

## A model of size dependent surface feeding in a stream dwelling salmonid

Robert L. Dunbrack & Lawrence M. Dill

Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

### Keywords:

Capture probability, Drift feeding, Foraging tactics, Gill raker spacing, Hunger, Feeding morphology, Reaction distance, Vision

### Synopsis

A model is developed which predicts the size composition of drifting surface food in the diet of a stream dwelling salmonid. Parameters included in the model are fish reaction distance to food, probability of successful capture (attack and ingestion), and surface drift size composition. Reaction distance and probability of successful capture were found to be functions of both fish length and food width. A test of the model showed no significant difference between its predictions and the actual diet composition of juvenile coho salmon, *Oncorhynchus kisutch*, collected in the field. The results are discussed in light of morphological considerations.

### Introduction

Food size dependent feeding by predatory fishes, defined as a non-correspondence between the size distribution of food in the diet and that in the 'environment', has been widely documented in standing water communities (Brooks & Dodson 1965, Galbraith 1967, Magnuson & Heitz 1971, Ware 1972, Wong & Ward 1972, Werner & Hall 1974, Moore & Moore 1976, Nilsson 1978, Gerking & Plantz 1980). Work on the causal mechanisms underlying this phenomenon has identified several factors possibly contributing to size dependency, viz. predator mouth morphology (Moore & Moore 1976, Wańkowski 1979, 1981), predator gill raker spacing (Brooks & Dodson 1965, Galbraith 1967, Magnuson & Heitz 1971), predator choice (O'Brien et al. 1976, Gibson 1980) and food size dependent reaction distance (e.g. Brooks & Dobson 1965,

Ware 1972, 1973, Werner & Hall 1974, Confer & Blades 1975, Moore & Moore 1976, Wańkowski 1979, 1981). Predictive feeding models incorporating various of these factors have shown significant agreement, under certain conditions, between predicted and actual size distribution of the diet (Ware 1973, Werner & Hall 1974, O'Brien et al. 1976, Eggers 1977, Gibson 1980).

To date these models have dealt exclusively with feeding in still water. Because size dependence is also a demonstrable characteristic of fish feeding in running waters (Elliott 1967, Metz 1974, Griffith 1974, Bisson 1978, Allan 1978, 1981, Ringler 1979), in this paper we adapt theory and techniques used previously for still water systems to the development of a predictive feeding model for fish in running water. The model is applied to the stream dwelling juveniles of the coho salmon, *Oncorhynchus kisutch*, feeding on prey floating on the water surface.

Received 19.11.1981 Accepted 19.7.1982

## Theory and methodology

### Feeding model

For a moving visual predator of size  $j$  which detects its prey on a two-dimensional surface, the relative rate at which it encounters food size  $i$ , while searching, will be a function of (1) its reaction distance for prey size  $i$  ( $RD_{ji}$ ), and (2) the density of prey size  $i$  ( $N_i$ ) which is potentially visible. Relative encounter frequency for food size  $i$  by predator  $j$  will then be:

$$(RD_{ji}) (N_i). \quad (1)$$

Addition of a velocity component would allow calculation of absolute rate of encounter. Such an expression was adopted by Laing (1938) to describe the rate of host finding by the parasitoid *Trichogramma evanescens*.

For a predator  $j$  searching at a distance  $H_j$  from a two-dimensional surface, expression 1 would be modified to:

$$(RD_{ji}^2 - H_j^2)^{\frac{1}{2}} (N_i) \quad (2)$$

(Ware 1973). Although Ware's model was developed for fish searching the benthos, it is readily adapted to fish searching the surface of a water column by inverting the search path (Fig. 1). In this case  $SW_{ji}$  (scanning width) is equal to  $(RD_{ji}^2 - H_j^2)^{\frac{1}{2}}$ , and expression 2 becomes:

$$(SW_{ji}) (N_i). \quad (3)$$

This expression describes relative encounter frequency equally well for a moving fish searching a stationary surface layer or a stationary fish searching a moving surface layer and would therefore be applicable to a stream dwelling fish feeding from a station.

To use expression 3 to describe the proportion of food size  $i$  in the diet of predator  $j$  it is necessary to multiply it by the conditional probability of successful capture of food size  $i$  by predator  $j$  given encounter ( $PC_{ji}$ ), and then divide the resultant expression by its summation for all prey size classes, thus:

$$F_{ji} = (SW_{ji})(N_i)(PC_{ji}) / \sum_i (SW_{ji})(N_i)(PC_{ji}) \quad (4)$$

where  $F_{ji}$  is the proportion of food size  $i$  in the diet of predator  $j$ . This is comparable to equation 1 of Confer & Blades (1975) for a fish searching in three dimensions.

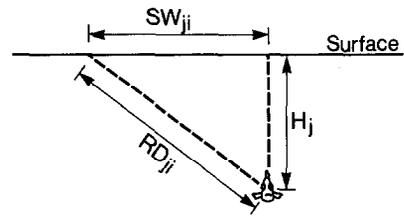


Fig. 1. Model of scanning width for surface feeding fish. Water is flowing into the page;  $H_j$  is the distance of the fish from the surface;  $RD_{ji}$  is the reaction distance of fish  $j$  to food  $i$ ;  $SW_{ji}$  is the scanning width of fish  $j$  for food  $i$ . Left side (fish's) would be a mirror image of the right.

### Reaction distance ( $RD_{ji}$ )

$RD_{ji}$ , the reaction distance of fish  $j$  to food size  $i$ , refers to the lateral reaction distance measured perpendicular to the long axis of the fish's body at some angle above the dorsal-ventral plane. If the visual volume of fish  $j$  for prey size  $i$  is assumed to be roughly spherical, then a reaction distance measured frontally can be substituted for the lateral reaction distance as has been done by other workers (Ware 1973, Werner & Hall 1974, Confer & Blades 1975).

Although this assumption of sphericity may not be strictly true (Confer et al. 1978, Luecke & O'Brien 1981) and may result in an overestimate of lateral reaction distance (Confer et al. 1978), this should have only a minor effect on the relative reaction distances (i.e. for different food sizes) because they should be reduced in a similar fashion. If only proportional diet composition is of interest (rather than rate of consumption), it would then be appropriate to substitute frontal reaction distance for lateral reaction distance. When the predator is searching at a distance  $H_j$  below the surface however, a source of error may come into play. A proportionally equal reduction in  $RD_{ji}$  will not result in a similar proportional reduction in  $SW_{ji}$ , as  $SW_{ji}$  for small prey will be reduced relatively more than  $SW_{ji}$  for large prey. This effect only becomes important when  $H_j$  is large relative to  $RD_{ji}$ . As  $H_j$  for the fish used in the test of the model (see below) was generally less than  $RD_{ji}$  for the smallest food items consumed, it is not felt that a significant error will be introduced by using frontal

reaction distance to estimate lateral reaction distance.

Frontal reaction distances were measured in a double laboratory stream channel lined with green plexiglass (Fig. 2). Juvenile coho salmon were seined from the Salmon River in Langley, B.C., anaesthetized (MS 222) and measured (fork length). They were then transported to the labo-

ratory and placed in one of the two channels. Only a single fish occupied a channel at any one time so that a total of two fish could be tested simultaneously. Fish generally held a station adjacent to an artificial rock placed at the downstream end of each channel. After a period of 24–48 hours, feeding trials were begun. Plecoptera nymphs were used as food. They were chosen because of their relatively constant body shape and color, both among species and over a wide size range. For a description of species and sizes used see Table 1. A trial consisted of introducing a nymph of known width through the delivery apparatus. Once in the channel the food (buoyed by an abdominal injection of air) floated downstream on the surface and at some point the fish initiated an attack. Experimental trials were preceded by a number of acclimation trials. A fish was considered acclimated to the experimental situation when it readily attacked a presented food item while occupying a position in the lower 30 cm of the channel. Approximately 10% of fish could not be acclimated and were not used. During experimental trials food items representing 10 size classes were introduced singly in random order. Each fish was presented with two food items from each size class for a total of 20 individual presentations per fish. Experimental trials were recorded on video tape and the record analysed for reaction distance (the distance between the fish and the food item when the fish initiated an attack) and attack distance (distance swum).

Effects of hunger were controlled by varying the intertrial interval to approximate the stomach emptying time (Dunbrack in preparation) for the food size presented at the beginning of the interval. The effect of hunger on both reaction distance and attack distance was also investigated directly by

Table 1. Species and size range (width) of Plecoptera nymphs used in reaction distance experiments.

Species	Width range used (mm)
<i>Acroneuria pacifica</i>	1.5–6.0
<i>Acroneuria californica</i>	1.25–5.6
<i>Isoperla</i> sp.	1.8–3.65
<i>Isoperla</i> sp.	0.5–1.4
Plecoptera sp.	0.5–0.75

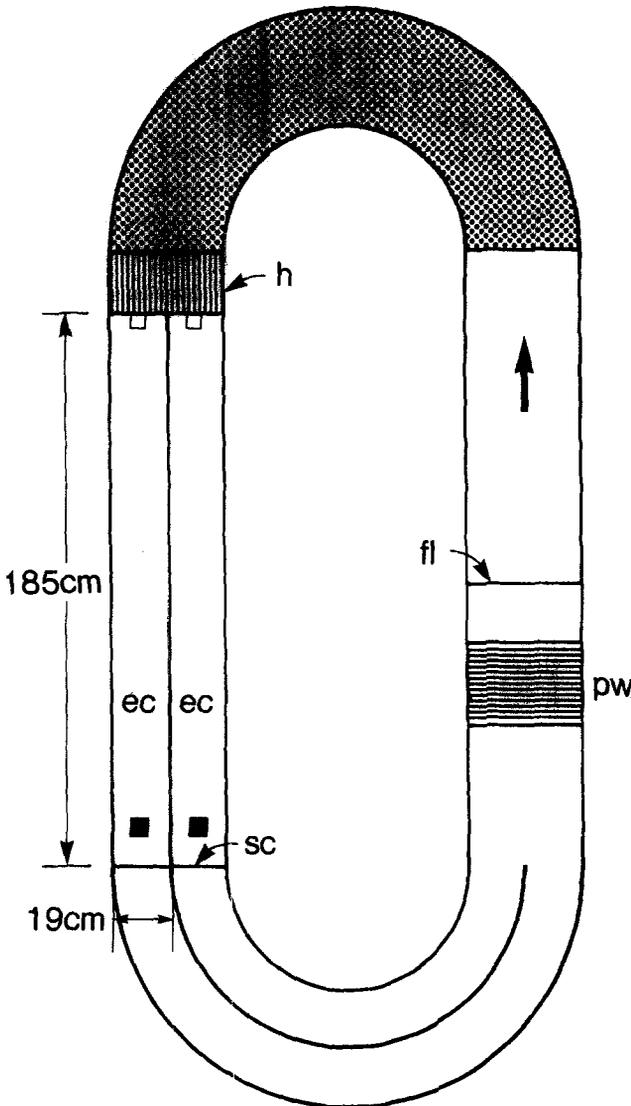


Fig. 2. Diagram of stream channel apparatus: pw-paddlewheel; sc-screen (5 × 3 mm mesh); ec-experimental channel; fl-filter (540uM); h-flow straightening honeycomb (20 cm elements, 3.5 mm diameter). Flow deflectors placed between horizontal baffles were installed in the shaded area. Arrow indicated the direction of water flow.

feeding starved (48 h) fish at short intervals until they no longer ingested food items.

A total of 12 fish were used in the initial reaction distance experiment: 4 of 40 mm ( $40.5 \pm 0.6$ ), 4 of 60 mm ( $59.1 \pm 0.7$ ) and 4 of 80 mm ( $80.6 \pm 0.7$ ). The water in the channel was maintained at 12°C and a depth of 18 cm. Mean water velocity was 20 cm sec<sup>-1</sup>. Light was supplied by four 75 watt floodlights suspended 50 cm above the water surface. These provided a mean surface illumination of 2160 lux. Turbidity of the water was 0 JTU (Hach Kit DR-EC/1) and pH was 7.

#### *Probability of successful capture (PC<sub>ji</sub>)*

PC<sub>ji</sub>, the probability that fish *j* will ingest food item *i* given that it comes within the fish's scanning width, can be subdivided into (i) probability of attack and (ii) probability of ingestion given attack.

#### *Probability of attack*

For a visual predator to attack a food item it must first see it. Under certain circumstances, such as a fish taking food off the benthos, this 'recognition success' (Ware 1973) can be a complex function involving both prey species and size. However, in a surface feeding situation much of this complexity disappears. Most food items (including terrestrial insects trapped on the surface, floating pupae and emerging adults) are of high contrast seen from below, and should be more or less equally recognizable. Brooks (1968) made a similar argument for open water zooplankton, referring to their 'nakedness to predation', as did Fahy (1980) in suggesting that all planktonic organisms are likely to be equally available to predators. Prey movement, which appears to affect both reaction distance and recognition success in still water systems (Ware 1973), is also less important in running water, as all available food is moving (albeit at different angular velocities) with respect to a stationary predator. It was therefore assumed that probability of attack determined for one type of prey would approximate that for other taxa in the surface drift.

Probability of attack as a function of food size and fish size was calculated by recording the outcome of each food presentation in the reaction

distance experiments described above. This provided a probability curve for food widths greater than 0.5 mm. Below this size it was difficult to follow the food on the video record and therefore difficult to tell if a fish had not reacted or if the food item had been caught in the delivery apparatus. An alternative technique was therefore used to estimate probability of attack for food items less than 0.5 mm in width. The technique involves comparing two sets of values which are considered to overestimate and underestimate true (actual) attack probability respectively. The actual value is taken as lying between the two.

The underestimate (experiment 1) was obtained by presenting individual coho, maintained in 15 liter aquaria (30 × 20 × 25 cm) with 100 zooplankton of uniform size (for species and sizes used see Table 2) and recording attack rate (attacks sec<sup>-1</sup>). Water conditions were as for the reaction distance experiments, and surface illumination (single 20 watt 'cool white' fluorescent bulbs, 12 cm above the surface) was 1300 lux. Although this illumination is less than that for the reaction distance experiments (2160 lux), both are well above the level at which feeding performance falls off (Brett & Groot 1963, Vinyard & O'Brien 1975). Single presentations of each food size class were made to six 40 mm and six 80 mm coho, generating a pair of attack rate-food

Table 2. Species, sizes and densities of zooplankton used in attack rate experiments. Experiment 1 was done at a constant initial density while in experiment 2 density was varied inversely as the cube of zooplankton body width.

Species	Width class (mm: mean ± S.E.)	Initial density relative to largest size class	
		Exp. 1	Exp. 2
<i>Daphnia pulex</i>	1.26 ± 0.03	—	1
<i>Daphnia pulex</i>	0.91 ± 0.02	1	—
<i>Daphnia pulex</i>	0.66 ± 0.02	1	7
<i>Daphnia pulex</i>	0.50 ± 0.01	1	—
<i>Daphnia pulex</i>	0.42 ± 0.02	—	28
<i>Daphnia pulex</i>	0.39 ± 0.02	1	—
<i>D. rosea</i>	0.33 ± 0.01	1	—
<i>D. rosea</i>	0.28 ± 0.01	1	—
<i>Ceriodaphnia reticulata</i>	0.21 ± 0.01	—	215
<i>Ceriodaphnia reticulata</i>	0.18 ± 0.006	1	—
<i>Diaptomus</i> sp. (nauplii)	0.1	1	1990

size curves. Rates were calculated from the number of zooplankton consumed over a time period chosen such that the relationship between total number of zooplankton consumed and elapsed time was still in a linear phase (no effect of declining density). This period varied from 30 sec for large and intermediate food sizes to 5 min for small sizes.

If an attack probability of 0 results in an attack rate of 0 and an attack probability of 1 results in the maximum attack rate for an initial density of 100 zooplankton of a particular size, then there should be a similarity between the normalized (i.e. maximum = 1) attack rate curve and the attack probability curve. This curve will underestimate actual attack probability because it will additionally be affected by decreases in reaction distance with decreasing zooplankton size.

The overestimate (experiment 2) was obtained through a variation of a technique used by Werner & Hall (1974). Conditions were as above except that the initial density of zooplankton within the fish's reaction field was adjusted to be inversely proportional to the cube of zooplankton width (for numbers used see Table 2). This equalizes the number of zooplankton within the fish's reaction field (for each food size) and therefore compensates for the effect of decreasing reaction distance (with decreasing food size) if the following conditions hold:

1. reaction distance is an increasing linear function of food width passing through the origin;
2. the fish is stationary;
3. handling time for all food sizes is the same at the initial density for each size class;
4. the body of water surrounding the predator extends in all directions further than the reaction distance for the largest zooplankton used; and
5. the fish's reaction field is spherical.

If the attack rate values so obtained are divided by the maximum observed attack rate, a curve is generated that should once again be similar to the attack probability curve. However:

1. reaction distance is likely to be an asymptotic function of food size (Ware 1973);
2. fish move while feeding and reaction field volume therefore tends to be proportional to the square rather than the cube of reaction distance (Confer

& Blades 1975, Eggers 1977);

3. handling time is probably less for smaller foods since they are easier to ingest and closer to the fish on average;
  4. reaction field is limited by the tank walls, increasingly truncating reaction volume for larger foods; and
  5. shape changes should have no effect on relative volumes of geometrically similar reaction fields.
- In all cases (except 5) this results in more small than large zooplankton being present in the fish's reaction field. If attack probability were constant (for all food sizes), attack rate would increase with decreasing food size. If attack probability decreases with decreasing food size, attack rate may decrease, but not as rapidly as attack probability. Thus the relative attack rate should in general overestimate attack probability.

#### *Probability of ingestion*

Probability of ingestion as a function of food size and fish size was determined by monitoring the outcome of attacks in both reaction distance and attack rate experiments.

#### *Test of the model*

A test of the model was carried out during April and May 1981 in the Salmon River. Pairs of coho were seined 24 h before they were to be used and kept individually in plastic bags containing approximately 15 liters of river water. This was to ensure that their stomachs would contain only food captured during the feeding trial. On the day of the experiment a single coho was introduced to a test pen (120 × 120 cm) placed in the stream. The fish remained in the pen for approximately 4 hours. The other fish was held as a control. The pen was enclosed by white nylon netting (mesh size 5 × 3 mm) that allowed water to flow through but kept the fish within the pen. The benthos was covered with clear plastic to encourage the fish to feed on the surface. Any debris adhering to the upstream face of the pen was cleared after two hours. Upon removal, test fish were anaesthetized, measured and their stomach contents removed by flushing (Meehan & Miller 1978). Control fish were treated in the

same fashion. After revival fish were released into the stream.

Surface drift items (terrestrial insects, adult insects, pupae and emerging adults of aquatic insects) from stomach contents of test fish as well as from surface drift samples taken simultaneously with the test and adjacent to the pen (0.25 mm mesh plankton net extending above the surface), were measured to the nearest 0.05 mm (maximum width) with a dissecting microscope and micrometer eyepiece. The size distribution of the surface drift provided values for parameter  $N_i$  of equation 4.

Whenever possible the fish in the pen was observed and its feeding movements recorded. A total of 10 fish were tested ranging in size from 39.5 mm to 50 mm. Incident illumination varied from 2000 to 7000 lux, turbidity averaged 10 JTU, mean water temperature was  $9.4^\circ\text{C}$ , mean surface velocity was  $20\text{ cm sec}^{-1}$  and mean water depth was 40 cm.

Using data obtained from the experiments on reaction distance and probability of ingestion as well as the size frequency distribution of the surface drift, the predicted size composition of the diet was calculated using equation 4 and the resultant prediction compared to the actual size composition of food obtained from stomachs of test fish.

## Results

### Reaction distance

Both reaction distance (Fig. 3) and attack distance (Fig. 4) were found to be increasing functions of food width and fish size. Except for its nonlinearity, the food size-reaction distance relationship of Fig. 3, regardless of fish size, is broadly similar to that reported previously in the literature (Brawn 1969, Werner & Hall 1974, Confer & Blades 1975, Vinyard & O'Brien 1976) and comparable to Ware's (1973) results for rainbow trout reacting to moving high contrast prey. Ware also reported a curvilinear relationship between food size and reaction distance which he attributed to light attenuation within the water column.

An increase in reaction distance with increasing predator body size has been noted previously by

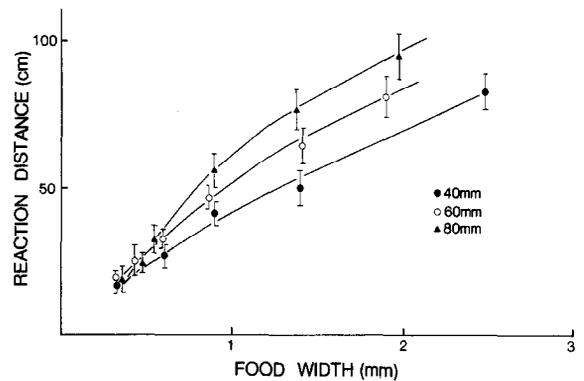


Fig. 3. Reaction distance (RD<sub>ji</sub>) as a function of food (stonefly) width and fish size. Lines fitted by eye. Vertical bars represent 1 S.E. In this and subsequent figures, 40, 60, and 80 mm refers to fish length.

Schmidt & O'Brien (unpublished, cited by O'Brien 1979) in arctic grayling, *Thymallus arcticus*, and by Breck & Gitter (1981) in bluegill sunfish, *Lepomis macrochirus*.

The relationships between relative satiation and relative reaction and attack distances are shown in Fig. 5. Relative satiation was defined as the ratio between cumulative weight of food consumed by a fish at the time of food presentation and total weight of food consumed when the fish no longer ingested food presented. Thus relative satiation varies from 0 at the beginning of a feeding series to 1 at the end. Relative reaction (and attack) distance was defined as the ratio between reaction (attack) distance measured for a particular presentation and

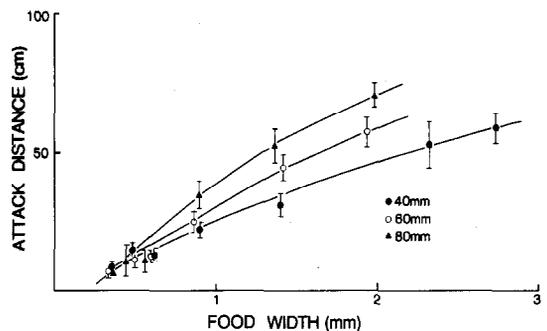


Fig. 4. Attack distance (distance swum by the fish from its station to the point of capture) as a function of food width and fish length. Lines fitted by eye. Vertical bars represent 1 S.E.

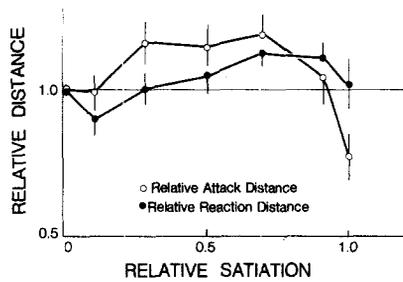


Fig. 5. Relative reaction distance (●-●) and relative attack distance (○-○) as functions of relative satiation. Data are pooled for 60 and 80 mm fish. Attack distance trend is significant ( $p < 0.05$ ), reaction distance trend is not. Vertical bars represent 1 S.E.

the expected reaction (attack) distance estimated (by least squares regression) from the data for that particular fish-food size combination obtained during the initial reaction and attack distance experiments. Thus relative reaction distance and relative attack distance could take on values greater than 1. Relative measures were used because of the difficulty of obtaining large numbers of stoneflies of uniform size. Because expected distances were calculated for each fish from previously obtained data, this treatment should reduce the confounding effect of interfish variation. Although both relative reaction and attack distances appear to increase initially and then decrease, only the decrease in attack distance with satiation is significant ( $r = -0.475$ ,  $p < 0.01$ ). The initial increase in both curves may be related to a priming of the reaction response due to the short interval ( $\bar{X} = 7.3$  min) between presentations.

#### Probability of successful capture

**Probability of attack.** – Food items larger than 0.75 mm width presented during the reaction distance experiments were attacked in all cases. Attack probability for these sizes is therefore taken as uniformly equal to 1.

The results of the first attack rate experiment (constant food density) are shown in Fig. 6. This depicts the relationship between normalized attack rate and food width for 40 mm and 80 mm coho. The corresponding attack probability curves are

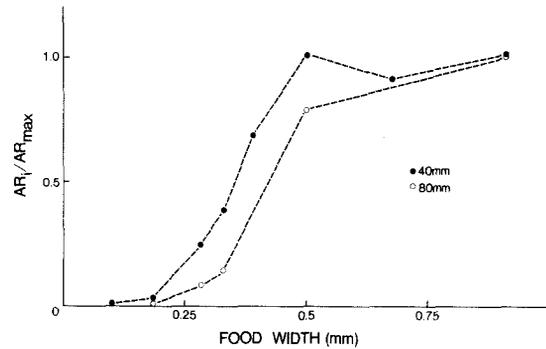


Fig. 6. Normalized attack rate as a function of food (zooplankton) width and fish length. Food density is constant.

indicated by the dashed lines in Fig. 8.

Fig. 7 shows the results of the second experiment (food density inversely related to food width). The ordinate expresses attack rate as a proportion of the maximum attack rate (as for the first experiment). The corresponding attack probability curves are shown in Fig. 8 as dotted lines. Since the curves derived from the constant density experiment should underestimate attack probabilities and those from the varying density experiment should overestimate them for any food width (see Theory and methodology), the actual probability curves would be expected to lie somewhere between the two and are estimated by the solid lines in Fig. 8.

Fig. 9 combines attack probability for large and small foods. The curve for 60 mm fish has been interpolated.

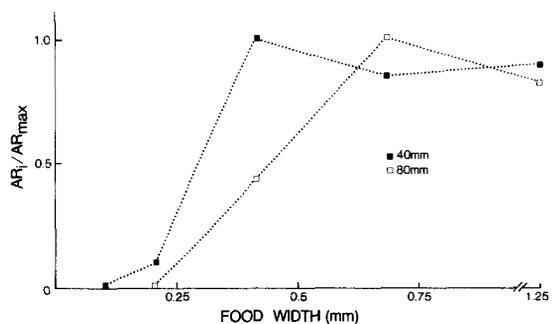


Fig. 7. Normalized attack rate as a function of food (zooplankton) width and fish length. Food density inversely proportional to cube of food width.

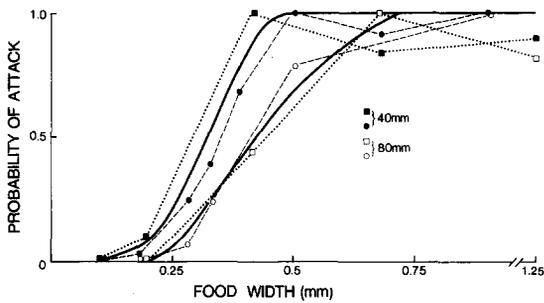


Fig. 8. Probability of attack as a function of food width and fish length. Dashed lines are identical to Figure 6; dotted lines are identical to Figure 7. Solid lines represent the best estimate of the probability of attack curves for 40 and 80 mm fish.

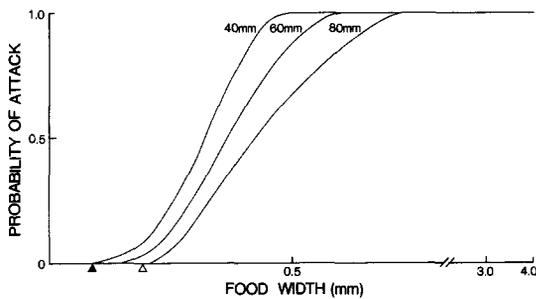


Fig. 9. Probability of attack for all food widths ingested. The line for 60 mm fish is interpolated. Arrows indicate the zooplankton widths corresponding to those lengths equal to the minimum gill raker spacings of 40 and 80 mm coho (▲—40 mm; △—80 mm).

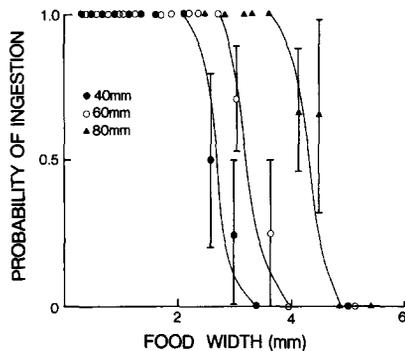


Fig. 10. Probability of ingestion as a function of food width and fish length. Data taken from reaction distance experiments. Points represent means of the ratio of prey ingested to prey attacked for 4 fish in each size class. Vertical bars represent 1 S.E.

### Probability of ingestion

The probability of ingestion given attack for the entire range of food widths ingested is shown in Fig. 10. This curve was obtained by observing attacks in the attack rate and reaction distance experiments. For prey <2 mm attack appeared to be invariably followed by ingestion. For larger prey (in the reaction distance experiments) probability of attack declined from 1 to 0 as food width increased, in a parallel fashion for 40 mm, 60 mm, and 80 mm fish.

Because of the nature of most surface foods (see above) they move only passively, and do not respond behaviourally to predator attacks. Thus it would seem justifiable to apply ingestion probabilities determined for floating stoneflies to other types of surface organisms. This is in contrast to planktonic taxa such as copepods which due to their rapid saltatory movements are sometimes able to avoid fish predators (Janssen 1976, Drenner et al. 1978, Gerking & Plantz 1980).

Probability of successful capture (PC<sub>ji</sub>) was obtained by multiplying attack probability (Fig. 9) by ingestion probability (Fig. 10) and is shown in Fig. 11, for the entire food size range (note change of scale on the abscissa).

### Test of the model

Predicted size composition of the diet (for three food width classes) was calculated for each test fish individually using equation (4) and appropriate values of SW<sub>ji</sub>, PC<sub>ji</sub> (both interpolated between the experimental data sets), N<sub>i</sub>, and H<sub>j</sub> (the latter from observation of the test fish). As drift composition did not vary significantly between trials all samples

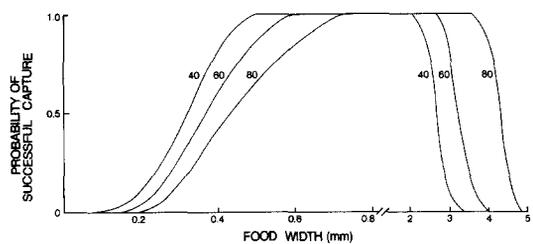


Fig. 11. Probability of successful capture (PC<sub>ji</sub>) for all food widths, and 3 fish sizes. Note change in scale along abscissa.

were pooled to provide a single estimate of Ni. The proportional predicted diet composition of each fish was then converted to a numerical value through multiplication by the total number of food items consumed by that fish. These values were summed for each food size class for all fish. This provided a single diet (essentially a weighted mean predicted diet) which could be compared to the actual diet composition pooled for all fish. Since no food was detected in any of the control fish, it was assumed that stomach contents of test fish represented only food consumed during the trials. The predicted and actual diets are shown in Fig. 12. A  $X^2$  goodness of fit test (2df) showed no significant difference between the actual and predicted values ( $X^2 = 0.308$ ,  $p > 0.1$ ). In contrast, there was a significant difference between actual diet composition and that predicted from a model not incorporating reaction distance or probability of successful capture (i.e. a model assuming fish capture food in the same proportion as it occurs in the drift) ( $X^2 = 96.2$ ,  $p < 0.001$ ).

Because the  $X^2$  test is designed to detect differences rather than describe similarities, given a sufficient sample size the prediction of any model can be shown to differ significantly from actual

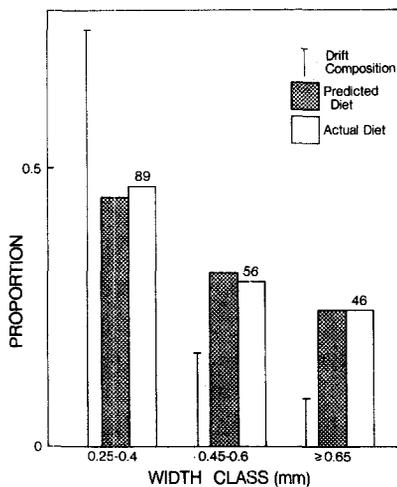


Fig. 12. Comparison of diet predicted by model and actual diet determined from stomach content analysis. Solid lines represent the proportion each size class forms of the total surface drift, open bars represent the actual diet composition, solid bars represent the predicted diet composition. Numbers of food items for each size class in actual diet are shown above the open bars.

Table 3. Sum of squared deviations, about predicted values, of 4 models (see text for details). For each model these values are compared to those for models C and D.

Model	Sum of squared deviations about predicted values	% reduction in sum of squares compared to:	
		model C	model D
A	22	99.5	97.8
B	950	78.6	6.3
C	4432	-	-338*
D	1012	77.2	-

\* increase

values. For this reason the data were subjected to additional analysis. The relative accuracy of different models can be determined by comparing the sum of the squared deviations between the predicted and actual number of food items of various size eaten. This was done for four models:

1. the model described in this paper (model A);
2. a model incorporating drift composition and probability of successful capture but not reaction distance (model B);
3. a model predicting that consumption will be proportional to the drift composition (model C); and
4. a model predicting numerically equal consumption of all food size classes (i.e. using the sample mean as the predictor) (model D).

The results are shown in Table 3. Model A was the lowest variance model giving a 97.8% reduction compared to model D and a 99.5% reduction compared to model C.

## Discussion

The reaction of a predator to food is by definition a behavioral phenomenon, but it is clear that such behavior must be physiologically or morphologically constrained. This can be illustrated through the relationship between reaction distance and fish size (Fig. 3).

There is evidence, based on optical theory, to suggest that a fish's visual acuity should increase with increasing eye size (reviewed by Northmore et al. 1978). While this may account for the trend of

increasing reaction distance with fish size, it is notable that measures of fish visual performance generally fall well within the limits set by acuity (Northmore et al. 1978). Thus acuity determines a maximum reaction distance that is then subject to behavioral modification. Although it is argued below that for any given food size reaction distance should be relatively invariant, the increase in reaction distance with fish size can be solely attributed to changes in visual acuity only if there are no additional body size correlates affecting reaction distance. The relationship between attack distance, food size and fish size (Fig. 4) is no doubt primarily due to the similar pattern of reaction distance although higher swimming speeds in larger fish could have a slight additional effect at larger food sizes.

The suggestion that attack distance decreases with increased satiation to a greater extent than does reaction distance (Fig. 5) seems reasonable in light of ecological considerations. While both reaction and attack are necessary components of predatory behavior, only attack is restricted to a predatory role. Reaction is a consequence of a fish's visual monitoring of its environment (e.g. for predators as well as food) which should be an almost continuous process, independent of hunger. Decreased reactivity with increased satiation would thus seem maladaptive. This does not appear to be the case for invertebrates such as the mantid *Hierodula crassa* whose 'awareness distance' decreases with satiation, although it decreases less rapidly than does attack distance (Holling 1966).

The attack rate experiments indicate that attack probability decreases with decreasing food size but suggest no mechanism. Ultimately minimum consumable prey size will be determined by minimum gill raker spacing (Galbraith 1967). When some prey dimension (usually length) exceeds this minimum gill raker spacing, prey will begin to be retained with increasing probability. Comparison of the zooplankton width corresponding to a length equal to the minimum gill raker spacing shows good agreement (for both 40 and 80 mm coho) with the end points (0) of the attack probability curves (Fig. 9).

While gill raker spacing may ultimately set lower

limits on minimum prey size, it does not seem likely that this would be a proximate mechanism in any except filter feeding fish (Brooks 1968). Fish actively selecting individual prey items would be expected to adopt the more energetically favourable tactic of ignoring prey which they have a low probability of ingesting. This has been suggested by Galbraith (1967) who found that minimum *Daphnia* length in trout stomachs was greater than the minimum gill raker spacing. If this is the case, minimum prey size must be proximally determined by another mechanism. One possibility lies in the fish's visual system. At rest, the teleost eye is focused for near objects and is characterized by a minimum sighting distance (Walls 1963, pp. 249–263). Since objects closer than this cannot be clearly resolved, this minimum sighting distance should effectively define a minimum prey size whose reaction distance equals the minimum sighting distance. Reaction distance for foods smaller than this should quickly fall to zero. There is some support for this pattern from the results of Ware (1973) and Wańkowski (1979) both of whom have reported that, for small foods, reaction distance decreases more rapidly than would be expected on the basis of food size alone. Additionally Walls (1963, p. 254) has suggested that small eyes have an advantage over large eyes with respect to near vision, smaller eyes having a shorter minimum near distance per se which would be augmented by the greater depth of field inherent in smaller lenses. This would result in smaller minimum prey size visible for smaller fish and could explain the fish size dependent attack rate for smaller zooplankton sizes reported in this paper as well as the observation of Moore & Moore (1976) that small flounder, *Platichthys flesus*, could detect smaller prey than could larger flounder. Depending upon the depth of field of the coho eye at rest, it is also possible that through accommodation fish could facultatively alter the lower size limit of prey detected, by increasing the minimum sighting distance. The advantage of this would lie in the corresponding increase in maximum sighting distance, increasing the total volume scanned. The optimal tactic might lie in periodically accommodating or linking accommodation to some en-

vironmental-physiological feedback mechanism such as hunger.

The shape of Fig. 11 is similar to that which Wilson (1975) has suggested characterizes most particulate feeding predators. As it reflects almost exclusively the capabilities of the predator however, this would seem to apply only where food can legitimately be treated as a single resource varying only in size. Predators engaged in more complex forms of predation involving prey with variable escape or detectability characteristics would tend to have correspondingly complex capture success curves with lower overall probabilities.

The curves of Fig. 11 are members of a family of curves along the food size axis each representing capture probabilities for a single predator size. From this it would be expected, under appropriate conditions of food availability, that mean food size in the diet should increase with increasing body size. This appears to be the case for juvenile coho (Dunbrack unpublished) and has been reported for several other fish including rainbow trout, *Salmo gairdneri* (Galbraith 1967, Bisson 1978), atlantic salmon, *S. salar* (Allen 1941), brown trout, *S. trutta* (Elliot 1967, Fahy 1980), yellow perch, *Perca flavescens* (Wong & Ward 1972), the flounder, *Platichthys flesus* (Moore & Moore 1976) and the gila topminnow, *Poeciliopsis occidentalis* (Gerking & Plantz 1980), among others.

A salient feature of Fig. 11 is the increase in absolute range of food sizes potentially eaten with increased body size. Werner (1974) obtained an analogous result in a study of handling time in different sizes of bluegill sunfish. Wilson (1975), although referring to interspecific body size differences, suggested this to be a common feature of capture probability curves. These upper and lower bounds may be critically associated with factors such as habitat selection (larger fish may be able to exploit food sources not available to smaller fish and vice versa, e.g. Wong & Ward 1972) but they also potentially result in an increase in diet breadth with body size. Whether or not this will be the case depends again upon the availability curve and the resource axis used to measure breadth. Increases in the size range of items consumed with increased body size have been noted in juvenile coho (Dun-

brack unpublished) as well as brown trout (Elliott 1967) and flounder (Moore & Moore 1976).

At the large end of the body size spectrum, probability of successful capture appears to be a function of mouth morphology. Wańkowski (1979, 1981) has expressed probability of ingestion as a function of PFR (food diameter/ fish length). Using roughly spherical food pellets he showed that ingestion probability fell from 1 at a PFR of 0.025 to 0 at a PFR of 0.07. While he did not directly investigate the effects of body size, he implies that absolute body size will have no effect on the PFR-ingestion probability relationship. With experimental data from fish ranging in length between 40 and 80 mm, it is possible to test this hypothesis for juvenile coho. If the abscissa of Fig. 10 is converted to PFR from food width, the PFR's corresponding to an ingestion probability of 1 are 0.05, 0.045 and 0.045 for 40, 60 and 80 mm coho respectively. PFR's corresponding to an ingestion probability of 0 are 0.085, 0.067 and 0.061. This suggests that at least maximum prey size cannot be considered a constant function of coho body length. The non-allometric relationship between body length and mouth width implied by this analysis is supported by head width measurements of juvenile coho taken by B. Hebden (personal communication) and this also seems to be the case for juvenile yellow perch (Wong & Ward 1972) and the flounder *Platichthys flesus* (Moore & Moore 1976).

Critical in any discussion of food selection by predators or consumers generally, is the identification of the sensory mode(s) employed by the predator for food detection and the consequent food characteristic(s) upon which selection will be based. Simple predictive and testable models such as the one developed here seem particularly suited to this end. Our model contains an hypothesis regarding modality (coho are visual predators) and an hypothesis based upon a food characteristic (size) both of which are supported by the outcome of the test. Although not trivial, the qualitative conclusions that coho are visual predators and that food selection is based on size would hardly seem surprising to a fish ecologist. The value of our model, however, lies in its quantification of the behavioural processes affecting food detection and

capture and the integration of these processes into a quantitative predictor of diet.

Implicit in the model is the hypothesis that diet composition is determined solely by reaction distance, probability of capture and ingestion, and food density (i.e. the fish are 'non-selective'). There is evidence to suggest this to be the case at low food densities (reviewed by Confer et al. 1978). In contrast, optimal foraging theory (reviewed by Schoener 1971, Pyke et al. 1977) argues that a food item *i*, once encountered, should be rejected in favour of continued search when:

$$(\text{return from } i) <$$

(mean rate of return) (handling time for *i*)(5)  
(this assumes a negligible handling cost, which seems reasonable for small foods). Thus depending upon the mean rate of return, optimal foragers should be more or less selective. The fish in the present study had stomachs <10% full at the end of the feeding trials. Using values for the weight of stomach contents of test fish, and assuming a constant feeding rate, the mean rate of return to test fish was estimated from equations in Elliott & Persson (1978) as  $3.5 \times 10^{-6} \text{ g sec}^{-1}$  (wet weight). Multiplying this by a handling time of three seconds (an upper limit for prey less than 1 mm in width; Dunbrack unpublished), gives the result that under the test conditions, optimally foraging coho should have consumed all foods weighing more than  $1.05 \times 10^{-5} \text{ g}$ , the approximate weight of an adult dipteran, a typical surface drift item, of width 0.2 mm. Smaller items should be ignored. In fact, at this food size, probability of attack and ingestion (Fig. 11) is <0.2. Thus, under these test conditions, the optimal foraging model and the present 'non-selective' model make nearly identical predictions.

If fish respond to higher food densities with increased selection, an optimal foraging prediction supported by observations of a direct relationship between stomach fullness and selectivity (Ivlev 1961, pp. 55-60, Moore & Moore 1976), the non-selective model could become inadequate as a predictor of diet composition at high levels of food availability. Under such conditions, the model could be modified to conform with energetically optimal tactic through truncation of the curves of Fig. 11 at that food size defined by inequality 5.

An additional factor potentially affecting diet composition is the possibility that two or more prey could be simultaneously visible, introducing a bias due to predator choice of the apparently largest one (O'Brien et al. 1976). The adequacy of the apparent size hypothesis to explain observed size selection at high food densities has been questioned (Gibson 1980, Gardner 1981, Eggers 1982), but the hypothesis has been shown to be consistent with the outcome of first choice experiments involving only two prey items (O'Brien et al. 1976, Gibson 1980). Since choice by apparent size can produce a bias in favour of relatively larger prey (O'Brien et al. 1976), the likelihood of its operation under the test conditions was investigated. Because the probability of a fish encountering two or more prey simultaneously is approximately zero, simultaneous encounter was arbitrarily defined as the encountering of two or more prey within a space of five seconds, an interval which should encompass any situation where choice by apparent size could occur. Mean encounter rate for all test fish, estimated from the number of items consumed, was found to be 0.014 in five seconds. Treating prey encounter as a Poisson process, the conditional probability of a fish encountering two or more prey, during any five second interval, given that it encountered at least one, was found to be 0.02. This value is so low that choice by apparent size could not have affected materially the outcome of the test, once again supporting the appropriateness of the nonselective model.

Food obtained from the surface drift constitutes an important energy source for coho (Mundie 1969, Johnson & Ringler 1980) as well as other stream dwelling salmonids (e.g. Elliott 1967, Metz 1974, Bisson 1978). An overall picture of coho food selection, however, requires the development of additional predictive models of subsurface and benthic feeding. Within the context of the model developed here this could be affected through changes in the parameters  $SW_{ji}$  and  $N_i$  of equation 4. For subsurface feeding,  $SW_{ji}$  becomes  $SA_{ji}$  (scanning area) which describes the cross sectional area of the volume scanned by the stationary predator (cf. Confer & Blades 1975) and  $N_i$  is the availability obtained through drift sampling. For a

benthic feeding coho, SAji describes the area of the fish's reactive field projected on the substrate below the fish and Ni is the epibenthic availability (cf. Ware 1973). The possibility of adapting our model to these two feeding situations is currently being investigated.

## Acknowledgements

We wish to thank A. Fraser who provided invaluable assistance in both the field and laboratory aspects of the study, as well as B. Hebden and R. Ydenberg who helped in the early stages. We also thank two anonymous referees who made helpful comments on the manuscript. The research was funded by NSERC Canada grant A6869 to LMD.

## References cited

- Allan, J.D. 1978. Trout predation and the size composition of stream drift. *Limnol. Oceanogr.* 23: 1231–1237.
- Allan, J.D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. *Can. J. Fish. Aquat. Sci.* 38: 184–192.
- Allen, K.R. 1941. Studies on the biology of the early stages of the salmon (*Salmo salar*). 2. Feeding habits. *J. Anim. Ecol.* 10: 47–76.
- Bisson, P.A. 1978. Diel food selection by two sizes of rainbow trout (*Salmo gairdneri*) in an experimental stream. *J. Fish. Res. Board Can.* 35: 971–975.
- Brawn, V.M. 1969. Feeding behaviour of cod (*Gadus morhua*). *J. Fish. Res. Board Can.* 26: 583–596.
- Breck, J.E. & M.J. Gitter. 1981. Visual acuity: increased reactive distance of bluegills (*Lepomis macrochirus*) with increased size. Abstract, Third Biennial Conference on the Ethology and Behavioral Ecology of Fishes, Normal, Illinois.
- Brett, J.R. & C. Groot. 1963. Some aspects of olfactory and visual responses in Pacific salmon. *J. Fish. Res. Board Can.* 20: 287–303.
- Brooks, J.L. 1968. The effects of prey size selection by lake planktivores. *Syst. Zool.* 17: 272–291.
- Brooks, J.L. & S.I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150: 28–35.
- Confer, J.L. & P.I. Blades. 1975. Omnivorous zooplankton and planktivorous fish. *Limnol. Oceanogr.* 20: 571–579.
- Confer, J.L., G.L. Howick, M.H. Corzette, S.L. Kramer, S. Fitzgibbon & R. Landesberg. 1978. Visual predation by planktivores. *Oikos* 31: 27–37.
- Drenner, R.W., J.R. Strickler & W.J. O'Brien. 1978. Capture probability: the role of zooplankton escape in the selective feeding of planktivorous fish. *J. Fish. Res. Board Can.* 35: 1370–1373.
- Eggers, D.M. 1977. The nature of prey selection by planktivorous fish. *Ecology* 58: 46–59.
- Eggers, D.M. 1982. Planktivore preference by prey size. *Ecology* 63: 381–390.
- Elliott, J.M. 1967. The food of trout (*Salmo trutta*) in a Dartmoor stream. *J. Appl. Ecol.* 4: 59–71.
- Elliott, J.M. & L. Persson. 1978. The estimation of daily rates of food consumption for fish. *J. Anim. Ecol.* 47: 977–991.
- Fahy, E. 1980. Prey selection by young trout fry (*Salmo trutta*). *J. Zool. Lond.* 190: 27–37.
- Galbraith, M.G. 1967. Size-selective predation on *Daphnia* by rainbow trout and yellow perch. *Trans. Amer. Fish. Soc.* 96: 1–10.
- Gardner, M.B. 1981. Mechanisms of size selectivity by planktivorous fish: a test of hypotheses. *Ecology* 62: 571–578.
- Gerking, S.D. & D.V. Plantz. 1980. Size-biased predation by the gila topminnow *Poeciliopsis occidentalis* (Baird and Girard). *Hydrobiologia* 72: 179–191.
- Gibson, R.M. 1980. Optimal prey-size selection by three-spined sticklebacks (*Gasterosteus aculeatus*): a test of the apparent-size hypothesis. *Z. Tierpsychol.* 52: 291–307.
- Griffith, J.S. 1974. Utilization of invertebrate drift by brook trout (*Salvelinus fontinalis*) and cut-throat trout (*Salmo clarki*) in small streams in Idaho. *Trans. Amer. Fish. Soc.* 103: 440–447.
- Holling, C.S. 1966. The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* 48: 1–86.
- Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press. New Haven, 302 pp.
- Janssen, J. 1976. Selectivity of an artificial filter feeder and suction feeders on calanoid copepods. *Amer. Midl. Nat.* 95: 491–493.
- Johnson, J.H. & N.H. Ringler. 1980. Diets of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*) relative to prey availability. *Can. J. Zool.* 58: 553–558.
- Laing, J. 1938. Host-finding by insect parasites. 2. The chance of *Trichogramma evanescens* finding its hosts. *J. Exp. Biol.* 51: 281–302.
- Luecke, C. & W.J. O'Brien. 1981. Prey location volume of a planktivorous fish: a new measure of prey vulnerability. *Can. J. Fish. Aquat. Sci.* 38: 1264–1270.
- Magnuson, J.J. & J.G. Heitz. 1971. Gill raker apparatus and food selectivity among mackerels, tunas, and dolphins. *U.S. Fish. Bull.* 69: 361–370.
- Meehan, W.R. & R.A. Miller. 1978. Stomach flushing: effectiveness and influence on survival and condition of juvenile salmonids. *J. Fish. Res. Board Can.* 35: 1359–1363.
- Metz, J.P. 1974. Die Invertebratendrift an der Oberfläche eines Voralpenflusses und ihre selektive Ausnutzung durch die Regenbogenforellen (*Salmo gairdneri*). *Oecologia (Berl.)* 14: 247–267.
- Moore, J.W. & I.A. Moore. 1976. The basis of food selection in flounders, *Platichthys flesus* (L.), in the Severn estuary. *J. Fish*

- Biol. 9: 139–156.
- Mundie, J.H. 1969. Ecological implications of the diet of juvenile coho in streams. pp. 135–152. *In*: T.G. Northcote (ed.) Symposium on Salmon and Trout in Streams, H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.
- Nilsson, N. 1978. The role of size-biased predation in competition and interactive segregation in fish. pp. 305–325. *In*: S.D. Gerking (ed.) Ecology of Fresh Water Fish Production, Blackwell, London.
- Northmore, D., F.C. Volkmann & D. Yager. 1978. Vision in fishes: color and pattern. pp. 79–136. *In*: D.I. Mostofsky (ed.) The Behavior of Fish and Other Aquatic Animals, Academic Press, New York.
- O'Brien, W.J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. *Amer. Sci.* 67: 572–581.
- O'Brien, W.J., N.A. Slade & G.L. Vinyard. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). *Ecology* 57: 1304–1310.
- Pyke, G.H., H.R. Pulliam & E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* 52: 137–154.
- Ringler, N.H. 1979. Selective predation by drift feeding brown trout (*Salmo trutta*). *J. Fish. Res. Board Can.* 36: 392–403.
- Schoener, T.W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2: 369–404.
- Vinyard, G.L. & W.J. O'Brien. 1975. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *J. Fish. Res. Board Can.* 33: 2845–2849.
- Walls, G.L. 1963. The vertebrate eye and its adaptive radiation. Hafner, New York. 785 pp.
- Wańkowski, J.W.J. 1979. Morphological limitations, prey size selectivity, and growth response of juvenile atlantic salmon, *Salmo salar*. *J. Fish Biol.* 14: 89–100.
- Wańkowski, J.W.J. 1981. Behavioural aspects of predation by juvenile atlantic salmon (*Salmo salar* L.) on particulate, drifting prey. *Anim. Behav.* 29: 557–571.
- Ware, D.M. 1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density and prey size. *J. Fish. Res. Board Can.* 29: 1193–1201.
- Ware, D.M. 1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Board Can.* 30: 787–797.
- Werner, E.E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. *J. Fish. Res. Board Can.* 31: 1531–1536.
- Werner, E.E. & D.J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55: 1042–1052.
- Wilson, D.S. 1975. The adequacy of body size as a niche difference. *Amer. Nat.* 109: 769–784.
- Wong, B. & F.J. Ward. 1972. Size selection of *Daphnia pulex* by yellow perch (*Perca flavescens*) fry in West Blue Lake, Manitoba. *J. Fish. Res. Board Can.* 29: 1761–1764.