tow, and *B. stilbius* were sampled with one net at two ranges of speed. Table 3 shows values of K calculated for these two species. For any one choice of speeds, values of K for *B. stilbius* are nearly constant within the class intervals where fish were retained by the mesh and caught in numbers large enough to yield useful estimates of C_1/C_2 , the ratio of catches obtained at the two speeds. Values of K for anchovy, on the other hand, were not constant. The latter result is not surprising, since widely different values of x_0 were obtained for the 1-m net and the IKMT whereas u_e would not be expected to differ for the two nets. Accordingly, the product of x_0u_e should not be the same for both nets, which violates the basic assumption used in calculating K with equation (8).

When values of K from Table 3 are used to calculate P_c from equation (7), the results agree with those obtained graphically for *B. stilbius* at the modal speeds, but not for anchovy. Apparently the calculated values of K for anchovy in Table 3 are too low, since they yield values of P_c which are too high, corresponding to values expected for reaction distances of about 2 to 3 m for both nets. Until avoidance behavior

is better understood, equation (8) should be used with caution.

SUMMARY AND CONCLUSIONS

The ideal sampler for plankton and nekton is one whose selective characteristics are known to be appropriate, qualitatively and quantitatively, for the problem under study. Major factors determining the selectivity of towed-net samplers are avoidance and mesh selection, both of which are strongly dependent on species, size or stage of development, and physical condition. Thus the theory of towed-net selectivity must be based on a combination of general principles and detailed knowledge of the physical characteristics and behavior of each species of interest, and of each net design as well.

This preliminary study deals with one aspect of selectivity: the basic principles of avoidance. A theoretical equation is derived for P_c , the minimum probability of capture, for animals which respond individually to an oncoming sampler by attempting to dodge. The theory is based on the amount of time animals allow themselves for avoiding the net, the animal's speed relative to the net, and the geometry of the encounter. Animals are characterized by their reaction distance, x_0 , and their escape speed, u_e . The net is characterized by the radius of its mouth opening, R , and its speed through the water, U . Equations (5) and (6) show the theoretical relationships between these variables and P_c ; Figure 3 illustrates these equations graphically.

TABLE 3.—Values of the product $x_0u_e = K$ for anchovy and *Bathylagus stilbius*, from equation (8). Anchovy data obtained with two nets towed at one speed, day and night. *B. stilbius* data obtained with one net towed at two speed ranges; K calculated using minimum, modal, and maximum speeds for each range.

Anchovy					<i>Bathylagus stilbius</i>				
Length (mm)	Catch ratios (1-m/IKMT)		K (cm ² /sec)		Length (mm)	Catch ratios (slow/fast)	K (cm ² /sec)		
	Day	Night	Day	Night			Minimum speeds	Modal speeds	Maximum speeds
7.75	0.735	0.764	758	665	47	0.667	5,600	6,500	11,800
8.75	0.492	0.565	1,470	1,240	52	0.222	11,200	13,300	20,700
9.75	0.431	0.524	1,850	1,360	57	0.244	11,000	13,000	20,300
10.75	0.209	0.827	2,410	488	62	0.200	11,500	13,600	21,100
11.75	0.242	0.417	2,280	1,690	67	0.204	11,500	13,500	21,000
12.75	0.847	0.133	435	2,710	72	0.218	11,300	13,300	20,800
					77	0.222	11,200	13,300	20,700
					82	0.238	11,100	13,000	20,400
					87	0.182	11,700	13,900	21,400
					92	0.149	12,100	14,400	21,900

Testing of the theory requires some knowledge of a species' escape speed as a function of size or stage of development and its reaction distance for one or more net designs under various circumstances, so that particular groups of animals in a sample can be associated with the proper values of x_0 and u_e in the theory. If the theory is known to be valid in a given instance, x_0 can be determined once u_e is known.

The theory was evaluated against four selected sets of catch data. Since not enough was known about the swimming ability of the species in question, assumptions had to be made about swimming speed as a function of size for each one. Aside from the major premise used in deriving the theory, that animals which can escape will do so, other assumptions made in carrying out analyses of catch data were: that reaction distance is essentially constant for any one species under a given set of circumstances (one net, towed at one speed, at one time of day) and that the size-frequency curve for a species is determined entirely by mesh losses, avoidance, and the population structure—the number of animals in each size class interval in the population.

The theory was first applied to daytime catches of *Stolephorus purpureus* with a 1-m net. Simultaneous measurements made with a plankton purse seine provided information on the population structure. This nearly ideal set of data permits direct calculation of the sampling efficiency of the 1-m net, so that an absolute test of the present theory could be made. First, the bias due to population structure was removed, by dividing the catch in each class interval by the population in that class interval; this procedure also converts the catch into values of P_c for fish large enough to be completely retained by the meshes, as equation (3) demonstrates. The adjusted catch curve (the solid line labeled C_L/N_L in Figure 4) can be directly compared with theoretical curves from Figure 3 (showing P_c for various values of relative reaction distance, x_0/R), when the length class intervals have been converted to speed class intervals by assuming that the fish swim 10 body lengths per second. Agreement between theory and observation appears to be good, with some exceptions. These may be due to sampling var-

iance, population variance, or failure of one or more assumptions used in matching *S. purpureus* to the theoretical parameters. In the latter case, the anomalies could be accounted for by incompetent avoidance behavior and school response instead of individual reaction to the net.

In the second example, the theory was used to evaluate catches of anchovy by two different nets, a 1-m net and an IKMT, towed at the same nominal speeds. Since population abundance was not determined for anchovy, an additional assumption had to be made: that the catch length-frequency curves were determined primarily by avoidance and mesh losses, as in the case of Hawaiian anchovy, where catches decrease 1,000-fold while the population decreases only by a factor of 10 in the same size interval. With this assumption, catch speed-frequency curves must also be curves of relative P_c as a function of size, or speed. Fitting the observed values to the theoretical P_c curves (Figure 5) yields a unique value for population density in each class interval, numerically equal to the catch at $P_c = 1.0$. For the anchovy, population densities of 75 and 60 animals per 100 ml wet plankton were obtained for the two samples analyzed by this method. In this case agreement between theory and observation, and between samples, seems excellent. Except for night tows with the 1-m net, values of P_c do not exceed 0.40 for the 1-m net and 0.12 for the IKMT. The only significant deviations from theory occur at smaller class intervals, where mesh losses are important. Mesh retention can be estimated quantitatively by extrapolating the theoretical curve toward smaller class intervals, for comparison with observed catches, as illustrated on the right-hand panel of Figure 5.

The third example makes use of length-frequency data for *Bathylagus stilbius* caught with an IKMT towed at two different ranges of speed. In this case, no satisfactory fit could be achieved for all larger class sizes of both sets of tows, when treated as a unit. If instead the analysis is performed using only one class interval at a time from the two sets of tows, as shown in Figure 7 and Table 1, the cause of the difficulty becomes clear. The estimated population densities have almost as great a range as do the

catches. Therefore the length-frequency curves are primarily determined by population structure, not avoidance. However, avoidance does account for the fact that faster tows caught nearly five times as many fish. Table 1 shows that P_c remained essentially constant for each set of tows over a wide range of class intervals, with values of about 0.3 for the fast tows and 0.07 for the slower ones.

The final example illustrates the use of avoidance theory for analysis of a more typical set of catch data: larvae and juveniles of the skipjack tuna caught with one net towed at one speed. The simplest way to account for the skipjack data is to assume that avoidance was more important than population structure (Figure 10). The Cobb pelagic trawl used to sample skipjack had two sizes of mesh, differing by a factor of three; the smaller mesh was used to line the cod end of the Cobb trawl. Catches of skipjack with this net fall into two groups differing in size by a factor of about three, suggesting that this trawl acts as two nets fishing in tandem. The large mesh forward end catches the largest fish, with a maximum P_c of the order of 0.03. The cod end catches smaller fish, with maximum P_c values of about 0.3. Fish of intermediate size are able to dodge the cod end but some 10% to 50% of these fish (depending on size) were retained by the larger meshes.

Analysis of four test cases leads to the conclusion that the elementary avoidance theory developed here does in fact provide reasonable interpretations of some samples obtained with towed nets. The theory's major virtue is its ability to provide relatively unambiguous estimates of probability of capture and thus of animal abundance in nature, which are not dependent on the accuracy of assumptions about swimming speeds or reaction distances. Even when the theory fails to account for observed features of the catch, it provides useful insight into the reasons for such failure and some indication of their magnitude. This is most clearly evident for losses through the mesh, but failures of the theory, or of the assumptions used in applying it, are also responsible for evidence uncovered here of incompetent avoidance behavior by smaller animals, effects of schooling on avoidance

success, and the fact that avoidance has only a minor effect on the length frequencies of *B. stilbius* samples. Given our present lack of knowledge of the behavior of animals when confronted by towed samplers, it might even be said that anyone using this theory should be most cautious in precisely those cases where the theory apparently works best. A case in point is the analysis of anchovy data presented on Figure 5. Agreement between observations and theory is relatively good in this case, so that it might be easy to forget that the slope of both curves, and the apparently valid estimates of reaction distance obtained from their slopes, depend entirely on the assumed relationship between the anchovy's length and its swimming speed. Similarly, Figure 7 shows the errors which can result from assuming that the speed of the net is constant. The best contribution to the study of plankton and nekton which the present theory could make is to stimulate further research which will make the theory obsolete.

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