Does the rate of foraging attempts predict ingestion rate for young-of-the-year brook trout (*Salvelinus fontinalis*) in the field?

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Abstract: To assess the costs and benefits of young fish adopting different behavioural tactics, field studies of juvenile salmonines have assumed that (but did not test whether) the rate of foraging attempts predicts ingestion rate. We tested this assumption by quantifying capture, ingestion, and rejection rates of potential prey items for individual young-of-the-year brook trout (*Salvelinus fontinalis*) in a lake. Overall, capture rate (a conservative estimate of the rate of foraging attempts) was only a fair predictor of overall ingestion rate (Kendall's $\tau = 0.54$) and only 46% of captured items (number/minute) were ingested. Surface capture rate was a poor predictor of surface ingestion rate ($\tau = 0.27$) and only 1% of captured items were ingested. In contrast, subsurface capture rate was an excellent predictor of subsurface ingestion rate ($\tau = 0.75$) and 93% of captured items were ingested. No benthic prey captures were observed. Fish that ingested a low proportion of captured items spent a greater proportion of time moving, moved faster, and pursued prey further than fish that ingested a higher proportion of captured items. Rejection of captured items can represent a significant and little appreciated component of the foraging cycle for young salmonid fishes.

Résumé : Dans leurs tentatives d'évaluer les avantages et les inconvénients des différentes tactiques comportementales adoptées par les jeunes chez le poisson, les études sur le terrain portant sur les jeunes salmonidés ont pris comme hypothèse, sans la tester, que le taux des tentatives pour capturer des proies est un indicateur du taux d'ingestion. Nous avons vérifié cette hypothèse en chiffrant les taux de capture, d'ingestion et de rejet de proies chez des ombles de fontaine de l'année (*Salvelinus fontinalis*) étudiés individuellement dans un lac. Au bilan, le taux de capture (une mesure prudente du taux de tentatives) constitue au mieux une variable prédictive passable du taux global d'ingestion ($\tau = 0{,}54$, Kendall) et en outre, seulement 46% des proies (numéro/minute) sont ingérées. Le taux de capture à la surface de l'eau est un mauvais indicateur du taux d'ingestion des proies capturées à la surface ($\tau = 0{,}27$); seulement 1% des proies capturées à ce niveau sont ingérées. Par contre, le taux de capture sous l'eau constitue un excellent indicateur du taux d'ingestion des proies capturées à ce niveau ($\tau = 0{,}75$); 93% des proies capturées ainsi sont ingérées. Aucune capture de proies benthiques n'a été observée. Les sujets qui ingèrent une faible partie des proies qu'ils capturent consacrent davantage de leur temps pour se déplacer, se déplacent plus rapidement et poursuivent leurs proies plus longtemps que ceux qui ingèrent une grande partie des proies qu'ils capturent. Le rejet de proies peut constituer un facteur important et méconnu du cycle d'alimentation des jeunes salmonidés.
[Traduit par la Rédaction]

Introduction

Theoretical and empirical studies have provided evidence that interindividual variation in foraging behaviour during early life stages of salmonine fishes can have important implications for their population dynamics (Elliott 1989, 1990*a*, 1990*b*; DeAngelis and Rose 1992; Chambers 1993; Van Winkle et al. 1993). The link between individual behaviour and population dynamics was examined, in part, by studies that investigated the costs and benefits experienced by individuals adopting different foraging, social, and antipredator tactics. Such studies commonly quantify foraging attempts to estimate the benefit of adopting one behavioural tactic over another.

Logistical problems associated with observing juvenile salmonines in the field have limited measurement of the various components of the foraging or predation cycle (search, locate, pursue, capture, ingest, or reject). The success of attempts to capture potential food items, usually termed a foraging attempt, was not assessed because of the difficulty of making overhead observations of small fish in shallow water. Consequently, earlier studies quantified the rate of foraging attempts (RFA; items attacked per unit time), a measure that includes foraging attempts that were unsuccessful (e.g., Grant and Noakes 1987*a*, 1987*b*; Nielsen 1992; McLaughlin et al. 1992, 1994). However, several field studies noted that unsuccessful foraging attempts (those ending in rejection of the captured item) can be frequent (Irvine and Northcote 1982; McNicol et al. 1985; Grant and Noakes 1987*a*, 1987*b*, 1988; Grant et al. 1989; Nielsen 1992; McLaughlin et al. 1992, 1994; McLaughlin and Grant 1994). Such studies assumed that the RFA is a good predictor of ingestion rate (items consumed per unit

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time), but this assumption has never been tested. Although it is apparent that the RFA overestimates ingestion rate, it is also possible that the RFA may not predict ingestion rate well.

We previously showed that only half of all potential prey items captured by lake-dwelling, young-of-the-year (YOY) brook trout (*Salvelinus fontinalis*) were successfully ingested (Biro and Ridgway 1995). Movement variables accounted for 12% of the variation in ingestion rates, whereas environmental variables accounted for 51%. Hence, distinguishing between captures ending in ingestion and those ending in rejection enabled an examination of the relative influence of behavioural (foraging activity) and environmental (distance to cover, temperature, etc.) variables on ingestion rates. Previous studies had inferred, on the basis of the RFA, that more active trout ingested more prey per unit time than less active trout in still-water pools (Grant and Noakes 1987*b*, 1988; Grant et al. 1989), but these active fish did not have significantly more prey items in the gut (McLaughlin et al. 1994; McLaughlin and Grant 1994).

Thus far, only laboratory studies have accurately quantified ingestion and rejection rates for juvenile salmonines. Capture and rejection of potential prey were successfully related to a number of factors in the laboratory, including the lack of experience with novel prey (Beukema 1968; Ware 1971; Bryan 1973), satiation (Bryan 1973), age (Godin 1978), relative prey size (Wankowski 1979, 1981; Dunbrack and Dill 1983), exposure to a dominant fish (Huntingford et al. 1993), reduced feeding motivation (Metcalfe et al. 1986, 1988), and the attention paid to capturing prey while under risk of predation (Metcalfe et al. 1987*a*, 1987*b*). However, numerous laboratory studies used foraging attempts as a measure of energy gain, and potentially important information about prey rejection was overlooked. Such studies investigated changes in attack distance with predation risk or with current velocity (Godin and Rangeley 1989; Gotceitas and Godin 1991; Martel and Dill 1993; O'Brien and Showalter 1993), changes in prey reaction fields (Dunbrack and Dill 1984), the benefits of social dominance (Abbott et al. 1985; Gotceitas and Godin 1992; Nielsen 1992), and the influence of predator experience on foraging (Ware 1971).

In this study, we observed the foraging behaviour of YOY brook trout while snorkeling in the shallow littoral zone of a small, clear lake and quantified whether potential prey items captured by trout led to successful ingestion or led to rejection. We assessed (*i*) how well capture rate (a conservative estimate of the RFA) predicts ingestion rate, (*ii*) the degree to which capture rate overestimates ingestion rate, and (*iii*) the relationship between the proportion of captured items ingested and an individual's foraging movements, body size, and aspects of the local environment where individuals were foraging.

Materials and methods

Study site

Fish were observed from 6 to 24 May 1993 in the nearshore littoral zone of Mykiss Lake (45°40′05 N, 78°10′20 W), Algonquin Provincial Park, Ontario, Canada. The small size (surface area = 23.5 ha) and clear water (Secchi depth = 4.8 m) made this lake ideal for detailed snorkeling observations as wave-related turbidity was rare. The study area encompassed an 800-m section of shoreline adjacent to the primary spawning area of brook trout in the lake. Densities of young trout within the study area ranged from 0 to 50 trout in a given 10-m shoreline transect (18 ± 15 trout per 10 m (mean ± SD); unpublished data). We observed young brook trout near and among fallen floating logs and inundated shoreline vegetation (distance from such habitat features = 9 ± 2 cm, $N = 120$) while fish were close to the surface (fish depth measured from the surface = 5 ± 4 cm, $N = 124$). Many were also observed within a few centimetres of floating logs that extended some distance offshore (mean distance from shore = 3.8 m, max. distance = 26 m). We observed fish ranging in size from 23 to 45 mm total length (31 ± 5 mm, $N = 124$), which was representative of the size range present at the study site. Reobserving a fish was unlikely given that observations were spaced over the entire study area.

Behavioural measurements

We observed YOY brook trout while lying motionless at the surface using mask and snorkel. Observations were made between 10:00 and 15:00 on days that were bright and relatively calm. Observations on the feeding and movements of fish were called out through the snorkel to a second person recording data while floating nearby; there was no indication that this method of communication disturbed the fish. Foraging behaviour was quantified using the method described in detail in McLaughlin et al. (1992) and Biro and Ridgway (1995). Briefly, the capture of potential prey and the number of body lengths traveled by the fish were estimated during alternate 5-s intervals for 5–6 min. With this information we calculated feeding rates, average search speed, speed while moving during search, prey pursuit distance, and the proportion of search time spent moving. Values for the movement parameters for each individual were calculated as the average of the 5-s interval estimates. Thus, each value used in the analyses represents the mean of measurements made for a single individual (i.e., sample size = number of individuals observed). Intervals with aggression were recorded but omitted from subsequent analyses because such instances represented less than 2% of the total observation time.

Fish were remarkably insensitive to the observer's presence, which allowed us to slowly approach individual fish to a distance of less than 1 m. A single observer (P.A.B.) was used to eliminate between-observer bias. Prior to commencing observations, the observer lay motionless for several minutes to ensure that the focal fish was not disturbed and was foraging freely. Close proximity of the observations and the magnifying effect of the mask underwater made it possible to distinguish the outcome of captures of potential prey, i.e., to distinguish captures ending in ingestion (retention of an item after its capture) from those ending in rejection (ejection of an item from the mouth after capture). A capture is hereafter defined as the closing of the jaws on or around a potential food item. We also recorded whether the capture was from the surface or subsurface. No fish captured items from the benthos. Items ingested were swallowed following minimal manipulation in the mouth and were difficult to identify except when quite large (e.g., Ephemeroptera nymphs). Conversely, fish rejected items immediately after capture in many cases or after several seconds in fewer cases and these were frequently identified as debris that littered the surface or to a lesser extent were suspended in the water column. See Wankowski (1979) for a detailed description of the sequence of movements involved in the capture, ingestion, and rejection of prey items.

Our definition of capture differs from that of a foraging attempt normally encountered in the literature, which in addition to captures, includes movements to inspect potential prey items and missed attacks (e.g., Grant and Noakes 1987*a*, 1987*b*, 1988; Grant et al. 1989; Grant 1990; Nielsen 1992; Keeley and Grant 1995). We did not record attempts failing to end in capture because we were limited in the amount of information that could be communicated using our methods and also because such attempts were infrequent relative to the frequency of captures. Thus, the capture rate (= ingestion rate + rejection rate) examined here is a conservative estimate of the rate of foraging attempts in comparison with other published studies.

Table 1. Correlation coefficients between total capture rate and total ingestion rate, surface capture rate and surface ingestion rate, and subsurface capture rate and subsurface ingestion rate.

Predictor of ingestion rate	τ	Y	α	β	*N*
Total capture rate	0.540	0.77	0.093	0.462	117
	(0.499–0.632)	(0.72–0.82)	(0.00–0.209)	(0.365–0.571)	
Surface capture rate	0.266	0.63	0.000	0.010	88
	(0.148–0.385)	(0.57–0.69)	(0.000–0.000)	(0.000–0.102)	
Subsurface capture rate	0.747	0.87	0.000	0.929	103
	(0.672–0.822)	(0.84–0.91)	(0.000–0.000)	(0.803–1.000)	

Note: Variables are Kendall's tau (τ) coefficient and associated Y value (see Materials and methods), and distribution-free estimates of the intercept (α) and slope (β). The 95% confidence intervals for each estimate are in parentheses.

Environmental measurements and body size

Following the observation period, the fish were captured with an aquarium dip net, their total length was measured to the nearest millimetre, and then they were released. The position of sedentary fish or the most frequently occupied position of active fish during the observation period was noted in relation to background features. Habitat measurements made from that position included (*i*) location of the fish in the water column relative to the surface (i.e., fish depth), (*ii*) water depth, (*iii*) distance of the fish from the nearest submerged or floating cover object (e.g., logs, inundated shoreline vegetation, boulders, shoreline), (*iv*) distance between the focal fish and the shore, and (*v*) percent overhead riparian cover (see Biro and Ridgway 1995 for details of our method). Near-surface water temperatures were recorded with an automatic temperature recorder (Tempmentor, Ryan Instruments Inc., U.S.A.) fixed on a floating log 10 m from shore and 20 cm below the water surface. The temperature reported for each individual was calculated as the mean temperature recorded between 10:00 and 15:00 each day.

Statistical analyses

The prediction of ingestion rate from capture rate presented some statistical problems not commonly encountered. First, the assumption of normality is violated. Second, ingestion and capture rate are not independent of one another and hence there is a built-in or "part–whole" correlation (Sokal and Rohlf 1981). Therefore, it is inappropriate to assume a null hypothesis of no association between ingestion rate and capture rate. In light of these problems, we used Kendall's tau (τ) statistic to evaluate the degree to which capture rate predicts ingestion rate because distribution-free confidence intervals can be obtained for the statistic (τ), slope (β), and intercept (α) that are not strongly affected by the part–whole correlation (W. Matthes-Sears, University of Guelph, Guelph, Ont., personal communication). In addition, the probability (Y) that an individual *i* has a greater ingestion rate than individual *j*, given that individual *i* exhibited a higher capture rate than individual *j*, can be calculated from τ (Hollander and Wolfe 1973). A value of Y = 0.5 indicates independence of ingestion and capture rates, while Y = 1 indicates that higher ingestion rates are associated with higher capture rates for all combinations of paired individuals *i* and *j*.

Parametric partial correlation coefficients were used to relate measures of individual foraging success (proportion of captured items ingested) to behavioural and environmental variables. Water depth was excluded from analyses because it was highly correlated with several variables and was uninformative. For example, fish were observed very near the surface irrespective of the wide variation in the distance from shore (mean = 3.8 m, range = 0.02–26 m) and depth (mean = 0.91 m, range 0.04–4.5 m). Several variables were transformed prior to analysis to meet the assumption of normality. Speed while moving and foraging rates were square-root transformed. Proportion of time spent moving and foraging rates expressed as a proportion were arcsine square-root transformed. Pursuit distance, habitat variables, and body size were $\log_{10}$ transformed.

Results

Capture rate as a predictor of ingestion rate

Total capture rate

The total, or overall, capture rate was only a fair predictor of the total ingestion rate (Fig. 1A; Table 1). The probability that individuals with a higher total capture rate also had a higher total ingestion rate was 0.77 (Table 1). The slope of 0.46 was moderately low (Table 1), indicating that on average only 46% of all captured items resulted in ingestion.

Surface capture rate

On average, individuals captured 54% of items from the surface ($SD = 0.35$, range 0–100%, $N = 117$). Surface capture rate was a very poor predictor of surface ingestion rate (Fig. 1B; Table 1). The probability that individuals with higher surface capture rates also had higher surface ingestion rates (0.63) was not much greater than the 0.50 expected when ingestion and capture rates are independent (Table 1). Only 1% of all items captured at the surface were actually ingested (Table 1).

Subsurface capture rate

The subsurface capture rate was an excellent predictor of subsurface ingestion rate (Fig. 1C; Table 1). The probability that individuals with higher subsurface capture rates also had higher surface ingestion rates was 0.87 (Table 1). Ninety-three percent of items captured from the water column were ingested (Table 1).

Foraging success

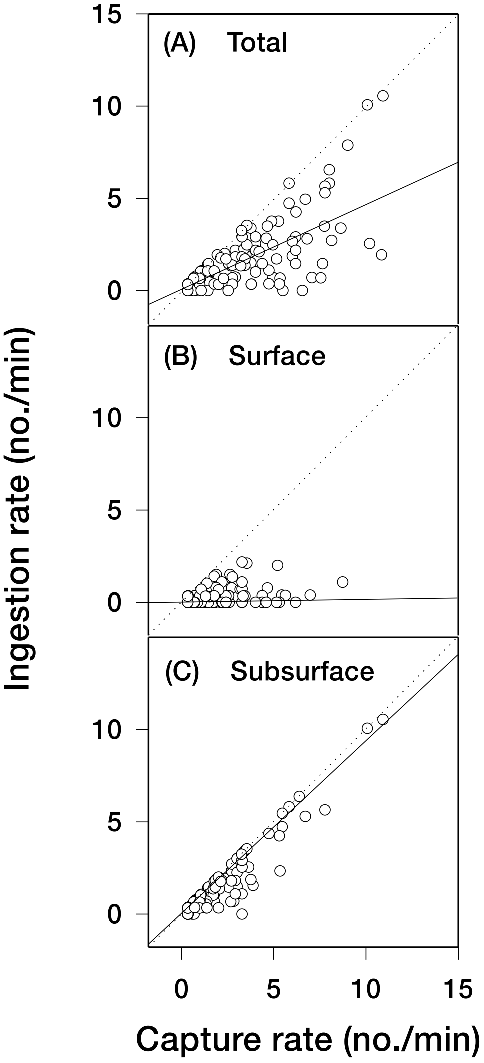
Total foraging success

Individuals varied substantially in their overall foraging success and tended to ingest either a very low proportion or a very high proportion of captured items (Fig. 2A). Individuals with low foraging success spent a greater proportion of time moving, moved faster, and pursued prey farther than fish with high foraging success (Table 2). Fish with low total foraging success captured more items from the surface than beneath the surface (total foraging success vs. proportion of captures from surface; $r = -0.63$, $P < 0.001$, $N = 117$). Individuals with high total foraging success were also located farther from shore, away from riparian canopy, and closer to submerged cover objects than fish with low foraging success (Table 2).

Surface foraging success

Surface foraging success was highly skewed right with 43%

Fig. 1. (A) Total ingestion rate versus total capture rate. (B) Surface ingestion rate versus surface capture rate. (C) Subsurface ingestion rate versus subsurface capture rate. Solid lines represent regressions calculated using parameters in Table 1. Broken lines (1:1) represent the relationship expected in the absence of rejection.



(38/88) of individuals ingesting less than 5% of the items they captured and few individuals ingesting more than 50% of the items they captured (Fig. 2B). Surface foraging success did not vary with foraging activity (Table 2). Fish with high surface foraging success were larger and closer to shore than those with low success (Table 2). Individual surface foraging success was not correlated with the proportion of items captured at the surface ($r = 0.014$, $P > 0.05$, $N = 88$).

Subsurface foraging success

Subsurface foraging success was highly skewed left with 43% (44/103) of individuals ingesting more than 95% of captured items, while only a few fish ingested less than 50% (Fig. 2C). Fish with high subsurface foraging success spent less time moving and did not pursue prey as far as those with low foraging success (Table 2). Fish with high subsurface foraging success were observed earlier in May, in areas with less overhead canopy, and closer to submerged objects than those with low success (Table 2). Unlike individual surface foraging success, subsurface foraging success increased with the proportion of items captured from the water column, although this correlation was relatively weak ($r = 0.28$, $P < 0.005$, $N = 103$).

Table 2. Partial correlation coefficients relating total, surface, and subsurface foraging success (proportion of captured items ingested) with measures of foraging movements, body size, and environmental variation.

Source of variation	Total success	Surface success	Subsurface success
Proportion of time spent moving	−0.32*	−0.11	−0.25*
Speed while moving	−0.22*	−0.08	−0.16
Pursuit distance	−0.42**	0.03	−0.28*
Total length	0.09	0.34*	0.10
Date	−0.18	0.05	−0.23*
Water temperature	−0.07	−0.04	−0.13
Overhead riparian cover	−0.29*	0.12	−0.20*
Distance from submerged cover	−0.38**	−0.13	−0.24*
Distance from shore	0.24*	−0.26*	0.07
Depth of fish in water column	0.14	0.13	0.02
N	108	81	98
R^2	0.39	0.23	0.27

*$P < 0.05$

**$P < 0.001$

Individual surface and subsurface foraging success

Individuals with high subsurface foraging success tended to have relatively high surface foraging success, although this correlation was weak ($r = 0.29$, $P = 0.012$, $N = 74$; Fig. 3). Further, few individuals had surface foraging success that was higher than or nearly equal to their subsurface foraging success (Fig. 3).

Discussion

Almost half of all items (number/minute) captured by YOY brook trout were subsequently rejected, given that 54 and 46% of all captured items were from the surface and water column, respectively. The degree to which capture rate overestimated ingestion rate differed greatly with the location in the water column where individuals captured prey. Overestimation, and therefore rejection rate, was extremely high for surface foraging but much lower for subsurface foraging; fish ingested only 1% of the items captured from the surface but ingested 93% of the items captured from the water column. Capture rate was at best a fair predictor of overall ingestion rate. The degree to which capture rate predicted ingestion rate also varied with the location in the water column where fish captured potential prey. Surface capture rate was a very poor predictor of surface ingestion rates, whereas subsurface capture rate was an excellent predictor of subsurface ingestion rate.

Rejection was clearly an important component of the foraging cycle for YOY trout in the lake environment. Rejection of captured items affected the utility of capture rate as a predictor and estimate of ingestion rate and the relative frequency of rejection was related to foraging activity, whereby actively foraging individuals experienced lower overall foraging success than sedentary individuals. Given these results, it may be incorrect to conclude that a given behavioural tactic associated

Fig. 2. Frequency distributions of individual foraging success. (A) Total foraging success. (B) Surface foraging success. (C) Subsurface foraging success. Arrows indicate the mean foraging success.

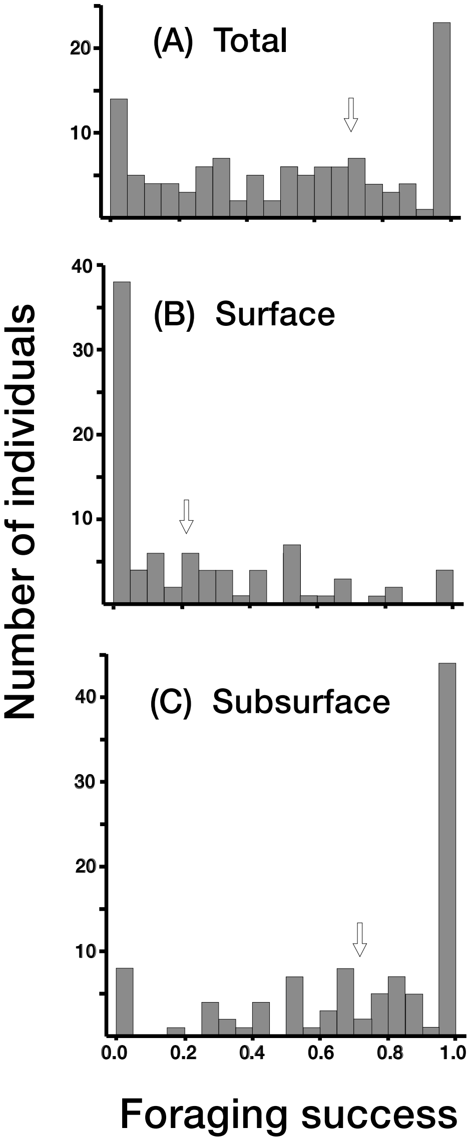
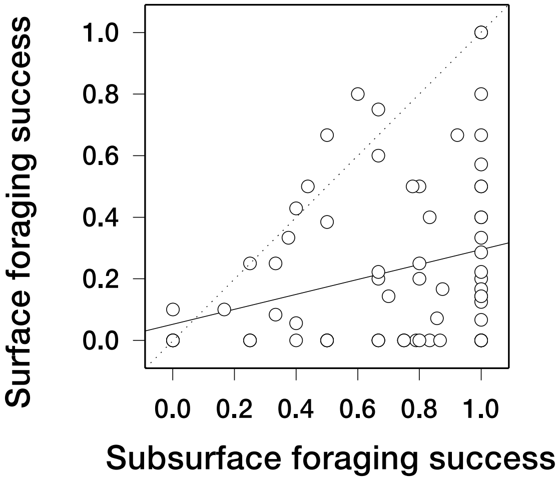


Fig. 3. Surface foraging success (SFS) versus subsurface foraging success (SSFS). The solid line represents the least-squares regression line (SFS = 0.053 + 0.243SSFS). The 1:1 line (broken) is provided for reference.



with high rates of foraging attempts necessarily has a greater energy intake rate than another tactic associated with a lower rate of foraging attempts, particularly when surface foraging is relatively frequent.

Rejection of captured items was also frequently observed in still-water side pools in streams (McLaughlin et al. 1994). In those pools, YOY brook trout that spent more time moving tended to forage relatively more from the surface and had higher rates of foraging attempts than fish that spent less time moving, suggesting a benefit for active compared with sedentary foraging individuals. However, the number of prey items in the gut did not vary significantly with activity (McLaughlin et al. 1994). Hence, the disparity between foraging rate and number of prey items in the diet may reflect high rejection rates for surface foraging.

Rejection was also frequently observed for fish in running water, especially for items captured from the surface (e.g., Williams 1981; McNicol et al. 1985; Stradmeyer and Thorpe 1987; McLaughlin and Grant 1994). Given that the rate of delivery of both invertebrate drift and debris increases with current (e.g., Grant and Noakes 1989; O'Brien and Showalter 1993), then rejection rate may also increase with current velocity and therefore the benefits of feeding in faster water may not be as great as foraging attempts would suggest (e.g., Grant and Noakes 1988; McLaughlin and Grant 1994). Although ingestion rate is a more reliable estimate of energy intake than foraging attempts, the energetic content of ingested items may vary and influence the reliability of that estimate. For instance, surface prey items tend to be larger than subsurface prey (McLaughlin et al. 1994) and presumably more profitable. If so, surface and subsurface ingestion rates would not be equivalent in terms of what we want them to estimate. In a particularly thorough field study, Nielsen (1992) investigated the benefits that juvenile coho salmon (*Oncorhynchus kisutch*) in dominance hierarchies in fast water had over floaters in slow water and found that there were no differences in the rate of foraging attempts among these behavioural tactics. However, the energetic content of the prey items ingested revealed that dominant fish had higher daily rations than subdominants and floaters, which accounted for their higher growth rates. Such an approach may be most informative, but it is impractical for very small fish that must be killed to sample stomach contents.

Incorporating realistic feeding conditions in a laboratory setting, such as spatial complexity in the environment, availability of several prey types, and natural debris, would greatly increase our understanding of prey discrimination by juvenile salmonids. It would improve the realism of models of reaction volumes and prey selection by drift-feeding juvenile salmonines (e.g., Dunbrack and Dill 1983, 1984; Grant and Noakes 1986), which are incorporated into more elaborate models of foraging and microhabitat choice (Hughes and Dill 1990; Hughes 1992*a*, 1992*b*). For example, O'Brien and Showalter (1993) incorporated natural stream debris into stream channels and found that adult grayling (*Thymallus arcticus*) reduced their attack distances and prey reaction distances when debris was common but they made no mention of fish rejecting prey or debris items; perhaps the greater visual acuity of adult fish allows better discrimination of prey from nonprey.

It is known that YOY brook trout in Mykiss Lake tend to spend either a very high or a very low proportion of time moving (Biro and Ridgway 1995). Given this observation and the relationship between total foraging success and time spent moving, two general foraging tactics may exist: active fish may feed on surface items with high capture rates but low foraging success and sedentary fish may feed on subsurface items with low capture rates but high foraging success. This may reflect a sampling behaviour for fish attempting to locate profitable feeding sites, or perhaps a few profitable prey that are ingested offset activity costs for the active fish with low foraging success. Wankowski and Thorpe (1979), for example, found that Atlantic salmon (*Salmo salar)* alevins grew fastest on large, compared with small, pellets even though the probability of fish rejecting a large pellet was 90%.

We did not observe YOY brook trout ingesting inedible debris items nor did we find nonprey items in a small number of fish stomachs examined ($N = 30$), leading us to conclude that the young trout often capture and reject inedible debris. Rejected items frequently included clumps of floating pollen, empty nymph cases, and tiny pieces of wood or vegetation, as reported in previous studies (Williams 1981; Stradmeyer and Thorpe 1987). The most eagerly pursued, and subsequently rejected, items on the surface were those that appeared translucent, such as empty nymph cases or insect wings. At times, the same individual captured and rejected the same debris item several times during an observation period.

We found that within individuals, subsurface foraging success was consistently higher than, and weakly correlated with, surface foraging success. This suggests that differences in the prey types captured, or the greater abundance of debris (relative to edible food) at the surface compared with that suspended in the water column, may account for the differences in within-individual foraging success. For example, surface rejection rates were lower for fish that were further from shore (partial $r = -0.21$, $P < 0.05$), which is consistent with our observations that debris tended to accumulate near shore among woody debris and shoreline vegetation.

Numerous studies have used the rate of foraging attempts as an estimate of ingestion rate to make inferences about the benefits of behavioural tactics adopted by individuals. We have demonstrated that our conservative estimate of the rate of foraging attempts may be an unreliable predictor of, and dramatically overestimate, ingestion rate, whereby prediction decreases and overestimation increases with the relative frequency of surface feeding. Patterns of rejection rates relative to ingestion rates may provide clues as to the basis of this behaviour, such as simple visual limitations or perhaps different sampling tactics. Finally, prey rejection is a neglected but potentially important component of the foraging cycle of young fish in the field that deserves further investigation.

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