Position Choice by Drift-Feeding Salmonids: Model and Test for Arctic Grayling (*Thymallus arcticus*) in Subarctic Mountain Streams, Interior Alaska

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We develop a model to predict position choice of drift-feeding stream salmonids, assuming a fish chooses the position that maximizes its net energy intake rate. The fish's habitat is represented as a series of stream cross-profiles, each divided into vertical strips characterized by water depth and velocity. The fish may select a focal point in any of these strips, and include several neighbouring strips in its foraging area. The number of prey the fish encounters depends on its reaction distance to prey, water depth, and water velocity; the proportion of detected prey the fish is able to capture declines with water velocity. The fish's net energy intake rate is its gross energy intake rate from feeding minus the swimming cost calculated by using water velocity at the fish's focal point. There was a close match between the positions predicted by this model and those chosen by solitary Arctic grayling (*Thymallus arcticus*) in the pools of a mountain stream in Alaska.

Les auteurs ont mis au point un modèle visant à prévoir la position des salmonidés qui se nourrissent en se laissant dériver dans un cours d'eau, en supposant au départ qu'un poisson se placera à un endroit lui permettant de maximiser son taux net de consommation d'énergie. L'habitat des poissons est représenté comme suit: une série de profils transversaux de cours d'eau, chacun divisé en bandes verticales caractérisées par la profondeur et la vitesse de déplacement de l'eau. Le poisson peut choisir un point central dans l'une ou l'autre de ces bandes et se déplacer dans plusieurs bandes adjacentes pour s'alimenter. Le nombre de proies que le poisson repère dépend de la distance de réaction qui le sépare de celles-ci ainsi que de la profondeur et de la vitesse de l'eau; le pourcentage de proies perçues que le poisson est capable de capturer diminue avec la vitesse de l'eau. Le taux net de consommation d'énergie du poisson équivaut au taux brut de consommation d'énergie au cours de l'alimentation moins l'énergie nécessaire à ses déplacements, valeur calculée en se servant de la vitesse de l'eau dans sa position principale. Les auteurs ont relevé une correspondance étroite entre les positions prévues par ce modèle et les positions choisies par des ombres arctiques (*Thymallus arcticus*) solitaires dans des étangs d'un cours d'eau de montagne situé en Alaska.

Drift feeding fish return to the same position, or "focal point", after each excursion to catch passing prey (Newman 1956; Kalleberg 1958; Jenkins 1969; Bachman 1984). Why do fish prefer one position over the multitude of alternatives? Several authors have proposed that fish select a position where the trade-off between swimming cost and the supply of drifting food, both of which increase with water velocity, maximizes net energy gain (Newman 1956; Jenkins 1969; Bachman 1981, 1984; Fausch and White 1981; Fausch 1984). Some authors add that the proximity of overhead cover, as a refuge from predators, is also important (Newman 1956; Jenkins 1969; Fausch and White 1981; Wilzbach 1985).

Despite this general consensus only Fausch (1984) has used these ideas to develop a quantitative model to predict feeding position choice by stream dwelling salmonids. Fausch's model worked well for predicting the position chosen by the dominant coho salmon (*Oncorhynchus kisutch*) in an artificial stream tank. However, we found his model to be poor at predicting the positions chosen by Arctic grayling (*Thymallus arcticus*) in stream pools, because it over-simplifies calculation of the fish's feeding rate. Fausch assumes that fish catch all prey passing through a "window" shaped like a pie slice (1/8th of a circle with a radius of two fish lengths), and uses the fastest water velocity, within two body lengths of the fish's focal point, to estimate the number of prey passing through this window. This method takes no account of water depth, the shape of the fish's reaction field, variations in water velocity within the fish's foraging area, or the influence of water velocity on the fish's ability to capture prey.

We propose a model to predict position choice by solitary stream salmonids that differs from Fausch's (1984) model in several ways. To estimate the rate at which the fish sees prey

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of different sizes we use data on the size-frequency distribution of prey, the fish's reaction distance to these prey, the topography of the stream bed, and the pattern of water flow. This approach owes much to the work on reaction distances, reaction fields and volumes, and prey selectivity of lake dwelling zooplanktivores (Confer and Blades 1975; Luecke and O'Brien 1981), recently applied to prey selection by drift-feeding salmonids (Dunbrack 1984; Dunbrack and Dill 1983, 1984; Grant and Noakes 1986). The model also includes a relationship for a decline in the fish's prey capture efficiency as water velocity increases. We use this model to predict position choice by solitary Arctic grayling in the pools of a mountain stream, and compare these predictions to the positions actually selected.

Methods

We first present our model, showing how habitat data and the fish's visual abilities are used to describe a fish's foraging area, how water velocity influences prey capture efficiency, and how these combine to determine the fish's net energy intake rate. We then apply our model to predict position choice of Arctic grayling.

A. The Model

Habitat and foraging area

Most pools of a mountain stream resemble one another in general morphology. A narrow, shallow jet of fast water enters the head of the pool, slows and disperses as it reaches the deeper belly of the pool, and finally enters the extensive shallow tail of the pool, where it may accelerate. We describe this architecture with a series of cross-profiles taken at 50 cm intervals along the length of the pool. We represent each cross-profile as a series of strips extending from the water surface to the stream bed. These strips are 25 cm (or occasionally 50 cm) wide, characterized by water depth and velocity, and centered on the position where depth and velocity are measured (Fig. 1).

The fish may select a focal point in any of these strips and include several neighbouring strips in its foraging area. Its focal point is equidistant from each side of the chosen strip and (for simplicity) a quarter of the way from the stream bed to the water surface.

Maximum capture distance

Imagine a fish feeding in swift water. To capture a passing prey item it must first see the prey and then intercept it before the prey is swept downstream. The proportion of prey that it sees, and is able to capture, should decline as water velocity increases. We have modelled the form of this decline in capture efficiency using the concept of "maximum capture distance" (MCD), which is the maximum distance from the fish's focal point, perpendicular to the current, at which the fish can intercept prey of a particular size (Note: this term was first used by Wankowski and Thorpe (1979); our definition is similar to
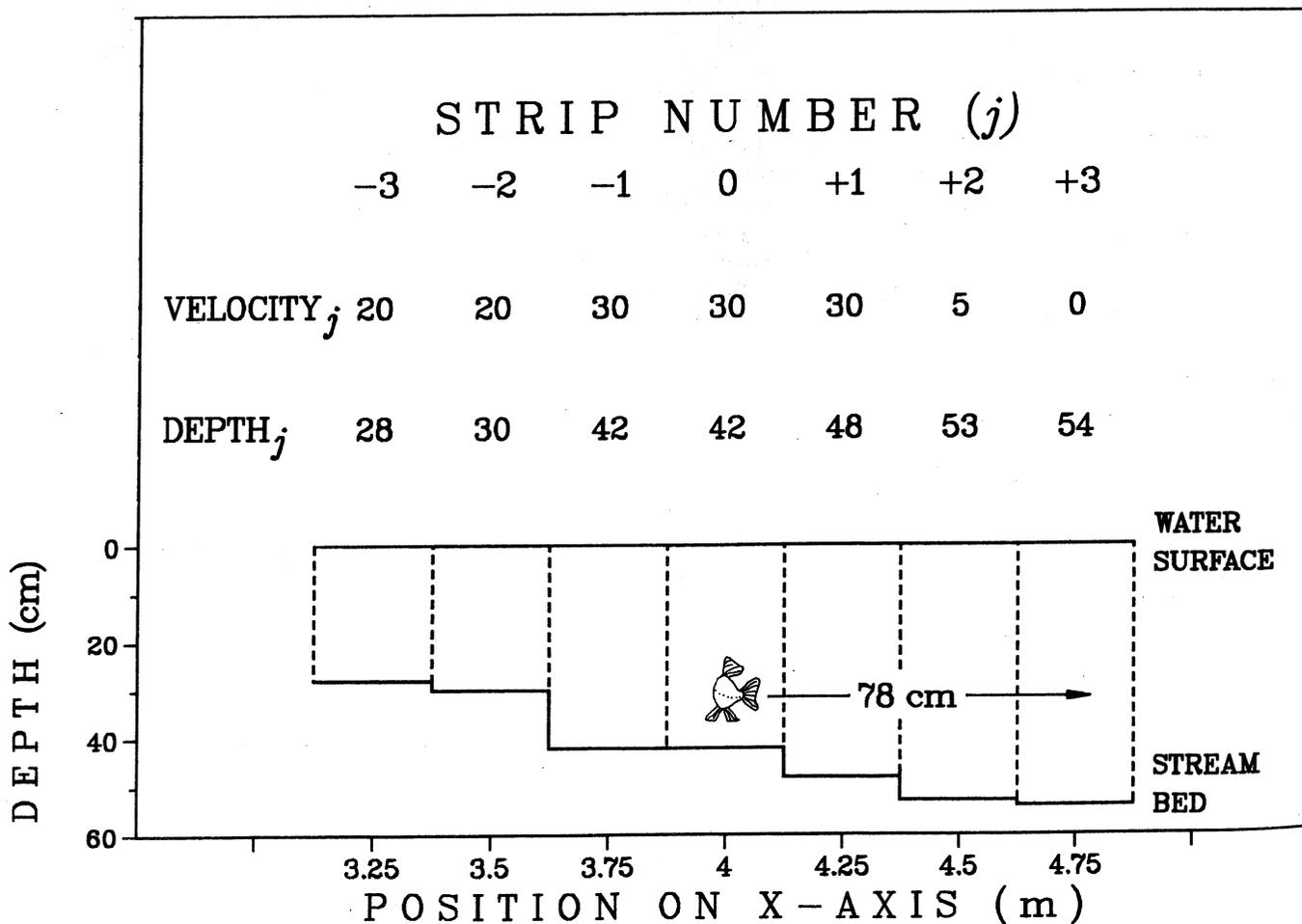

FIG. 1. Part of a stream cross-profile, looking upstream, showing how the habitat and the grayling's foraging space are described. Seven strips j ($j = -3, ..., +3$) are shown, each characterized by a water velocity and depth measurement. The fish's focal point is in strip 0 and, because the fish's reaction distance to the largest prey is 78 cm (see later), the seven strips encompass its foraging area.
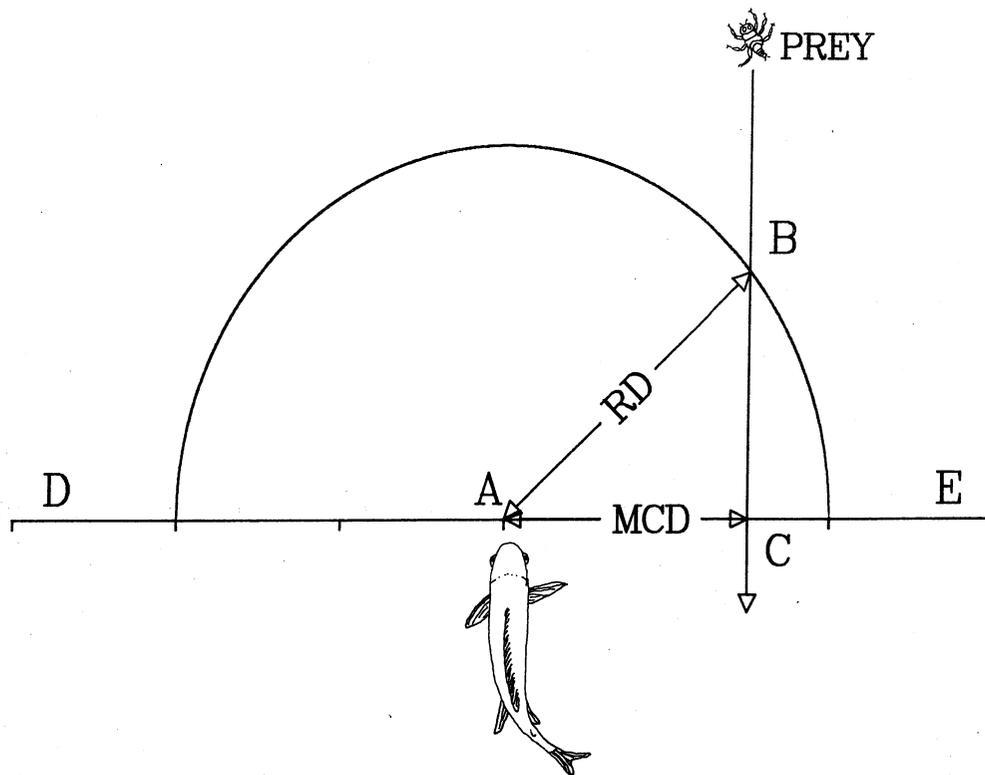
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FIG. 2. Geometry of prey interception, seen from above. A is the fish's focal point, AB its reaction distance to the approaching prey, and AC the maximum capture distance. The fish will see the prey at B and must intercept it before it crosses the line DE.

theirs, but more restrictive). To derive a relationship for MCD we assume that the water velocity in the fish's foraging area is V, that the fish detects each prey item at its reaction distance (RD), that the fish begins intercepting each prey item as soon as it sees it — i.e. there is no time lag, but see Godin and Rangley (1989) — and travels at its maximum sustainable swimming speed ($VMAX$). We constrain the fish to capture prey items before they cross a line perpendicular to the current passing through the focal point. This assumption is not realistic but there is little information available with which to improve it.

Under these conditions the relationship between MCD and RD, $VMAX$, and V can be derived as follows (Fig. 2). When line segment $AC = $ MCD, the time it takes the fish to travel this distance (Time fish $= TF$) will be the same as the time taken by the prey to travel line segment BC (Time prey $= TP$), and the fish will catch the prey just as it crosses line DE. To travel AC, relative to the streambed, the fish must swim AB relative to the water. $AB = RD$ and $BC = V \cdot TP$ and since $TP = TF = RD/VMAX$, then by substitution $BC = V \cdot RD/VMAX$. Therefore, using Pythagoras' theorem:

(1) $\quad \text{MCD} = \sqrt{RD^2 - (V \cdot RD/VMAX)^2}$

The relationship between maximum capture distance and water velocity is illustrated in Fig. 3, for several combinations of RD and $VMAX$. (Note that both RD and $VMAX$ are expected to depend on fish size.) This is a two dimensional argument but can be generalized to three dimensions, as below.

Calculating net energy intake

The fish's net energy intake rate is the balance of its gains from feeding and its swimming cost. To estimate the fish's feeding rate we first calculate the cross sectional area of each

strip j ($j = -3, \ldots, +3$), within which the fish will capture prey in each of three size-classes i ($i = 1, 2, 3$). Fig. 4 shows how these capture areas (CA_{ij}) are defined.

Once the values of CA_{ij} are known, it is possible to calculate the total energy content of the prey passing within capture range of the fish, or gross energy intake rate (GEI), as follows:

(2) $\quad \text{GEI} = \sum_{i=1}^{3} \sum_{j=-3}^{+3} CA_{ij} \cdot V_j \cdot PC_i \cdot PE_i \cdot 3\,600/1\,000\,000$

where V_j is the average water velocity in strip j, PC_i is the concentration of prey in size class i, and PE_i is the energy content of prey in size-class i. The $3\,600/1\,000\,000$ term is necessary because CA_{ij} and V_j have units of centimetres and seconds while PC_i and GEI have units of metres and hours.

We use the water velocity at the fish's focal point (e.g. V_o in Fig. 1) to calculate swimming cost (SC), i.e. we ignore the small incremental cost of prey attack. Net energy intake rate (NEI) is then simply: NEI $=$ GEI $- SC$.

B. Application of the Model to Predict Position Choice of Grayling

Position choice experiments

We performed position choice experiments during the summers of 1986 and 1987 in the pools of Twelvemile Creek, a second order mountain stream (at about 65°25′ N, 145°30′ W), Yukon River Drainage, interior Alaska.

To provide an XY coordinate system with which to record the location of habitat measurements, and the position choice of grayling, we laid a grid consisting of 1 m squares on the stream bed, using 3-mm white nylon cord. The X axis of this
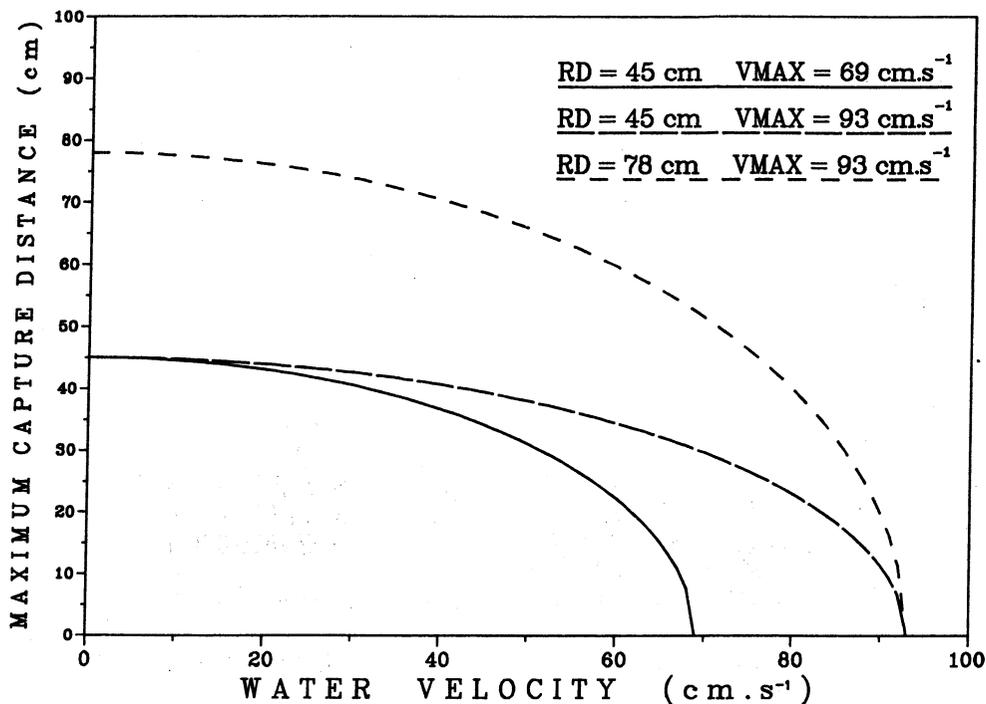
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FIG. 3. Relationship between the maximum capture distance and water velocity, showing the influence of reaction distance (*RD*), and interception speed (*VMAX*).
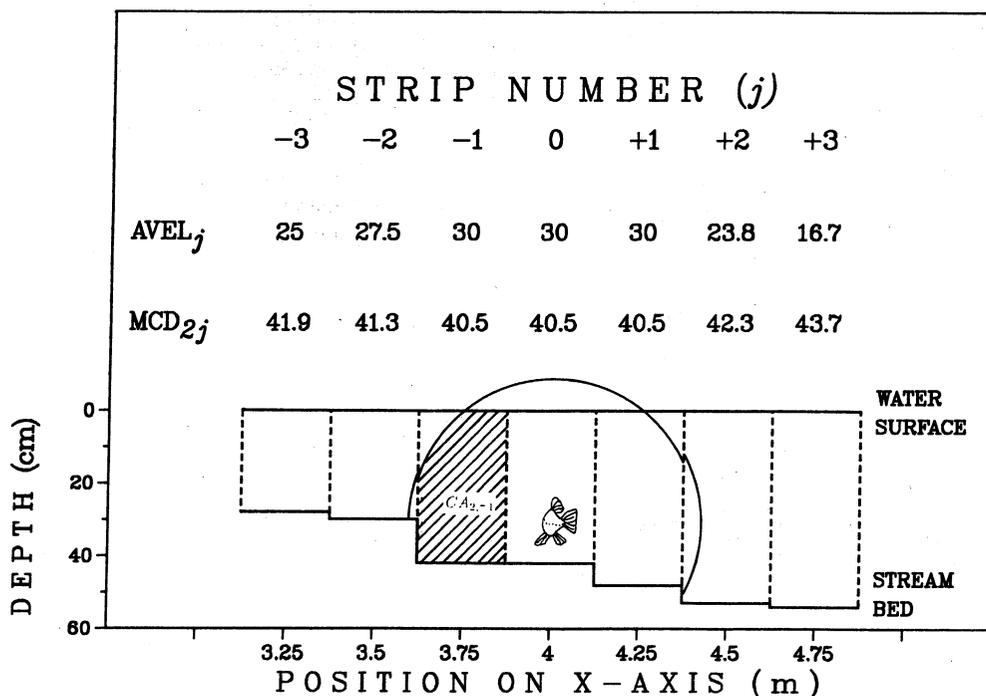

FIG. 4. Area within which the fish can capture prey in size-class $i = 2$. The $AVEL_j$ are the means of the water velocities in the strips the fish must cross to intercept prey in strip j, weighted by the average distance the fish travels in each strip. The MCD_{2j} are the maximum capture distances for prey in size-class $i = 2$ appropriate for strip j. These are calculated using Eq. 1, in which $RD = 45$ cm (the appropriate RD for prey in size-class $i = 2$), $V = AVEL_j$, and $VMAX = 69$ cm·s^{-1} (the appropriate $VMAX$ for a 30 cm grayling). The areas of each strip j within which the fish will capture prey in size-class i (CA_{ij}) are the overlaps between strip j and a circle with radius MCD_{ij} centered on the fish's focal point. $CA_{2,-1}$ is shaded. Note that this is the same cross section as illustrated in Fig. 1 and that the radii of the arcs that encompass the CA_{2j} happen to be the same for strips -1, 0, and $+1$ but not for strips -2 or $+2$.

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TABLE 1. Design and results of position choice experiments — showing fork lengths of fish used in each pool, dates of introduction and observation, and the coordinates of the position selected by the fish, predicted by our model, and predicted by Fausch's (1984) model.

	Date introduced	Date observed	XY Coordinates of selected position	XY Coordinates of predicted position (This paper)	XY Coordinates of predicted position (Fausch 1984)
Yellow Flower Pool 1986					
200 mm fish[a]	10 July 1986	11 July 1986	6.50, 3.50	6.50, 3.75	1.00, 2.25
280 mm fish	9 July 1986	10 July 1986	6.50, 3.50	6.00, 3.75	0.50, 3.50
Waterfall Pool 1986					
193 mm fish[a]	10 July 1986	11 July 1986	3.00, 2.00	2.50, 2.25	0.50, 2.50
325 mm fish	8 July 1986	10 July 1986	4.00, 2.00 and 3.00, 2.00	2.50, 2.25	0.50, 2.50
Yellow Flower Pool 1987					
275 mm fish[a]	19 July 1987	21 July 1987	7.50, 3.75	6.50, 4.00	0.00, 4.00
300 mm fish	6 August 1987	7 August 1987	7.50, 3.75	6.50, 4.00	0.00, 4.00
Bedrock Pool 1987					
250 mm fish[a]	4 August 1987	5 August 1987	6.50, 4.25	5.50, 4.25	1.00, 5.00
280 mm fish	Natural resident	19 July 1987	6.50, 4.50	7.00, 4.00	1.00, 5.00

[a]The positions of these fish are illustrated in Fig. 5.

grid was parallel to the current. We mapped Yellow Flower Pool on 7 September 1986 and 14 July 1987, Waterfall Pool on 15 September 1986, and Bedrock Pool on 3 September 1987. In Yellow Flower Pool and Bedrock Pool water depth and average water velocity were measured at 0.5 m intervals on the X-axis and 0.25 m intervals on the Y-axis except in the tail of each pool, where measurements were 0.5 m apart on both axes. In Waterfall Pool the measurement interval was 0.5 m on both axes and we interpolated values to give a 0.25 m interval on the y-axis. Water velocity was measured with a Marsh McBirny current meter.[2] We did not map the pools at the same time we recorded fish position, however, fish occupied the same positions at the time of mapping as in the position choice experiments we report here.

The grayling in Twelvemile Creek take advantage of the long summer days to feed continuously, often maintaining the same feeding position 24 h a day (N. F. Hughes, pers. obs.). Evidently they rarely become satiated, at which time we would expect them to move to low velocity resting positions. Occasionally fish do select resting positions, but this is apparently in response to very low drift abundance, not satiation (N. F. Hughes, unpubl. data). Their behavior makes it possible to determine a grayling's preferred feeding position quite easily, and describe it with a single XY coordinate.

To prepare for the position choice experiments we block-netted the upstream and downstream ends of each pool to prevent wild fish from entering, and removed unwanted resident fish with rod and line or seine. Most experimental fish were caught with rod and line and introduced into the pools soon after capture, but one was a natural resident. We ran two position choice experiments in each of four pools (Yellow Flower Pool 1986 and Yellow Flower Pool 1987 are considered separately because bottom topography and pattern of water flow changed markedly during the spring breakup of 1987); the design of these experiments is given in Table 1. We observed the fish from a camouflaged observation tower 4 m high, and recorded each fish's focal point on a scale map of the pool. To assign coordinates to each fish's position we rounded the loca-

tion of its focal point to the nearest 0.5 m on the X-axis and the nearest 0.25 m on the Y-axis.

Parameters obtained from the literature

All parameters, other than data on water depth and velocity, were derived from the literature. To estimate the concentration of drifting invertebrates we used an equation developed by LaPerriere (1981, 1983) for interior Alaskan streams in the immediate vicinity of Twelvemile Creek. This equation describes the relationship between the mean summer concentration of drifting invertebrates at a station and the mean summer discharge at that station, allowing us to predict invertebrate drift concentration in our experimental pools from stream discharge data. We used data from Imnaviat Creek (Table 2), a beaded tundra stream in Northern Alaska, to approximate the size composition of the drift (Ries 1988). In both Imnaviat Creek, and interior Alaskan streams, chironomids dominate the invertebrate fauna (Oswood 1989), and the mean size of drifting invertebrates is very similar (0.59 mg in Imnaviat Creek, based on Table 2 and the length/weight relationship given in Rogers et al. (1976), and 0.63 mg in LaPerriere's study of interior Alaskan streams). These similarities make us comfortable applying size composition data from Imnaviat Creek to Twelvemile Creek. Note that floating food items and possible localized inputs from cover vegetation are not accounted for by the model.

The equations we used to estimate the abundance and energy content of the prey, the reaction distance of fish to these prey, and the swimming performance of grayling are given in Table 3.

Values for prey abundance, prey energy content, and reaction distance, for the three prey size-classes are given in Table 4. Reaction distance increases asymptotically with fish length but hardly changes for fish over 19 cm in length, so we used the same values for all the fish in our experiments. Values of $VMAX$ ranged from 63 cm·s^{-1} for the smallest fish to 71 cm·s^{-1} for the largest fish. Swimming cost varied with water velocity at the focal point, and with fish size.

Predicting position choice

To predict fish position choice we use our model to estimate the fish's NEI at all possible focal points in a pool (for compar-

[2]Reference to trade names or manufacturers does not imply government endorsement of commercial products.

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TABLE 2. Length frequency of invertebrate drift in Imnaviat Creek, summer 1985 (Ries 1988).

i	Size-class i (mm)	PL_i Midpoint of size-class i (mm)	PP_i Proportion of prey in size-class i
1	0.5–2.5	1.50	0.58
2	2.6–5.0	3.75	0.38
3	5.1–8.0	6.50	0.04

ison we did the same using Fausch's (1984) model). The number of possible focal points equals the number of strips in all the cross-sections taken to describe the pool. The XY coordinates of these possible focal points correspond to the XY coordinates at which water depth and water velocity were measured. We predict the grayling will choose the focal point where NEI is greatest. These calculations also allow the construction of a NEI contour map for the pool.

Results

The positions predicted by our model are quite close to those selected by the grayling (Table 1) and similar in physical character, lying in the center of the current near the deepest part of the pool (Fig. 5, Table 5). By comparison the positions predicted by Fausch's (1984) model are much further from the positions selected by the grayling, and quite different in physical character, lying in slow water at the head of the pool, within two fish lengths of very fast water.

In each of the pools, both fish selected the same (three pools), or very similar (one pool) positions. The larger fish in Waterfall Pool did use a second position that was distinctive from the one used by the smaller fish, but this appeared to be a resting position rather than a feeding position. Each of the models also predicted the same, or similar positions, for both the fish in each pool (Table 1).

On average our model ranked the positions selected by the fish in the top 4% of available positions while ranks for the positions predicted by Fausch's (1984) model were much lower (Table 5).

To show how our model functions, we compared the predictions of the full model to two reduced versions (Table 6). In reduced version A the fish pays no swimming cost, while in

version B maximum capture distance is independent of water velocity, remaining at the fish's reaction distance. The predictions of version A are the same, or very close, to those of the full model, while the positions predicted by version B are mostly further upstream, in the center of fast current, at the head of the pool.

Discussion

The similarity between the positions predicted by our model and those selected by the grayling supports the hypothesis that grayling choose positions which maximize their net energy intake rate. Our model's predictions are substantially more accurate than those of the only other available model (Fausch 1984), because our model includes more realistic assumptions about the number of prey the fish detects and the influence of water velocity on the prey capture abilities of the fish.

The prevailing view — that fish maximize their net energy intake rate by selecting a water velocity that optimizes the trade-off between food supply and swimming cost (Jenkins 1969; Bachman 1981, 1984; Fausch and White 1981; Fausch 1984) — is probably too simple. Removing swimming cost from our model results in little or no change in its predictions, demonstrating that trade-offs involving cost are not necessary to predict position choice in this particular situation. This is because the spatial variation of swimming costs and gross energy intake are such that the position that provides the greatest gross energy intake also provides the greatest net energy intake, after the subtraction of swimming costs. This does not mean that swimming costs are unimportant; at lower drift densities than we use here, trade-offs involving costs become important in determining the predicted position (N. F. Hughes, unpubl. data).

There is an important trade-off in our model between the number of prey items that a fish sees, and the proportion of these it is able to capture. The number of prey the fish sees increases with water depth and velocity, compared to only velocity in Fausch's model, while the proportion of detected prey the fish is able to capture declines with water velocity (there is no such decline in Fausch's model). The importance of this trade-off is shown by comparing the predictions of the full model with those of reduced verison B, in which the fish catches all the prey it sees, irrespective of water velocity. The

TABLE 3. Equations used to estimate parameters in the model, and their sources. PC_i is the abundance of prey in size-class i, PE_i is the energy content of prey in size-class i, RD_i is the reaction distance of the fish to prey in size-class i, $VMAX$ is the fish's maximum sustainable swimming speed, SC is the fish's swimming cost. V is the average water velocity at the fish's position (cm·s^{-1}), PP_i and PL_i are parameters from Table 2. FL is fish fork length (cm), FW is fish weight (g) which was estimated from fish length by regression ($Log(FW) = -2.03 + 3.03 \cdot Log(FL)$), SF is mean summer discharge, this was about 0.25 m^3·s^{-1} in the study reach (unpubl. data).

Parameter	Units	Equation	Source
PC_i	number·m^{-3}	$PC_i = PP_i \cdot e^{(-0.45 \cdot \ln(SF) - 1.702)}$	Adapted from LaPerriere (1981).
PE_i	J	$PE_i = 0.7274 \cdot PL_i^{2.62}$	Adapated from Cummins and Wuycheck (1971) and Rogers et al. (1976).
RD_i	cm	$RD_i = 12 \cdot PL_i (1 - e^{(-0.2 \cdot FL)})$	Estimated from data given by Schmidt and O'Brien (1982)[a].
$VMAX$	cm·s^{-1}	$VMAX = 36.23 \cdot FL^{0.19}$	Jones et al. (1974).
SC	J·h^{-1}	$SC = 10^{(C+M \cdot V)} \cdot 19 \cdot FW/1000$ where $C = 2.07 - 0.37 \cdot Log(FL)$ and $M = 0.0410 - 0.0196 \cdot Log(FL)$	Derived from graphical models in Brett and Glass (1973)[b].

[a]Developed using data for 3–13 cm grayling feeding on Arctic zooplankton at 1354 lx.
[b]Using data for sockeye salmon (*Oncorhynchus nerka*) at 10°C.

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TABLE 4. Values for prey concentration (PC_i), prey energy content (PE_i) and reaction distance (RD_i) for each size-class of prey, calculated by using equations from Table 3.

Size-class (mm)	PC_i (number·m^{-3})	PE_i (J)	RD_i (cm)
0.5–2.5	0.1976	2.10	18
2.6–5.0	0.1295	23.21	45
5.1–8.0	0.0136	98.08	78

predictions of version B are considerably poorer than those of the full model.

Several authors have suggested that overhead cover influences choice of feeding positions by stream salmonids (Newman 1956; Jenkins 1969; Fausch and White 1981), implying that fish select positions that optimize the trade-off between net energy intake rate and predation risk. This idea is appealing

because predation risk may be high in well-lit midstream positions, which allow the highest net energy intake rate, and low beneath overhead cover, where light conditions reduce the ability of fish to see prey (Wilzbach 1985). In addition, it has been shown that fish do trade off predation risk and food intake rate in many situations (Werner et al. 1983; Power 1984; Dill and Fraser 1984; see Dill 1987 for a review).

Predation risk may not be an important determinant of position choice for relatively large fish, however. In this study, grayling selected positions in the deepest (Yellow Flower Pool) or second deepest (Bedrock Pool) depression, in the center of the current. These positions were often a long way from the "bolt holes" they used to hide in when alarmed. Jenkins (1969) gave a very similar physical description for the positions chosen by brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) in a semi-natural stream channel, and found that fish chose the same positions soon after channel construction that
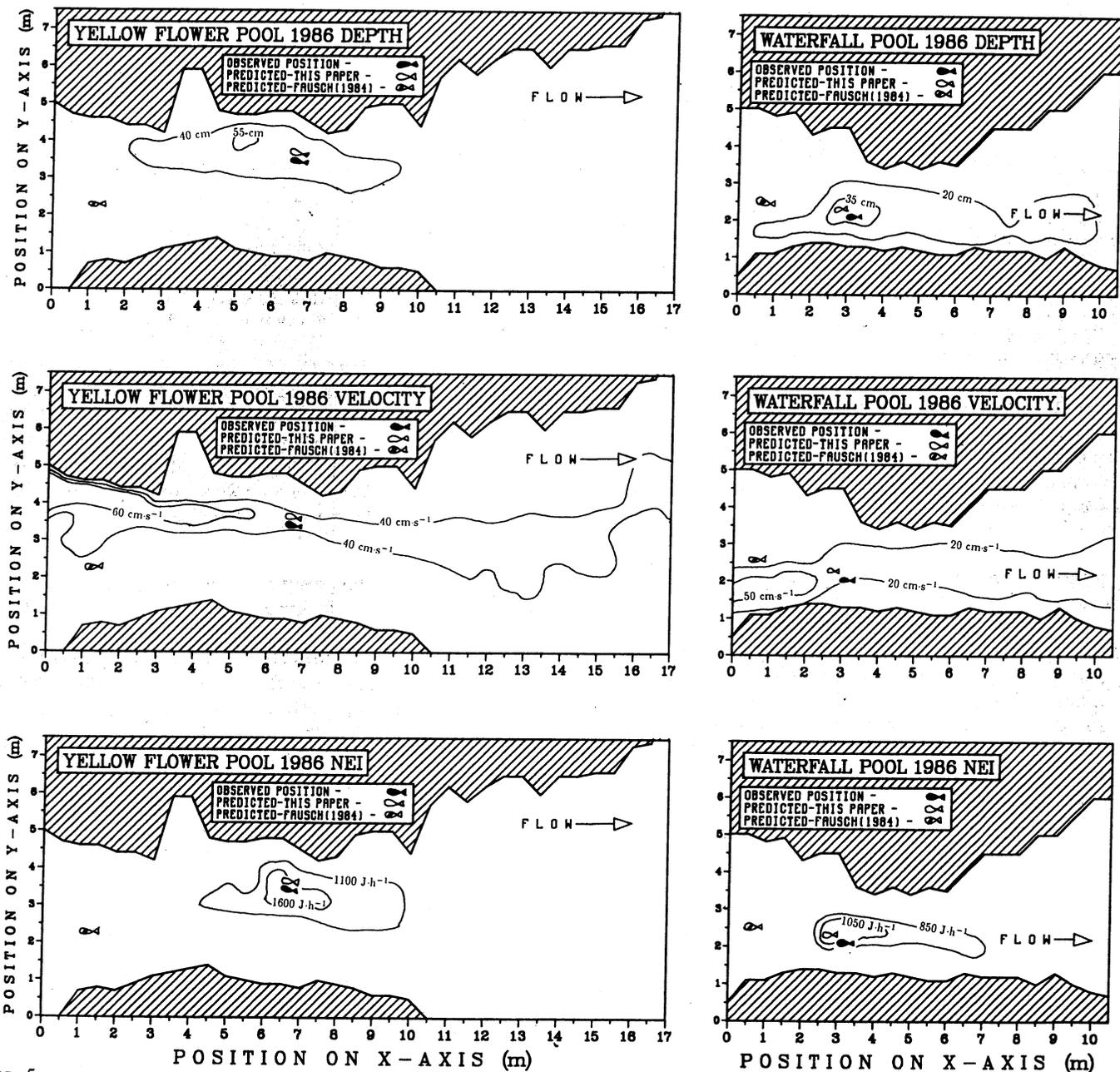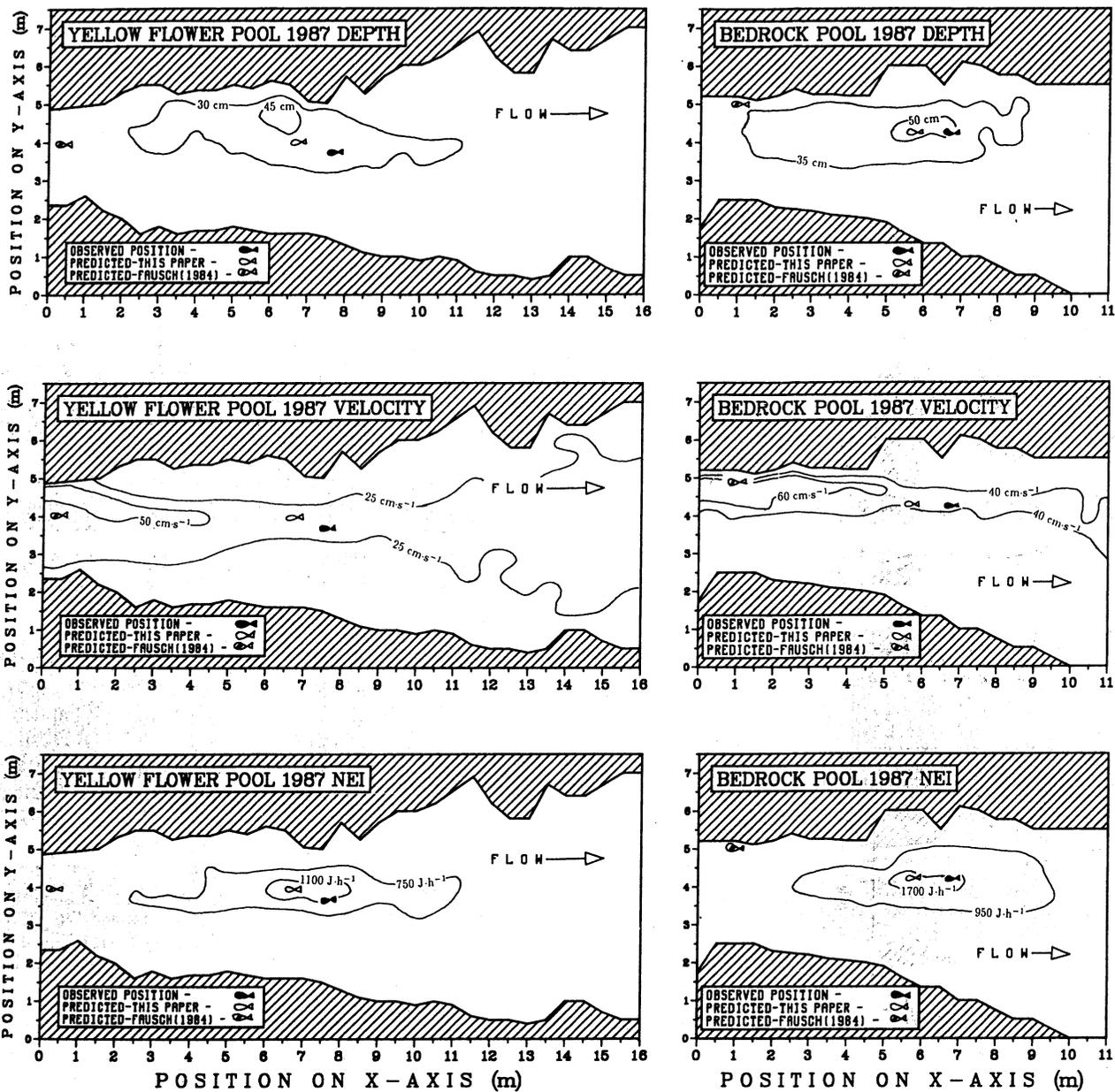

FIG. 5

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YELLOW FLOWER POOL 1987 DEPTH

BEDROCK POOL 1987 DEPTH

YELLOW FLOWER POOL 1987 VELOCITY

BEDROCK POOL 1987 VELOCITY

YELLOW FLOWER POOL 1987 NEI

BEDROCK POOL 1987 NEI

POSITION ON Y-AXIS (m)

POSITION ON X-AXIS (m)

OBSERVED POSITION –
PREDICTED-THIS PAPER –
PREDICTED-FAUSCH(1984) –

FLOW ⟶

FIG. 5. (*Continued*)
Observed and predicted fish position choices, in relation to water depth (cm), water velocity (cm·s⁻¹), and predicted net energy intake (NEI; J·h⁻¹), for 200 mm fish in Yellow Flower Pool (1986), 193 mm fish in Waterfall Pool (1986), 275 mm fish in Yellow Flower Pool (1987), and 250 mm fish in Bedrock Pool (1987).

they chose later, when overhead cover had developed. Similarly, Bachman (1984) showed that brown trout in his study pool spent most of their time feeding in midstream, clearly visible from overhead. These observations suggest that large salmonids select their feeding positions on the basis of water depth and flow, not on the proximity of overhead cover.

Applications of the Model and Future Developments

By varying the values of parameters in our model it should be possible to explain a wide range of position choice behavior. For example — some parameters, such as VMAX, swimming cost, and reaction distance depend on fish size, while others such as prey size and prey concentration depend on location, time of day, and season. Preliminary simulation results suggest that these variations can explain why stream salmonids move

into faster, deeper water as they grow, and change their positions daily and seasonally (N. F. Hughes and L. M. Dill, unpubl. data). Ideas incorporated in this model have already been used to predict the size composition of the diet (Dunbrack and Dill 1983; Grant and Noakes 1986).

In future it should be easy to adapt our model to include more information on the environmental variables that affect a fish's energy intake. Two useful relationships might be the influence of temperature on swimming costs, which could be included using data from Brett and Glass (1973), and the relationship between light intensity and reaction distance. In some cases these additions will be necessary to explain position choice behavior — such as why fish often move into low velocity resting positions at night (Kalleberg 1958; Edmundson et al. 1968), when the abundance of invertebrate drift is greatest.

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TABLE 5. Comparison of physical features at positions selected by the fish with the positions predicted by our model and by Fausch's (1984) model, showing water depth and velocity at each position, and the fastest velocity within two fish lengths either side of each position. Also shown are the ranks our model gave to each position. Only one fish from each of the four pools is included in this table, because positions selected by the second fish were identical or very similar (see Table 1).

	Water depth (cm)	Water velocity ($cm \cdot s^{-1}$)	Fastest water within two fish lengths ($cm \cdot s^{-1}$)	Ranking of position by our model
Yellow Flower Pool 1986 — 200 mm fish				
Observed position	56	50	50	9th of 477
Predicted — this paper	50	40	50	1st of 477
Predicted — Fausch (1984)	10	0	100	338th of 477
Waterfall Pool 1986 — 193 mm fish				
Observed position	43	20	28	22nd of 286
Predicted — this paper	37	33	40	1st of 286
Predicted — Fausch (1984)	5	0	35	134th of 286
Yellow Flower Pool 1987 — 275 mm fish				
Observed position	42	25	30	2nd of 486
Predicted — this paper	42	30	30	1st of 486
Predicted — Fausch (1984)	17	5	110	155th of 486
Bedrock Pool 1987 — 250 mm fish				
Observed position	50	55	55	10th of 318
Predicted — this paper	54	40	45	1st of 318
Predicted — Fausch (1984)	34	10	130	229th of 318

TABLE 6. Coordinates of feeding positions predicted by the full model and two reduced models for Yellow Flower Pool (1986), Waterfall Pool (1986), Yellow Flower Pool (1987), and Bedrock Pool (1987), Twelvemile Creek.

	Predicted position		
	Full model	Reduced version A (no swimming costs)	Reduced version B (MCD = RD)
Yellow Flower Pool 1986			
200 mm fish	6.50, 3.75	6.00, 3.75	4.00, 3.25
280 mm fish	6.00, 3.75	6.00, 3.75	4.00, 3.25
Waterfall Pool 1986			
193 mm fish	2.50, 2.25	2.50, 2.25	2.00, 1.75
325 mm fish	2.50, 2.25	2.50, 2.25	2.50, 2.25
Yellow Flower Pool 1987			
275 mm fish	6.50, 4.00	6.50, 4.00	3.00, 3.75
300 mm fish	6.50, 4.00	6.50, 4.00	3.00, 3.75
Bedrock Pool 1987			
250 mm fish	5.50, 4.25	5.50, 4.25	2.00, 4.50
280 mm fish	7.00, 4.00	5.50, 4.25	2.00, 4.50

Incorporating information about the fish's internal state will also be necessary to predict position choice in some situations. For example, fish that become satiated and cease feeding should move to low velocity resting positions, and there is evidence that increased hunger causes fish to move into faster water (Huntingford et al. 1988). A dynamic programming version (Mangel and Clark 1988) of the model might be the best way to include the influence of the fish's internal state on its decision making and position choice.

To explain some aspects of position choice and feeding behavior it may be necessary to alter some of the model's cen-tral ideas. For example, we assume attack speed (*VMAX*) to be the fish's maximum sustainable swimming speed, but in fact it is controlled by the fish and may be slower than this, or as high as maximum burst speed. We also constrain the fish to catch prey upstream of a line perpendicular to the current, whereas real fish may intercept prey further downstream. In reality we suspect that solitary grayling choose an attack speed and inter-ception trajectory that minimize the cost of prey capture, and that they pursue all prey large enough to offset capture cost (see Godin and Rangley (1989) for further discussion). In future, similar ideas could be used to explain both position choice and prey capture behavior with a single model.

Acknowledgements

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