

# The functional response of drift-feeding Arctic grayling: the effects of prey density, water velocity, and location efficiency

W. John O'Brien, Michael Barfield, and Karen Sigler

**Abstract:** An important aspect of a predator–prey system is the functional response of the predator to changing prey densities. We studied the feeding rate response of drift-feeding Arctic grayling (*Thymallus arcticus*) on a small invertebrate prey, *Daphnia middendorffiana*, at densities ranging from 0.01 L<sup>-1</sup> to 1.8 L<sup>-1</sup> and current velocities of 25, 32, and 40 cm·s<sup>-1</sup>. We videotaped the feeding of grayling to determine the duration of the search and pursuit components of the feeding cycle and the location efficiency of grayling feeding at different current velocities. Feeding rate increased approximately as the prey density to the 0.4 power from 0.01 to 1.25 prey·L<sup>-1</sup>, above which the feeding rate dropped. Current velocity had no significant effect on feeding rate. Search and pursuit times dropped with increasing prey density, but neither was affected by current velocity. However, current velocity reduced both maximum location distance and location efficiency. The lack of increase in feeding rate with increasing current velocity may be due to a trade-off between the increasing likelihood of encounter and decreasing location efficiency as current velocity increases. These data suggest that grayling could effectively feed in a variety of stream habitats with different current velocity.

**Résumé :** Un aspect important du système prédateur–proie est la réponse fonctionnelle des prédateurs aux changements de densité des proies. Nous avons étudié chez l'Ombre arctique (*Thymallus arcticus*), un poisson qui se nourrit dans la dérive, la variation du taux d'alimentation à même des *Daphnia middendorffiana*, de petites proies invertébrées dont la densité variait de 0,01 L<sup>-1</sup> à 1,8 L<sup>-1</sup> à des vitesses de courant de 25, 32 et 40 cm·s<sup>-1</sup>. L'alimentation de l'ombre a été enregistrée sur bande vidéo pour déterminer la durée des composantes de recherche et de poursuite du cycle alimentaire et l'efficacité de la localisation de la proie durant l'alimentation à diverses vitesses de courant. Le taux d'alimentation augmente à peu près en fonction de la densité des proies à un exposant de 0,4 à des densités de proies variant de 0,01 et 1,25 proie·L<sup>-1</sup>; au-delà de ces valeurs, le taux diminue. La vitesse du courant n'affecte pas de façon significative le taux d'alimentation. Le temps consacré à la recherche et à la poursuite diminue en fonction inverse de la densité des proies, mais n'est pas affecté par la vitesse du courant. Cependant, la vitesse du courant diminue la distance maximale de localisation et son efficacité. L'absence d'augmentation du taux d'alimentation en fonction de la vitesse du courant peut être due à un compromis entre la probabilité plus élevée de rencontre à une vitesse de courant élevée et la baisse de l'efficacité de la localisation. Ces observations indiquent que l'ombre peut s'alimenter de façon efficace dans une gamme étendue de cours d'eau à diverses vitesses de courant.

[Traduit par la Rédaction]

## Introduction

One of the most important aspects of foraging is the relationship between prey density and feeding rate, commonly referred to as the functional response of the predator. Solomon (1949) was the first to introduce the idea that Holling (1959a, 1959b, 1965) later explored in detail. The standard way of modeling the functional response is to divide the to-

tal time per prey into search time and pursuit (handling) time (Pulliam 1989). Search time is often modeled by assuming a random prey distribution and a random search. If a constant volume is searched per unit search time, then the functional response is given by the disk equation (Holling 1959b; Pulliam 1989):

$$FR = \frac{ap}{1 + aph}$$

where FR is the feeding rate,  $a$  is the attack rate,  $\rho$  is the prey density, and  $h$  is the handling (including pursuit) time. This is an example of a Type 2 functional response (Holling 1959a), which increases at a steadily decreasing rate until reaching a plateau. At low prey densities, FR is proportional to  $\rho$  (which is assumed also in many other functional response models), whereas at high prey density, FR approaches a constant value of  $1/h$ .

Whereas the functional response has been studied in many animal groups, both vertebrate (Witz 1996; Morgan et al. 1997; O'Donoghue et al. 1998) and invertebrate (O'Neil

Received June 27, 2000. Accepted May 17, 2001. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on September 11, 2001.  
J15837

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1997), there is relatively little known about the functional response of fish, especially drift-feeding fish. The general foraging ecology of fish has been well studied (Lazzaro 1987; O'Brien et al. 1990; O'Brien and Evans 1992) in part because of their ease of handling and relatively straightforward behavior. Drift feeding in streams, in particular, has attracted a lot of interest (Dahl and Greenberg 1998) because of its importance to the growth and well-being of stream fish (Deegan et al. 1997), as well as its potential impact on drifting invertebrates (Friberg et al. 1994). There is not, however, a great deal known about drift feeding in Arctic grayling. O'Brien and Showalter (1993) demonstrated that the search window width (greatest lateral distance at which prey are attacked after excluding the lateral-most 5% of attacked prey on each side) of drift-feeding Arctic grayling (*Thymallus arcticus*) was reduced with increasing current velocity and increased debris in the stream water. The width of the search window declined from about 80 cm at a low velocity ( $11.6 \text{ cm}\cdot\text{s}^{-1}$ ) to 45 cm at the highest velocity tested ( $55.7 \text{ cm}\cdot\text{s}^{-1}$ ) (O'Brien and Showalter 1993). There is preliminary evidence that velocity not only reduces the size of the search window but may also erode the efficiency of location within the window. Interestingly, Hughes (1992a, 1992b) found that grayling generally preferred the most rapid water that was available in a small mountain stream.

The functional response is "essential in developing models of foraging behavior and ecological interactions"; for example, the form of the functional response can determine the stability of a predator-prey system, the magnitude of fluctuations in prey density, and the nutrition of the predator (Abrams 1990). For drift-feeding Arctic grayling, their prey (stream aquatic insects) often have synchronized hatches and emergences that at these times could produce large numbers of prey in the drift. At other times and locations, the density of prey in the drift may be very low (for example, data in Hinterleitner-Anderson et al. 1992 show a 25-fold range of *Baetis* densities). Therefore, grayling may feed at many different prey densities.

In this work, we directly investigated the effect of increasing prey density and stream velocity on the feeding rate of Arctic grayling and on the average time that the fish spent searching (related to the attack rate in the disk equation) and attacking each prey (the overwhelming majority of handling time). We also attempted to estimate the probability that a prey item at a given water velocity and location lateral to a searching fish was located as it passed (location efficiency). We hypothesized that feeding rate would be proportional to prey density at low densities and then level off at high prey densities. We also hypothesized that feeding rate would increase, and location efficiency would decrease, with increasing current velocity.

## Materials and methods

We investigated the drift feeding of Arctic grayling at the Toolik Lake Field Station (TLFS) on the shores of Toolik Lake, Alaska ( $68^{\circ}38'00''$ ,  $149^{\circ}36'15''$ ). Two to four fish were observed each summer from 1995 to 1997 (location efficiency estimation was based on similar experiments in 1992). The fish, 31.5–34.5 cm total length, were obtained from a wild population in the Kuparuk River about 8 km north of Toolik Lake. The Kuparuk has only

large adult fish, with small fish inhabiting its tributaries (Deegan et al. 1997).

The experiments were done in a 500-L experimental stream designed after Vogel (1981). Water was filtered daily so the turbidity was low. The stream was housed in a 4-m-high "polar tent" with a semitranslucent fabric that allowed about 20% full sunlight. Grayling visual acuity (measured by maximum distance at which they respond to prey) is fairly constant above about 1000 lx (Schmidt and O'Brien 1982). Because light level during the trials was above this, they were not believed to be an important factor. The observation portion of the stream is 1.5 m long and 0.61 m wide (with water depth of 0.16 m) with Plexiglas® windows on each side. Water was recirculated (moved from the back to the front of the channel) through a 25-cm-diameter pipe using a propeller driven by an electric motor. A rheostat regulated the speed of the propeller giving stream velocities up to  $65 \text{ cm}\cdot\text{s}^{-1}$ . The front end of the stream is fitted with a diffuser to spread the current across much of the stream width and with flow straighteners to reduce turbulence (see O'Brien and Showalter 1993 for more details).

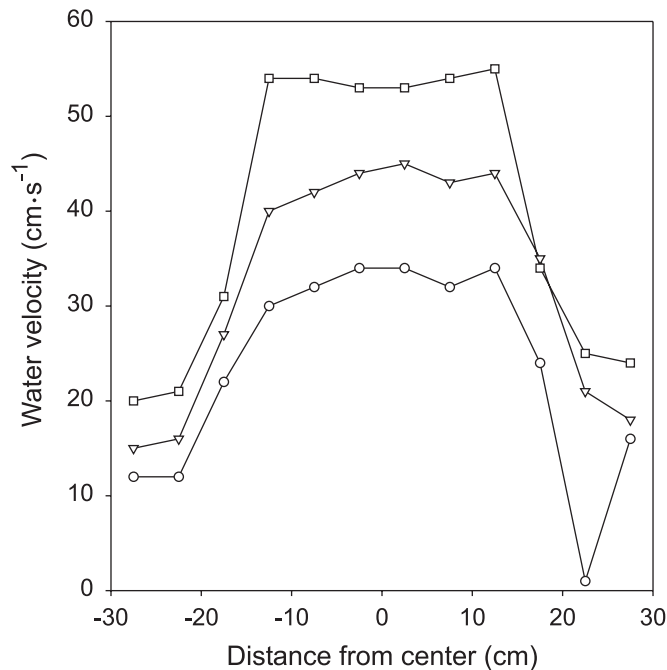
## Feeding rate experiments

A given experiment (run) consisted of feeding a single fish on a constant density of small prey, *Daphnia middendorffiana*, 2.5–3.0 mm long. *Daphnia middendorffiana* were used as prey because they are similar in size to stream-drifting invertebrates, they are nearly uniform in size, and large numbers of them can be easily collected from a nearby pond (pond MS-1, 50 m east of TLFS). The major drift species in the Kuparuk is the mayfly *Baetis*, which varies in length from about 2 to 4 mm (Lee and Hershey 2000). In 1995 and 1996, prey densities used were from 0.01 to  $1.25 \text{ prey}\cdot\text{L}^{-1}$  (a total of 41 runs). Because the feeding rate did not saturate in that range, additional runs were done at high densities ( $0.6$ – $1.8 \text{ prey}\cdot\text{L}^{-1}$ ) in 1997 (24 runs), but only at slow and medium water velocities. In all experiments, the initial prey density was created by slowly adding the appropriate number of prey to the back of the stream behind the fish. The prey were added over a time period calculated to equal the turnover time of the stream at the current velocity being used. The prey density was kept constant by adding a prey item each time the fish ate a prey item. Prey were added at the back of the stream, out of sight of and behind the fish. The experiment was continued until the fish had fed on slightly more than 100 prey. The feeding was videotaped using a Panasonic Palmcorder® PV-IQ204 mounted 1.2 m above the stream. Because prey were not visible on the videotape, an observer (who could see the prey) looking into the side of the stream indicated each attack verbally and kept track of the number of attacks and total time elapsed.

Feeding rates were determined at three different average stream velocities: 25, 32, and  $40 \text{ cm}\cdot\text{s}^{-1}$  (peak velocity about 35, 45, and  $55 \text{ cm}\cdot\text{s}^{-1}$ , respectively). Stream velocity was measured with a Marsh-McBirney current meter (Marsh-McBirney, Inc., Frederick, Md.) at 5-cm increments across the channel (see Fig. 1). Water temperature was maintained at  $12^{\circ}\text{C}$  using an Aquanetics® chiller (Aquanetics Systems, San Diego, Calif.), which automatically warms or cools the water. For data presented here, each fish was used at all prey densities for that year (0.01, 0.05, 0.25, and  $1.25 \text{ L}^{-1}$  for 1995–1996; 0.6, 0.9, and  $1.8 \text{ L}^{-1}$  for 1997).

It was not possible to completely plan the experiment. Grayling are extremely agonistic and subdominant fish will not feed, so they had to be kept separate. Also, fish had to be held for 4–8 days before they were used for feeding trials. Some fish would not feed in the experimental stream, others would feed for a number of runs and then refuse, and others could be used for many runs. Therefore, the data is based on a fairly small number of fish and predominantly those that tended to be the most willing to feed in the experimental stream.

**Fig. 1.** Current velocity across the experimental stream. The average velocities are  $25 \text{ cm}\cdot\text{s}^{-1}$  (circles),  $32 \text{ cm}\cdot\text{s}^{-1}$  (squares), and  $40 \text{ cm}\cdot\text{s}^{-1}$  (triangles).



### Feeding cycle components

The Palmcorder® tapes were analyzed using a Panasonic AG-6300 tape deck with a Panasonic Remote Controller A505. The time and position of the fish at the start and end of each attack was determined, from which search times and pursuit times were determined. Pursuit time is the length of time that it takes the fish to swim to a located prey and attack it. Because the fish apparently immediately searches after an attack, the time from one attack until the start of the next pursuit was considered to be the search time.

### Location efficiency experiments

We also analyzed a series of 13 runs using five stream velocities at a prey density of  $0.01 \text{ L}^{-1}$  performed during 1992 using the procedure described above. We attempted to estimate the location efficiency, which is the probability that a prey item is attacked as it passes a fish searching for prey (we call it location efficiency because we assume that the fish attacks any prey it locates). This location efficiency is assumed to be a function of prey velocity and the lateral distance from the fish to the path of the prey item. Because the prey used cannot be seen on the videotapes, location efficiencies could not be determined by simply dividing the number of prey attacked by the total that pass the fish at a given velocity and position. However, it can be shown that if the prey are randomly distributed, the maximum likelihood estimator of the location efficiency is the number of prey attacked divided by the expected value of the number that pass the fish (at a given velocity and position). Therefore, we assumed that the prey were randomly distributed (because of mixing in the return channel) and traveled at the water velocity in straight lines parallel to the sides of the stream. The prey can swim in still water, but the distance they could travel in the few seconds that it takes to traverse the channel would likely be negligible. Because we measured water velocity in 5-cm increments, we conceptually divided the width of the stream into twelve 5-cm-wide "tracks" across the width of the stream. From the videotapes, we determined the fish location (track) at all times, from which we calculated the expected number of prey pass-

ing the fish for each fish track – prey track combination. This was the product of the prey density, water velocity at the prey's location, track cross-sectional area, and time that the fish was in the given track. We also noted the location of the fish when it began to move toward each prey item (presumably its position when it located the prey item) and the position at which it ate the prey item. This allowed us to determine the actual number of attacks for each fish track – prey track combination. Using the water velocity of each prey track, we were able to estimate the efficiency as a function of lateral distance and water (prey) velocity.

These experiments were done at a very low prey density ( $0.01 \text{ L}^{-1}$ , which is five prey in the entire system) to minimize the chance that the fish would be attacking one prey item as another passed. Because five different rheostat settings were used and there were 12 generally different current velocities across the stream for each, there were a large number of velocity – lateral distance pairs (39 velocities and 12 lateral distances). The expected and observed number of prey items for each was generally less than 10, so the ratio would be very inaccurate. Therefore, to give the efficiencies, the data were lumped into ranges of stream velocity and lateral distance, and then the ratio of the total attacked prey to expected number of prey was determined for each; this gives the best estimate as long as efficiency is constant across each range of velocities and distances. A total of 639 prey items were captured in these runs, the expected number of prey ranging from 9.7 to 253 for the different efficiencies calculated (all expected prey numbers were above 50 except at the most lateral distance).

### Statistical analysis

The feeding rates and attack and pursuit times were analyzed using regression and analysis of variance (ANOVA). The factors affecting these dependent variables were prey density (the covariate in the regressions), water velocity, the individual fish used, and their interactions. The 1996–1997 data spanned a wide range of prey densities ( $0.01$ – $1.25 \text{ L}^{-1}$ ), and each fish was used at each density for at least one of the water velocities. Therefore, these data were first analyzed without the 1997 data. For the regressions, we excluded only terms involving interactions between the fish and water velocity (because we did not have data for each fish at each velocity), allowing us to test for effects of density, velocity, and individual fish and interactions between density and the other two factors. Logarithmic transformations of the dependent variables and prey density gave linear relationships, homogeneous variance, and normal residuals. We then performed the regressions including 1997 data at  $0.6 \text{ prey}\cdot\text{L}^{-1}$  and  $0.9 \text{ prey}\cdot\text{L}^{-1}$ , because these are within the range of densities for 1995–1996. One reason for initially excluding these data is that by their inclusion, the tests of the effect of the individual fish and the fish–density interaction could be influenced by the fact that different densities and a narrow range of densities were used in 1997. Because these terms were not significant using the 1995–1996 data, it should be possible to include the 1997 data (except at the highest density) in the regression of the dependent variables on prey density alone.

For the ANOVAs, because we did not have replicates for each fish at each prey density and water velocity, we excluded any terms involving the individual fish and so tested for the effect of prey density, water velocity, and their interaction. The dependent variables were again logarithmically transformed. ANOVAs used only 1995–1996 data, because one water velocity was absent in the 1997 data.

For the location efficiency data, differences between each pair of water velocities at the same lateral distance were tested. Under the null hypothesis that the efficiencies were the same (equal to the efficiency obtained by combining the data for the two velocities), we calculated the expected number of prey captured for each velocity. Under the assumptions made, the actual number captured



should be a Poisson random variable with this mean, so this distribution was used to test the significance of the difference.

## Results

### Feeding rate experiments

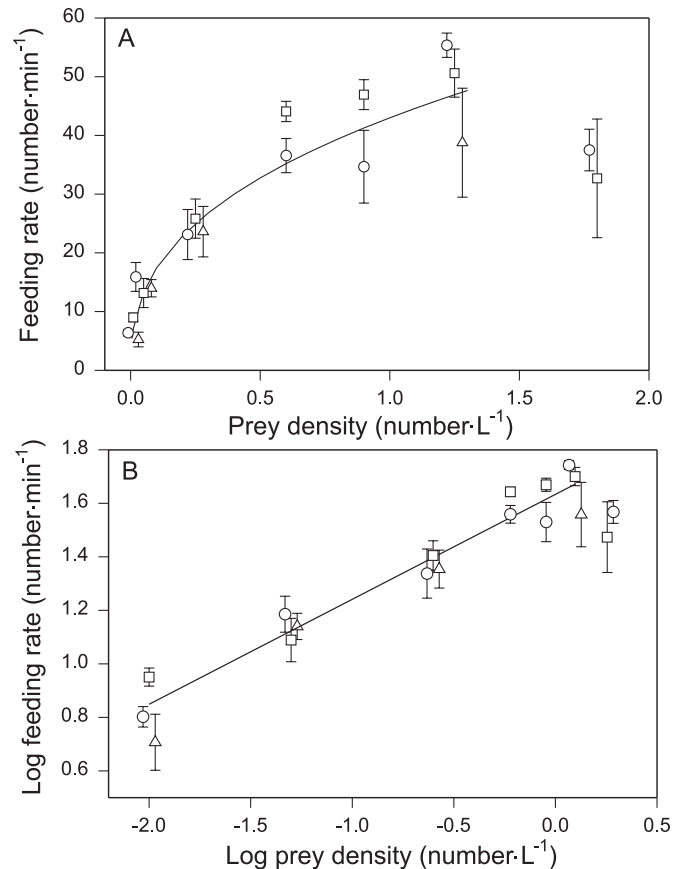
The feeding rates are shown in Fig. 2a. The feeding rate increases with prey density up to  $1.25 \text{ L}^{-1}$  and then falls at  $1.8 \text{ L}^{-1}$ . There is no apparent consistent effect of stream velocity. We first analyzed the 1995–1996 data, which included prey densities of 0.01, 0.05, 0.25, and  $1.25 \text{ L}^{-1}$ , using all data for which we had at least one run at each density for each fish. We performed a regression for the logarithm of the feeding rate, with logarithm of the prey density as a covariate and the individual fish and stream velocity and interactions between each of these and prey density as other factors. (We could not test for fish–velocity interactions because we did not have data for each fish at each velocity.) The prey density was highly significant ( $p < 0.001$ ), but all other factors were not ( $p > 0.4$  in all cases). We also performed an ANOVA with prey density and speed (and their interaction) as factors. Density was again highly significant ( $p < 0.001$ ), whereas speed ( $p = 0.187$ ) and speed–density interaction ( $p = 0.374$ ) were not. We then performed a regression of logarithm of feeding rate on logarithm of density (eliminating the factors not found to be significant) and obtained the relation  $\text{FR} = 41.1p^{0.381}$ . This regression had  $R^2 = 0.82$  and a lack-of-fit  $p = 0.769$ , indicating that the regression fit the data well.

For the 1997 data, prey densities of  $0.6 \text{ L}^{-1}$  and  $0.9 \text{ L}^{-1}$  fell within the range of densities for the above regression. The mean feeding rate at  $0.9 \text{ L}^{-1}$  was almost exactly on the regression line given above, whereas at  $0.6 \text{ L}^{-1}$ , it was a little higher. However, the prey density of  $1.8 \text{ L}^{-1}$  fell outside the range of the previous regressions, and the average feeding rate was well below the regression, indicating the relation above does not hold above  $1.25 \text{ prey} \cdot \text{L}^{-1}$ . We therefore repeated the regressions described above for all data except that at  $1.8 \text{ prey} \cdot \text{L}^{-1}$  and again found that the fish, speed, and their interactions with density were not significant ( $p > 0.15$ ), whereas density was highly significant ( $p < 0.002$ ). The regression using only density gave a relation of  $\text{FR} = 43.0p^{0.392}$  with  $R^2 = 0.84$  and again a good fit (although in this case the residuals are borderline normal, with  $p = 0.056$  on the Anderson–Darling test). A plot of the feeding rate data with logarithmic axes and including the regression line is shown in Fig. 2b (the same regression line is also shown in Fig. 2a).

### Search and pursuit times

The two major components of the feeding cycle of drift-feeding grayling are search and pursuit of located prey. Search time ( $t_s$ ) is dramatically affected by prey density, falling from an average of 7.9 s at the lowest density measured to under 1.3 s for all densities of  $0.6 \text{ prey} \cdot \text{L}^{-1}$  or greater. Regressions and ANOVAs as described for the feeding rate were performed on the logarithms of search and pursuit times. Regression results presented here include all prey densities except  $1.8 \text{ L}^{-1}$ , but the results using 1995–1996 data alone were similar. For search time, none of fish, speed, or the interaction of either with density was significant ( $p > 0.35$ ), whereas the logarithm of density was highly sig-

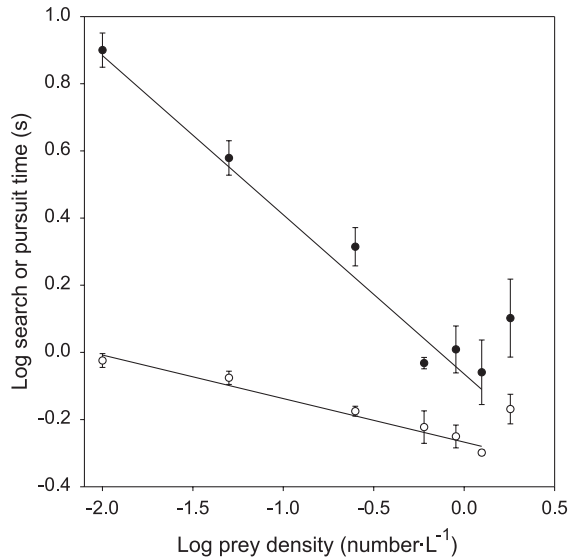
**Fig. 2.** Feeding rate of Arctic grayling as a function of *Daphnia middendorffiana* density for different current velocities. The average water velocities are  $25 \text{ cm} \cdot \text{s}^{-1}$  (circles),  $32 \text{ cm} \cdot \text{s}^{-1}$  (squares), and  $40 \text{ cm} \cdot \text{s}^{-1}$  (triangles). Bars indicate  $\pm$  standard error, with sample sizes generally 3 or 4 (in two cases each, the sample size is 2 or 5). Some of the points have been offset horizontally a small amount for clarity. (a) Linear scales on axes. (b) Base-10 logarithmic scales.



nificant ( $p < 0.001$ ). Only the density was significant for the ANOVA. The regression equation using only the density was  $t_s = 0.863p^{-0.476}$  with  $R^2 = 0.82$ , a goodness-of-fit  $p = 0.52$ , and a regression  $p < 0.001$  (Fig. 3). Therefore, the search time did not drop as the reciprocal of the density (as often assumed, as in the disk equation), but approximately as the reciprocal of the square root of the density. The search time was higher than the regression at a prey density of  $1.8 \text{ L}^{-1}$ .

With pursuit time ( $t_a$ ), the speed–density and fish–density interactions were close to significant ( $0.05 < p < 0.1$ ), whereas speed ( $p = 0.166$ ) and fish ( $p = 0.775$ ) were not. Density was again highly significant ( $p < 0.001$ ). For the ANOVA, water velocity was highly significant ( $p < 0.001$ ), and the water velocity–density interaction was almost significant ( $p = 0.06$ ). On average, slower water velocity led to longer pursuit times. The regression equation using only density was  $t_a = 0.540p^{-0.130}$ , which was highly significant ( $p < 0.001$ ) with  $R^2 = 0.64$  and a goodness-of-fit  $p = 0.68$ . Pursuit time, therefore, decreased slowly with increasing density (except at the highest density, see Fig. 3). Because

**Fig. 3.** Search and attack time of Arctic grayling feeding on different densities of *Daphnia middendorffiana* (both axes are logarithmically transformed). Solid circles represent search times, and open circles represent pursuit times. Bars indicate  $\pm$  standard error, with sample sizes from 6 to 12.



the search time was much higher at most densities, the pursuit times are generally less important.

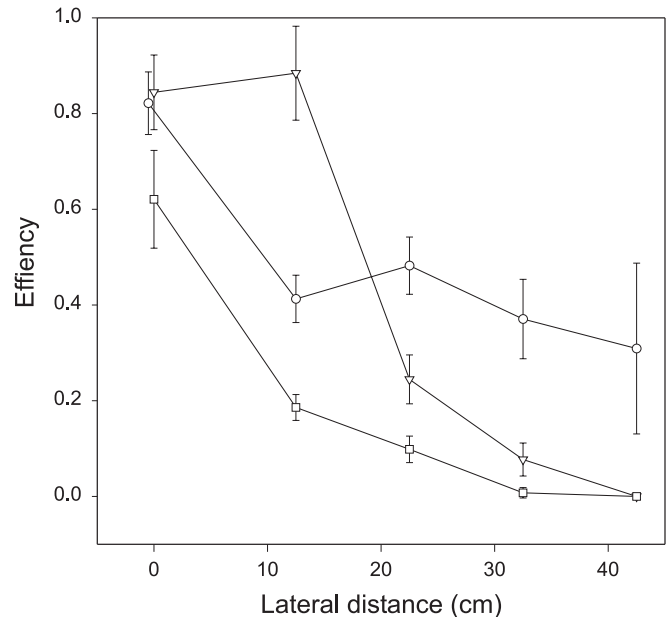
#### Location efficiency experiments

Increased stream velocity reduced the efficiency with which grayling located prey (Fig. 4). There is some irregularity at 12 cm lateral distance from the fish. At all other distances, the efficiencies decline in order of velocity. There is much uncertainty about each value, because it is determined by dividing by the expected number of prey. The actual number can depart significantly from the expected value owing to chance and to a nonrandom distribution of prey. However, we are mostly interested in the apparent fact that the efficiency averaged across the channel decreases with increasing water velocity. This seems quite likely, and the data in this figure support that hypothesis, at least at the highest velocity. Notice that there is not 100% efficiency, even right in front of the fish. Given our assumption of random prey and a constant efficiency across each range of water velocities and lateral distances, the number of prey caught for each point is a Poisson random variable. This distribution was used to construct the error bars shown and to test for differences owing to water velocity at each lateral distance (a cutoff of  $p = 0.05/3$  was used because there were three comparisons each). The three efficiencies at 0 lateral distance did not differ significantly, nor did the medium and fast water results at the two most lateral positions. All other differences were significant under the assumptions given (which may understate the error of each estimate).

#### Discussion

Drift-feeding Arctic grayling show a functional response that is a Type 2 functional response, except for the decrease at the highest density. The feeding rate at the lowest prey density ( $0.01 \text{ L}^{-1}$ ) is about 5–8  $\text{prey}\cdot\text{min}^{-1}$ . The feeding rate

**Fig. 4.** Location efficiency of Arctic grayling feeding on low densities of *Daphnia middendorffiana* at different water velocities. Velocities range from 6 to  $25 \text{ cm}\cdot\text{s}^{-1}$  (circles), 26 to  $45 \text{ cm}\cdot\text{s}^{-1}$  (triangles), and 46 to  $65 \text{ cm}\cdot\text{s}^{-1}$  (squares). Bars indicate  $\pm$  standard error. The low-velocity point at 0 lateral distance has been offset slightly for clarity.



rises at prey densities up to  $1.25 \text{ prey}\cdot\text{L}^{-1}$  and then drops at the highest prey density. The feeding rate is usually expected to approach a plateau at high densities (for example, all of Holling's types), and that is what we expected to find when we ran the 1997 high-density runs. The feeding rates at  $0.6 \text{ prey}\cdot\text{L}^{-1}$  and  $0.9 \text{ prey}\cdot\text{L}^{-1}$  were similar, and that at  $1.25 \text{ prey}\cdot\text{L}^{-1}$  is not a great deal higher, so it is possible that a plateau is reached there. However, a steadily increasing curve (as described by the regressions above) seems to fit the data better. At the highest density, the feeding rate drops. Although it is generally assumed (and often found) that feeding rate plateaus at high density, it is clearly possible that the observed drop in feeding rate at very high density is real. For example, when too many prey are visible at once, the fish may hesitate before attacking; this is consistent with the increase in average search time observed at the highest density.

The feeding rate increase was less than proportional to density even at the lowest densities. A possible reason is that our lowest densities were out of the linear range. Therefore, we plotted the reciprocal of the feeding rate versus the reciprocal of the prey density and the ratio of feeding rate to prey density versus feeding rate (Holling 1959b), both of which are linear for the disk equation of Holling (1959b). Both plots were curved, indicating that the disk equation does not fit the data.

For all but the highest density, the feeding rate is proportional to about the 0.4 power of the density, so that grayling double their feeding rate with an increase of about five times in prey density. A proportional rate of increase is expected if the fish spends most of its time searching and if the average search time is inversely proportional to the density. The

measured search times and pursuit times show that most time is spent in search at low prey densities, but the average search time was not inversely proportional to density. Abrams (1990) shows that departures from proportionality may result from the predator either decreasing the proportion of the time it spends in feeding or increasing its attack threshold as prey density increases. Both these (with certain assumptions) lead to an initial increase in feeding rate as the square root of prey density, not far from our results. There is experimental evidence for a drop in predator effort with increasing prey density. For example, Holling (1966) observed that the maximum distance at which a mantis will react to prey increases with increasing hunger. Similarly, grayling may be willing to attack prey further laterally when prey density is low and concentrate on closer prey at high density. This would certainly make sense in maximizing net energy gain. The average lateral distance of attacked prey does decrease with increasing density but not enough to totally account for the slow increase in functional response. However, it may be that the grayling has a higher attack threshold at higher prey density, which only incidentally affects lateral distance of attacks.

Another interesting aspect of the functional response is the lack of effect of stream velocity. Although increased velocity should cause the fish to encounter more prey, the feeding rate did not significantly change. This cannot be accounted for solely by the reduction in the search window with increasing water velocity that O'Brien and Showalter (1993) reported. They reported a 33% decrease in window width with stream velocity increasing from below 20 cm·s<sup>-1</sup> to almost 60 cm·s<sup>-1</sup>. Further, they predicted that feeding rate would increase with increasing velocity, at least for velocities from 10 cm·s<sup>-1</sup> to 45 cm·s<sup>-1</sup>. Clearly this is incorrect.

One possible explanation for feeding rates not increasing with increasing stream velocity is that the search window width and location efficiency decrease as a function of stream velocity. This could have the effect of keeping grayling feeding rates about constant with changing stream velocities. For the lowest density, multiplying the stream velocity, cross-sectional area, prey density, and average efficiency gives an estimate of the expected feeding rate. These values are 7.7, 9.5, and 6.1 prey·min<sup>-1</sup> for low, medium, and high water velocities, respectively, compared with observed feeding rates of 6.4, 9, and 5.2 prey·min<sup>-1</sup>. At higher prey densities, the effect of stream velocity should be reduced because the grayling spends less time searching and more in pursuit. Even without the drop in efficiency, because the highest stream velocity used was only 60% higher than the lowest and the feeding rate increased only as the 0.4 power of prey density, the effect of stream velocity should not be great (about 20%, because  $1.6^{0.4} \approx 1.2$ ).

Given that the feeding rate does not increase with current velocity, one might expect that grayling in a natural stream would select feeding positions in slow currents where respiratory costs should be lower. Hughes and Dill (1990) found that removing swimming costs from their model made little or no difference to the predictions as to what current velocity the fish might choose. Furthermore, they found that grayling commonly chose feeding positions in water as rapid as 55 cm·s<sup>-1</sup>, although they also chose slower current positions. We also observed grayling feeding in currents as high as

55 cm·s<sup>-1</sup> in the Kuparuk River, and in an experimental stream where two different flow velocities could be created, grayling consistently chose to be in the faster current (O'Brien, personal observation). Hughes (1992a, 1992b) also found that dominant Arctic grayling chose the most rapid current available, whereas subdominant (i.e., smaller fish) settled for feeding sites in slower water. Interestingly, there are no "small" grayling in the Kuparuk River, suggesting that big fish take most, if not all, profitable feeding sites and smaller, subdominant fish cannot grow (Deegan et al. 1997). Consistent with this idea that most if not all profitable feeding sites are taken is the fact that many fish lose weight during years of low flow where there may be fewer profitable feeding sites (Deegan et al. 1999).

Although grayling are adept swimmers and do not have to swim very hard at these high stream velocities, they still expend more energy at high velocities than at low velocities. One possible advantage to being in fast flowing water is that attack distances are very short owing to reduced search window width. This would mean less time and energy spent attacking each prey, possibly resulting in an energy savings and an increase in the percentage of time spent searching. Also, faster currents may be able to carry larger prey.

## Acknowledgments

The work was supported by a series of grants from the National Science Foundation (including DEB-9211775, OPP-9400722, and OPP-9615949). A number of postdoctoral, graduate, and undergraduate students helped in this research, including Nancy Costa, Andrew Dzialowski, Amy Slaymaker, Steve Swaffar, and Kathy Tamberello. Dr. Cynthia Annett helped greatly in the final writing. The staff at the Toolik Lake Research Station provided essential help and an atmosphere conducive to hard work and fun.

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