Three-Dimensional Prey Reaction Field of the Juvenile Coho Salmon (*Oncorhynchus kisutch*)

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Filmed observations of the feeding behaviour of juvenile coho salmon (*Oncorhynchus kisutch*) cruising in a large aquarium were used to determine the three-dimensional shape of their reaction field, and to estimate the cross-sectional area of the effective volume searched for prey (scanning area). Reaction distance was greatest above the horizontal visual plane and ahead of the transverse visual plane, and this corresponds to the feeding behaviour of fish observed in the wild. The scanning area for a given size of prey was obtained by plotting all captures as projections on the transverse plane. This distribution of points was then divided into a series of concentric bands characterized by prey attack probabilities, which were then used as weighting factors in the final calculation of the scanning area. Our results and techniques are discussed in relation to previous studies of fish reaction fields, and a simple method of estimating scanning area for salmonids is suggested.

On a utilisé des observations filmées du comportement alimentaire de saumons cohos (*Oncorhynchus kisutch*) juvéniles se déplaçant dans de grands aquaria pour déterminer la forme tridimensionnelle de leur champ de réaction et pour évaluer l'aire transversale du volume réel parcouru à la recherche de proies (aire d'exploration). La distance réactionnelle était plus élevée au-dessus du plan visuel horizontal et en avant du plan visuel transversal; cela correspond au comportement alimentaire observé chez les saumons sauvages. On a calculé l'aire d'exploration pour une taille donnée d'une proie en portant sur un graphique toutes les captures comme projections sur le plan transversal. Cette distribution des points a ensuite été divisée en une série de bandes concentriques caractérisées par les probabilités d'attaque des proies, probabilités qui servirent ensuite comme facteurs de pondération dans le calcul final de l'aire d'exploration. On présente les résultats et techniques en fonction des études antérieures sur les champs de réaction du poisson et on élabore une méthode simple pour l'estimation de l'aire explorée par les salmonidés.

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Selective feeding on large prey by predatory fish has been related to the greater visibility of larger prey items (Brooks and Dodson 1965; Ware 1972, 1973; Werner and Hall 1974; Confer and Blades 1975; Moore and Moore 1976; Wańkowski 1979, 1981; Dunbrack and Dill 1983). Models incorporating a positive relationship between prey size and the distance at which prey will be detected and attacked (reaction distance) have shown good agreement between predicted and actual dietary size-class frequencies (Ware 1973; Werner and Hall 1974; O'Brien et al. 1976; Eggers 1977; Gibson 1980; Dunbrack and Dill 1983). In the construction of such models it is often sufficient to specify only the relative reaction distance (RD) to various sizes of prey, but if quantitative diet predictions are required, or if the feeding space is constrained, actual RDs and the shape of the reaction field (the visual field surrounding the fish) must also be included (Confer et al. 1978). The relationship between prey size and frontal RD has been obtained for several fish species, but relatively less work has been done on the shape of reaction fields and how this may affect the prey encounter process.

As a cruising fish moves through the water column, it searches a somewhat cylindrical volume whose longitudinal axis is the fish's trajectory. For such a predator, the rate at which it encounters prey will be directly proportional to the effective cross-sectional area of this search volume, which we term "scanning area." Confer et al. (1978), in their study of the reaction field of cruising lake trout (*Salvelinus namaycush*), approximated the dimensions of this cross section using the means of observed RDs to prey attacked adjacent to the transverse plane (the plane perpendicular to the fish's longitudinal body axis and passing through both eyes). Luecke and O'Brien (1981) described the reaction field of stationary bluegill sunfish (*Lepomis macrochirus*) in terms of 0.95 and 0.05 detection probability contours for a number of visual planes, including the transverse one. The reaction field map they constructed provides a useful model of prey encounter for a fish such as the bluegill, which tends to pause after each capture and search for the next prey item from a stationary position (Luecke and O'Brien 1981), but it is not entirely appropriate for a cruising predator, which may perceive its prey somewhat differently. For example, the movement of a cruising predator could affect the detectability of prey items by altering their apparent motion, or the length of time they are present in the predator's reaction field. More importantly, the technique of dividing the reaction field into discrete visual planes, used by both Confer et al. (1978) and Luecke and O'Brien (1981), while convenient from a descriptive point of view, leads to an estimate of the scanning area that is based only on attacks made adjacent to the transverse plane. Not only does this ignore the role that the remainder of the reaction field plays in prey detection, but it is likely to result in a biased estimate of the scanning area. This bias stems from the fact that attacks directed in or close to the transverse plane represent only a small portion of all attacks, most of which are directed ahead of this plane. The probability that a prey item will be detected as a function of its distance from the fish's search trajectory, necessary information for an unbiased estimate of the volume searched, is not explicitly contained in such mean RDs and can only be obtained by examining the role of the entire reaction field in prey detection.

In the work described here, an attempt is made to identify this bias and provide a description of the scanning area based on the entire reaction field. To facilitate comparison of the results of this study with those of Confer et al. (1978) and Luecke and O'Brien (1981), a reaction field map is also constructed.

Methods

Experimental Procedure

The experimental apparatus consisted of a plywood tank 70 × 70 × 90 cm (length × width × depth). The inside of the tank was coated with white nontoxic epoxy paint, and the bottom and sides were marked off in a 5 × 5 cm grid of black lines. Lighting was provided by four 75-W flood lights, which gave a surface illumination of approximately 600 lx. Two video cameras suspended 130 cm above the water surface provided paired video records of feeding bouts for stereo analysis.

Prey items (*Daphnia pulex*, mean width 1.26 ± 0.14 (SD) mm) were introduced to the tank via two horizontal and diagonally opposed pipes situated at a depth of 35 cm, through which water taken from the tank outlet was circulated back to the tank by a centrifugal pump. This technique of prey introduction produced a relatively even distribution of *Daphnia* from top to bottom, as no significant difference in *Daphnia* density was found in a comparison of eight "top" (400-mL cylindrical sampler centered at 17.5 cm depth) and eight "bottom" (centered at 52.5 cm) samples taken within 3 min of the introduction of 1000 *Daphnia* to the tank.

The five juvenile coho salmon (*Oncorhynchus kisutch*) used in the experiments (Table 1) were seined from the Salmon River, Langley, B.C., and maintained in the laboratory in individual aquaria. A single fish was placed in the tank 2 d prior to the beginning of recorded feeding bouts and on the day following introduction was fed as during recorded bouts to familiarize it with the feeding regime. To initiate a feeding bout, 10 *Daphnia* were introduced to the tank via the pipes and the pump was turned off. During the subsequent feeding period, an observer above the tank activated a light whenever a capture was made. The light was not visible to the fish but appeared on both video records and thus served to synchronize the two recordings and to allow discrimination (and deletion) of attacks made on nonfood items. To minimize the effect on RD of the initial movement imparted to the prey by the pump, captures made within 20 s of pump stoppage were ignored. Also ignored were captures made within 5 s of a previous capture, the intent being to eliminate short RDs to prey fortuitously encountered adjacent to a prior capture. A total of 12 feeding bouts were filmed between 9 a.m. and 12 noon on each day experiments were run.

TABLE 1. Body length and number of attack sequences analyzed for each of the five fish used in the experiment.

Fish	Fork length (mm)	Attacks analyzed
1	55	76
2	50	70
3	54	71
4	58.5	84
5	56	4
		$\Sigma = 305$

During an attack sequence, the fish initially oriented its body axis in the direction of the intended prey item. This was followed by a rapid acceleration from cruising velocity (which averaged 8.1 ± 0.56 (SE) cm · s^{-1}) in a straight line towards the prey. Prey capture was typically followed by deceleration and body rotation away from the attack trajectory. Attack parameters were defined as follows (see Fig. 1): reaction distance (RD) is the snout-to-snout distance between fish positions just prior to orientation and at capture; attack bearing (β) is the angle in the horizontal plane between the body axis prior to orientation and the attack trajectory; attack elevation (ϵ) is the angle between the attack trajectory and the horizontal plane (the search trajectory is assumed to be horizontal). Thus defined, RD is not necessarily equivalent to sighting distance. It is possible that prey are sighted at one distance but not attacked until this distance has been reduced to some threshold that may be subject to behavioural modification (Dunbrack and Dill 1983).

3-D Analysis

For each attack sequence, the paired video records were used to obtain the coordinates (x, y, z) of three points: the fish's head and tail just prior to orientation to the prey and the fish's head at the point of capture. This was done for a total of 305 attack sequences distributed among five fish (Table 1). The paired head and tail positions provide an estimate of the fish's search trajectory necessary to calculate attack bearing. The details of the technique used for 3-D analysis and estimation of attack parameters are described in Dunbrack (1984), along with simulations to determine the accuracy of the method.

Reaction Field Map

The coho reaction field was mapped in three planes: transverse (through the eyes), horizontal (along the mid-body line), and sagittal. Each of these was in turn taken as forming the equatorial plane of a sphere (attack initiation at the center) and an attack was included in a particular plane if the capture occurred within ±30° latitude of it. Each of these planar belts was further divided into eight equal sectors, which thus measured 60 × 45° (Fig. 2).

Scanning Area

All prey items captured above and ahead of the fish were plotted as projections on the transverse plane with their distance from the origin being equal to their perpendicular distance from the search trajectory. This distribution of points was divided into a series of concentric bands characterized by attack probabilities that, assuming that prey were evenly distributed throughout the water column, can be estimated from the relative density of attacks within each band. A weighted cross-sectional

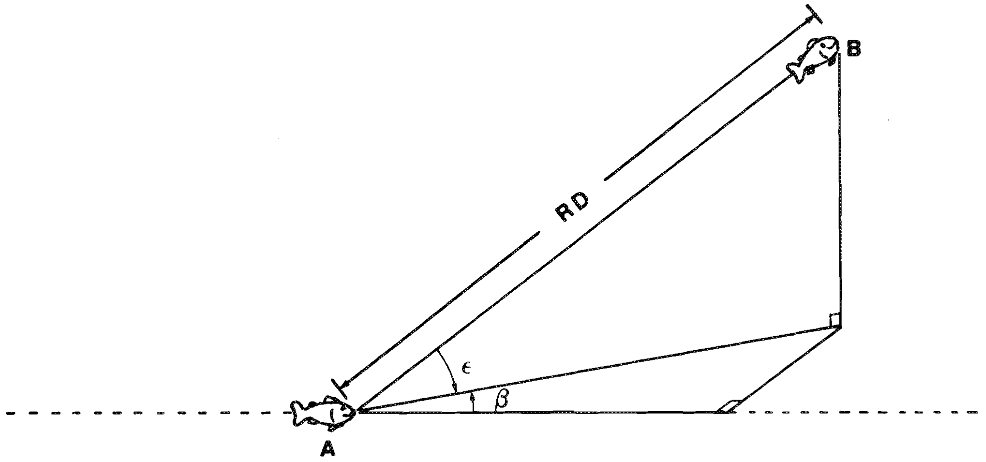

FIG. 1. Geometry of the attack parameters. A, position of the fish just prior to attack initiation; B, position at point of prey capture; β, attack bearing measured in the horizontal plane; ε, attack elevation between the horizontal plane and the attack trajectory; RD, reaction distance.

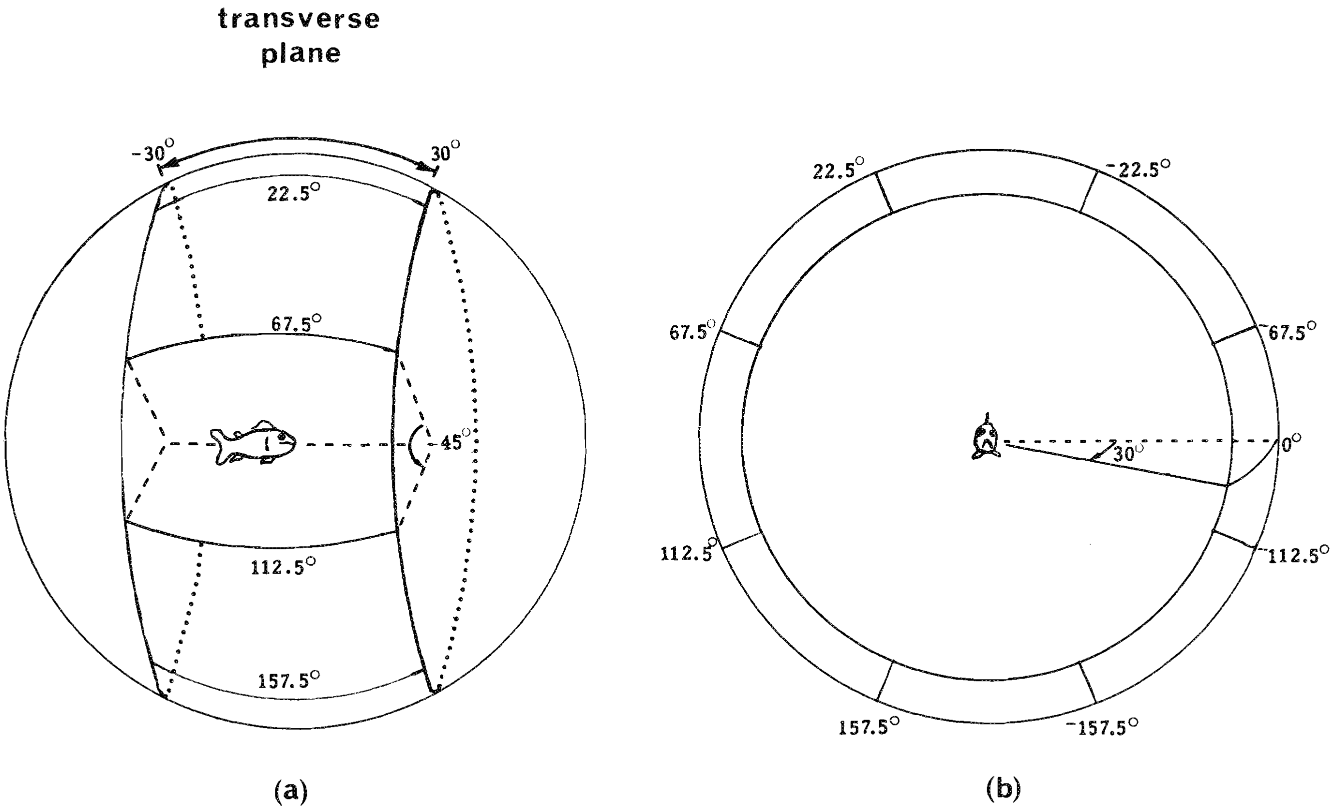

FIG. 2. Lateral (a) and frontal (b) views of the visual sectors comprising the transverse plane. In this case the transverse plane is the equatorial plane and the sectors lie between ±30° latitude. Lines of longitude are 45° apart so that each sector is 60 × 45°.

area of the search volume can then be obtained by multiplying the area of each attack probability category by its corresponding attack probability and summing over all categories. This is the scanning area.

Results

Reaction Field Map

Values of attack bearing (longitude) and elevation (latitude) for each of the 305 sequences analyzed are shown in Fig. 3. This figure contains no information on RD. The data are plotted in polar coordinates in Fig. 4 to show the relationship between RD and angular orientation for each of the three attack planes. There is a tendency for RD to increase with increasing elevation. This trend is significant for both the sagittal (ANOVA $F_{4'69} = 6.1$, $p < 0.001$) and transverse ($F_{4'163} = 6.3$, $p < 0.001$) planes. In the sagittal plane (Fig. 4a) the maximum mean RD is directly above the fish and the minimum is directly below. In the transverse plane (Fig. 4c) the minimum mean RD is still directly below the fish, but the maximum mean RD is now in the 22.5–67.5° sector. Although RD appears to increase laterally in

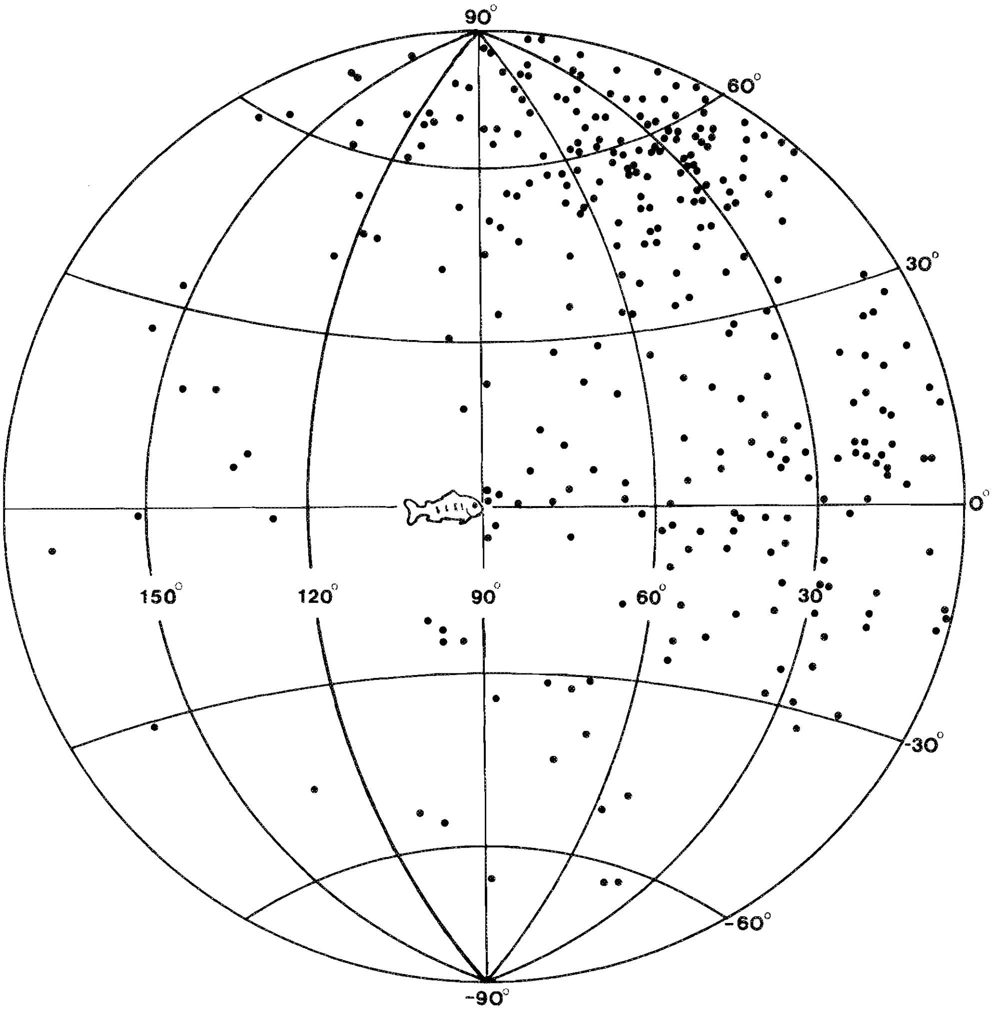

FIG. 3. Bearing (β, longitude) and elevation (ϵ, latitude) of the 305 attacks analyzed. The fish's left hemisphere has been reflected upon the right hemisphere.

the horizontal plane (Fig. 4b), this trend is not significant ($F_{2'110} = 0.4$).

The pattern of attacks observed in a study such as this will be affected to a certain extent by the size of the apparatus relative to the potential reaction field of the fish. If the apparatus is too small, much of the reaction field will be truncated and observed RDs will be shorter than in a larger tank. To investigate the effect that truncation of the reaction field may have had on the results, the data were reexamined after all attacks made towards and within 30 cm of a wall, the surface, or the bottom were eliminated. It was felt this procedure would rectify most truncation problems, as less than 5% of all RDs were greater than 30 cm. The only substantial changes occurred in the lateral sectors of the horizontal and transverse planes, where mean RDs increased 23 and 17.2%, respectively (Fig. 5). Using this correction, RD in the horizontal plane was now significantly greater laterally than frontally ($F_{2'78} = 3.9$, $p < 0.05$).

Scanning Area

All attacks above the horizontal plane and not expected to have been affected by truncation (see above) were plotted as projections on the transverse plane. Concentric lines were drawn around areas of approximately equal attack density (Fig. 6) and the attack probability for prey within each band calculated as $D_j/D_{\max}$, where $D_{\max}$ is the attack density in the band closest to the attack trajectory and D_j is the attack density in band j. The weighted estimate of that portion of the scanning area above the horizontal plane obtained using this technique (i.e. $\Sigma_j(\text{AREA}_j)(D_j/D_{\max}) = 932\ \text{cm}^2$) was 1.2 times that found using only mean RDs in the transverse plane ($776\ \text{cm}^2$). A good estimate of the scanning area below the horizontal plane could not be obtained using this procedure because of the low number of attacks recorded there.

Discussion

Specific visual adaptations should develop in response to a variety of selection pressures. For a visual predator a significant component of this selection will be related to foraging activities, and we would therefore expect directional prey detection ability to be correlated with mode of foraging. Coho salmon feed while holding a station in running water or actively searching in still water and, like most predators, encounter prey primarily in the forward directed hemisphere. In the field, because of their generally low position in the water column and the presence of much surface food, more of their attacks are directed above than below the horizontal plane (K. J. Puckett, Dep. of Biosciences, Simon Fraser University, pers. comm.). The relatively large

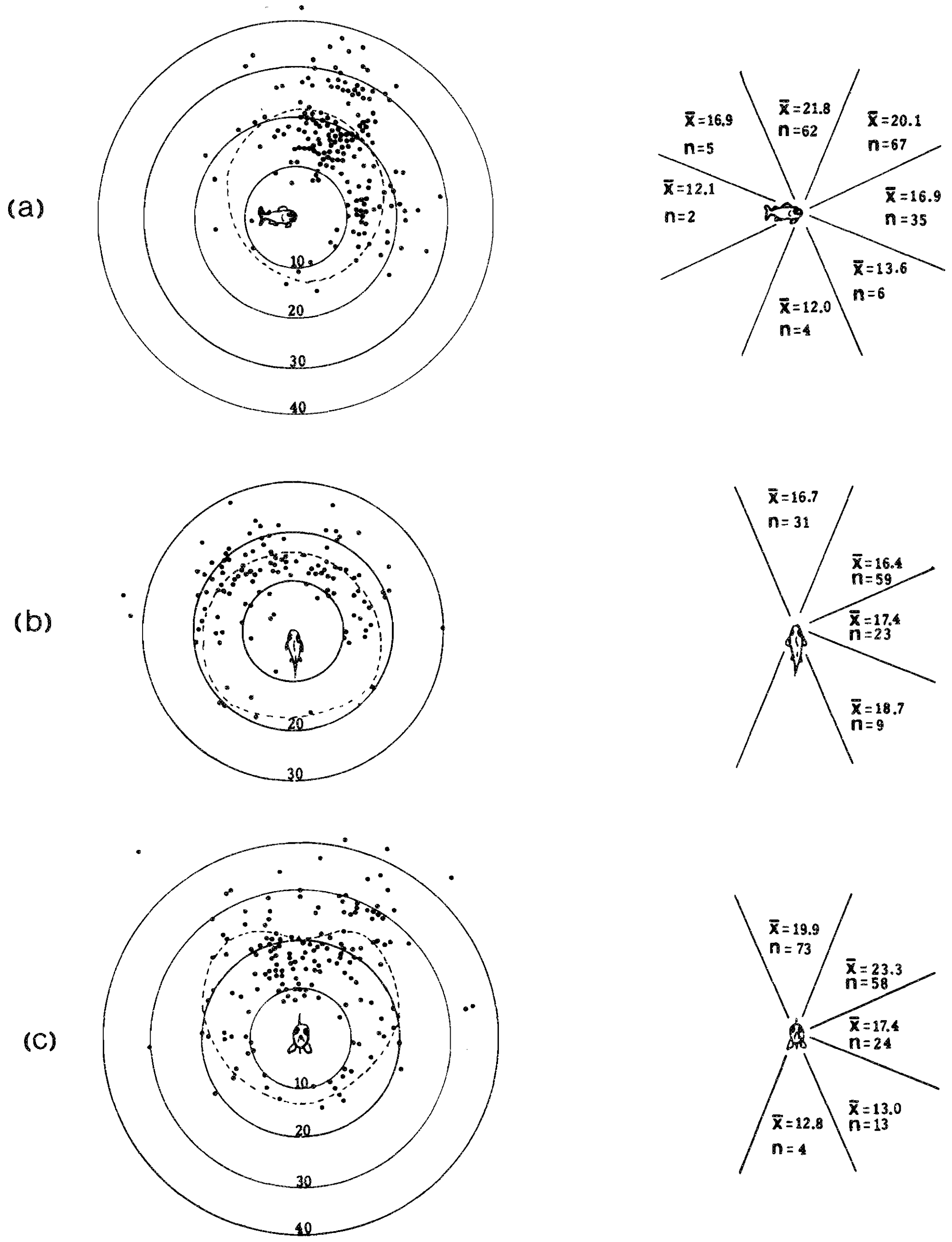

FIG. 4. Left: attacks plotted on polar coordinates for sagittal (a), horizontal (b), and transverse (c) visual "planes". Concentric circles represent distances from the fish's snout (cm). Broken lines are drawn through the mean RD value for each sector. Right: mean RD ($\bar{x}$) and number of attacks (n) observed for each sector of each visual "plane". Equivalent right- and left-hand (fish's) sectors are pooled.

RDs ahead and above observed in this study are thus generally consistent with coho foraging behaviour under natural conditions.

The detailed shape of the reaction field can reflect a number of proximal factors, not all of which are entirely related to vision and none of which can be easily partitioned as to effect. For example, within that portion of the visual field ahead and above, RD was greatest adjacent to the transverse plane (Fig. 4a). This could reflect corresponding patterns of visual acuity and sensitivity, but could also be related to the skewed distribution of prey encountered there (resulting from the fact that prey close to the search trajectory will normally be attacked before they reach the transverse plane), or to the increasing apparent rate of prey movement, which may enhance visibility, as prey are approached by the cruising fish.

The potential influence of the mode of foraging on the observed reaction field means that the results of various studies must be compared with caution. Confer et al. (1978) measured the attack field of lake trout searching for food while swimming in a glass aquarium. Their methodology was quite similar to ours and the two studies should therefore be directly comparable. If the probable effect of attack field truncation in their study is taken into account, the results are quite similar. This may reflect the fishes' phylogeny, similarities in the way

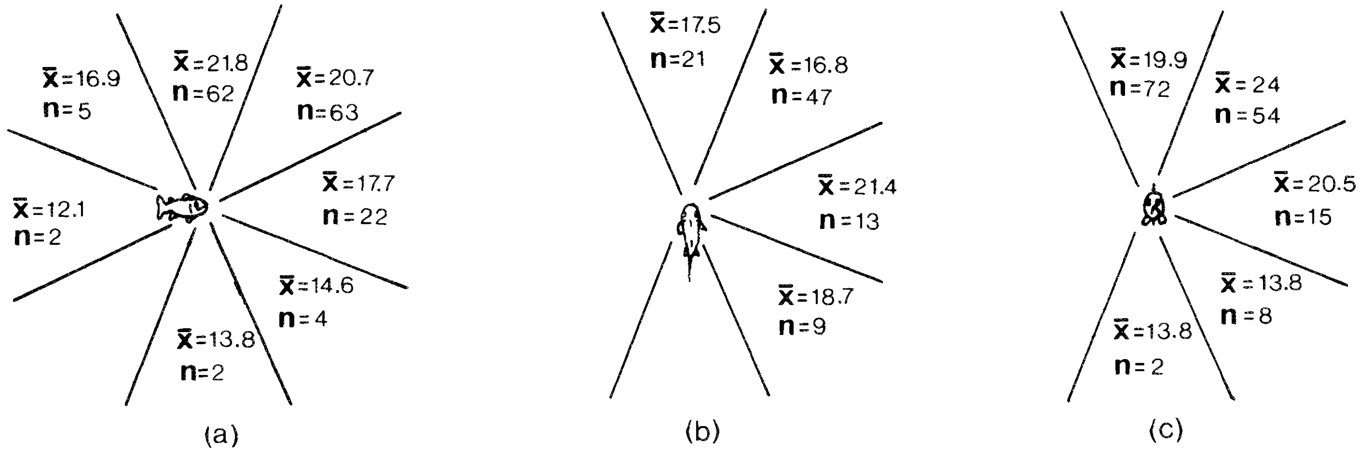

FIG. 5. Mean RD ($\bar{x}$) and number of attacks (n) observed for each visual "plane", after the data were corrected for potential truncation of the reaction field (see text and Fig. 4 caption for details).

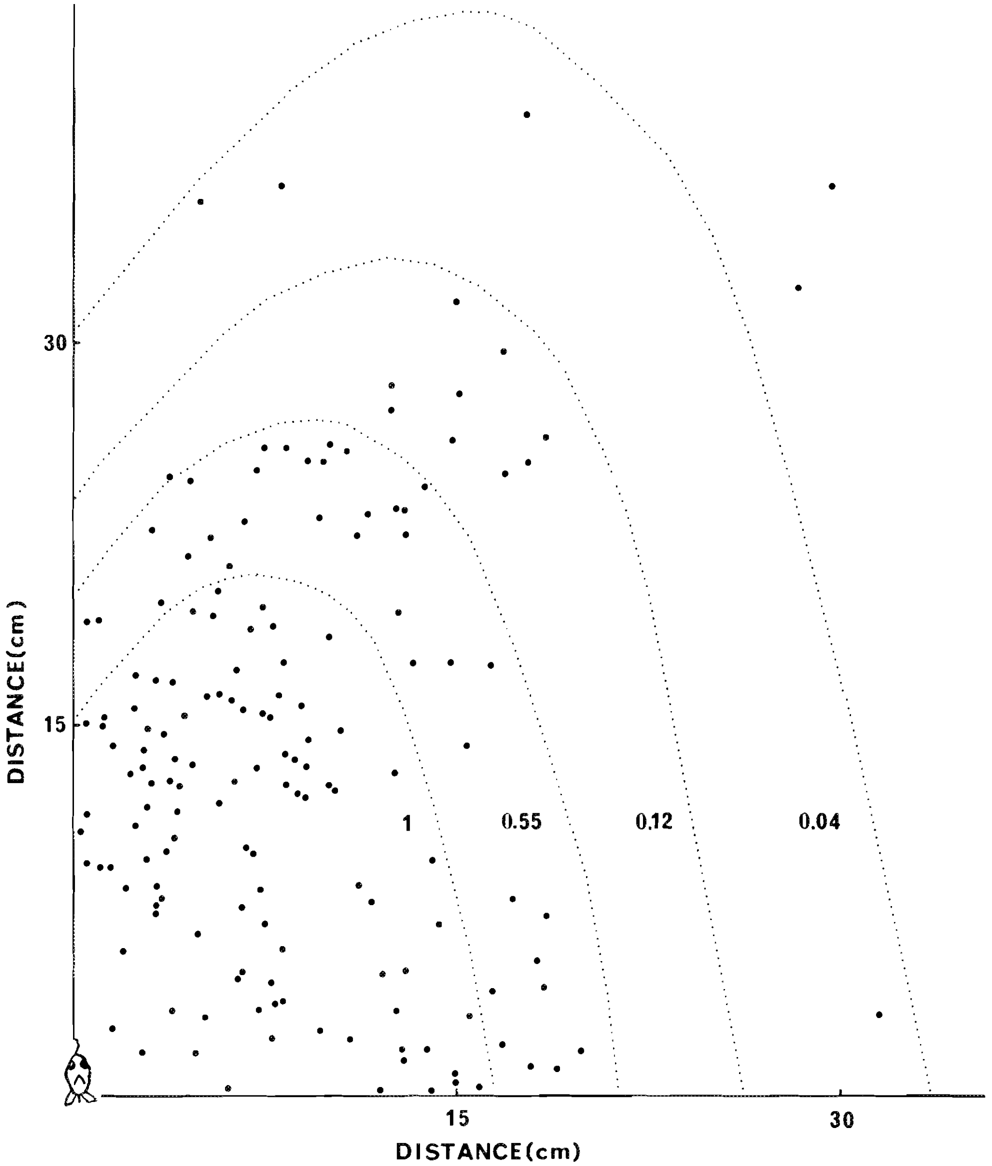

FIG. 6. Plot of all attacks not expected to have been influenced by truncation (see text), projected on the transverse plane. X- and Y-axes are perpendicular distances from the fish's search trajectory. The shape of the concentric curves was obtained by visual inspection and conforms generally to the RD data (Fig. 5c). Numbers represent the relative probability of attacking prey falling within the corresponding concentric band ($D_j/D_{\max}$; see text).

they encounter prey, or both. Although the probabilistic interpretation of prey encounter we use here owes much to Luecke and O'Brien (1981), the procedure they employed in evaluating the prey location ability of bluegill is quite different from ours. They presented prey to stationary fish; there were thus no apparent movement cues available to the fish to aid prey detection. The relatively low prey location ability they observed in the transverse plane may be related to this technique, which seems to stress acuity (i.e. the ability to resolve an object) and may underestimate the importance of peripheral visual sensitivity to real or apparent prey movement in more dynamic prey encounter situations.

The weighted cross-sectional area of the search volume (scanning area) calculated using our technique is 20% larger than that obtained by the method of Confer et al. (1978), a difference that at low prey densities would be directly translated into a similar increase in predicted feeding rate. A change of this magnitude could be significant in modelling fish production or the impact of predation in low-productivity habitats.

An obvious drawback of our technique is its time consuming nature. Examination of the data, however, suggests a simpler estimate. It has been shown that the portion of the scanning area above the horizontal plane (Fig. 6) is approximately 1.2 times larger than the equivalent area obtained by drawing a curve through the mean RDs of Fig. 5 (transverse plane). If this relationship also holds for that portion of the scanning area below the horizontal plane, a total scanning area can be calculated. If it is then assumed that the volume searched is cylindrical, the search radius (R) giving an area of identical size to this total scanning area is approximately 20% larger than the RD in the forward sector of the horizontal plane in our large tank (frontal RD), i.e. $R \approx 1.2\text{RD}$. Confer et al. (1978) found that the frontal RD of lake trout in a narrow aquarium (RDn) was approximately 30% larger than that observed when their fish were cruising in a larger tank ($\text{RDn} \approx 1.3\text{RD}$). Some of this difference, which they related to the increased difficulty of locating prey in any particular direction as search volume expands, is probably attributable to reaction field truncation. Correction for this effect in our study increased frontal RD by 5%. A slightly larger correction (5–10%) should apply to the "large" aquarium data of Confer et al. (1978) because of the considerably smaller size of their aquarium. Therefore, RDn may actually be closer to 1.2RD, and thus may approximate R. This suggests that a measurement of frontal RD, which is readily obtained, can be used as the radius of a hypothetical circular area approximating the scanning area. Although this approximation is empirically derived for coho salmon, it may prove useful for other cruising or stream dwelling salmonids with reaction fields of similar shape. It would be of less utility in very shallow water (such as in many streams) where the actual shape of the scanning area becomes important. The use of the scanning area model in predicting diet composition under such conditions is being explored by the first author.

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