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Morphological and behavioural differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow- vs. fast-running water

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Synopsis

Morphology and resource use were compared among recently-emerged brook charr, *Salvelinus fontinalis*, sampled from field locations differing in current speed. Individuals from faster running water were slightly longer, and had more fusiform body shapes and larger caudal fin heights, than individuals from slower running water. In addition, individuals from faster running water also directed more foraging attempts toward the middle of the water column and fewer toward the benthos and water surface. They also ate more dipteran larvae, fewer aquatic crustaceans, and fewer insect pupae and adults. Individuals located in the slowest and fastest current speeds made fewer foraging attempts per min, on average, than individuals located in current speeds of intermediate magnitude. Dry weight of stomach contents did not vary significantly with current speed, however. The form of the relationship between body shape and current speed suggests that it is adaptive. Small-scale variation in the location of foraging sites may account for some of the individual variability in resource use often reported for stream salmonids. Variation in the locations of foraging sites may also entail a trade-off between an individual's swimming effort and the quality of prey it consumes.

Introduction

Studies comparing individuals varying in morphology, physiology, or behaviour can be valuable in a variety of contexts including (i) evaluating the role that individual variation plays in the mechanisms regulating population sizes (DeAngelis et al. 1991), and (ii) establishing functional links between morphology or physiology and other aspects of an individual's ecology (e.g. habitat use, diet) (Ehlinger 1990, Wainwright 1991).

Salmonids can display substantial individual variation in morphology, life-history, and behaviour. Such variation is possibly most spectacular in the reproductive biology of males where, in populations of many species, some males mature at an early age, are small, and attempt to sneak matings with females, while other males mature later, are large, and fight with other males for access to females (Gross 1985, Hutchings & Myers 1988). Variation in morphology and age at maturity also occurs in females (Thorpe 1989). Individual differences in foraging morphology and behaviour are known as well, as exemplified by the four feeding morphs of arctic charr, *Salvelinus alpinus*, found in Lake Thingvallavatn, Iceland (Skúlason et al. 1989). While such examples are remarkable and important to study, important but less conspicuous variation undoubtedly occurs within many other populations (e.g. Taylor & McPhail 1985a).

Previous studies of salmonids reported that fish from populations facing arduous hydrodynamic conditions had more fusiform body shapes than fish from populations facing less arduous hydrodynamic conditions. In some cases the variation has been observed among populations from rearing habitats differing in current speed (e.g. Riddell & Leggett 1981, Swain & Holtby 1989). In others it has been observed among populations differing in the migration distance between their rearing streams and the sea (e.g. Taylor & McPhail 1985b,c, Fleming & Gross 1989). Such patterns are believed to reflect strong selection pressure for sustained swimming ability in the populations experiencing the faster currents or longer migration distances. The differences in morphology can also be associated with differences in social and foraging behaviour (e.g. Swain & Holtby 1989).

If the patterns among populations reflect a functional relationship between morphology and sustained swimming ability, then it is reasonable to expect that similar patterns between morphology and current speed along with corresponding differences in behaviour may also occur among individuals from the same population (Bennett 1987). Recently-emerged brook charr, *Salvelinus fontinalis,* display broad variation in the current speeds where individuals forage, and fish foraging in running water are more sedentary (relative to the stream bottom) and more aggressive than those foraging in still water (Grant & Noakes 1988). In this study, we examine the morphology, the use of the water column, and the types and amounts of prey consumed by charr foraging at locations differing in current speed. Variation in the mensural characters influencing swimming ability could be important at this state of development because recently-emerged salmonids often face current speeds that are strong relative to the fish's sustained swimming ability (Heggenes & Traaen 1988). Moreover, variation in current speed is expected to influence a fish's rate of encounter with prey, its swimming costs, and therefore its net rate of energy gain and growth rate (Fausch 1984, Grant & Noakes 1987a, 1988, Godin & Rangeley 1989, Hughes & Dill 1990, Simonson & Swenson 1990).

Methods

Study sites and data collection

Our study was conducted at three sites located on the Credit River drainage system near Guelph, Ontario, Canada (43°33′, 80°15′). A more detailed description of the sites is given in McLaughlin et al. (1992), and a description of the drainage system and fish species at these sites or locations nearby is provided by Cunjak (1988). The charr are permanent residents in these streams, and the streams have not been stocked in 20 years (Ontario Ministry of Natural Resources, personal communication).

The recently-emerged fish we observed and collected were all free swimming and attempting to capture prey. Behavioural observations were made between 09:00 and 17:00 h from 1 April to 3 May 1988. Foraging behaviour was quantified using the interval method described in McLaughlin et al. (1992). An observer arrived at an observation site and waited 5 min for fish to recommence their activity, and 5 min more to ensure that they were feeding normally. A focal individual was selected and its fork length was estimated visually to the nearest 0.25 cm. Waiting 10 min before selecting a focal fish should have minimized any bias toward 'bold' or 'hungry' fish since, on average, charr this size return to an area within 2 min after being disturbed by an observer (Grant & Noakes 1987b). Also, for a sample of fish captured after observation the estimated fork lengths were not significantly different from measured lengths (paired $t = 0.57$, $p > 0.50$, $N = 90$, median absolute difference = 0.1 cm).

After selecting a focal fish, the number of body lengths traversed (relative to the stream bottom) was estimated to the nearest length over 5 sec intervals and recorded on microcassette tape. We also identified whether the movement during an interval was associated with search for prey, pursuit of prey, aggression, or flight (see McLaughlin et al. 1992). Vertical location in the water column to where each pursuit was directed was categorized as surface, midwater, or benthic. Observation periods lasted 4.2 to 17.1 min (median = 6.5). Afterward we attempted to capture the focal individual using aquarium dip nets, and then returned to measure water temperature and current speed in the area where the individual was observed. Current speed was measured with a Pigmy Teledyne-Gurley current meter rated for currents down to 1 $cm \cdot s^{-1}$. Current speeds below this were evaluated by releasing silt particles into the water column. Current speed was estimated as 0 $cm \cdot s^{-1}$ if the particles fell straight down and 1 $cm \cdot s^{-1}$ otherwise. Since the fish were swimming in the water column it was possible to estimate current speed at the position where an individual was holding station. For fish that moved relative to the stream bottom, current speed was estimated as the average of several measurements taken in the area traversed by the fish.

Our behavioural observations provided measures of the proportion of search time spent moving and the proportions of benthic, midwater, and surface foraging attempts. The proportion of search time spent moving was estimated as the proportion of intervals involving search where the focal fish moved one body length or more.

We videotaped fish swimming in still-water pools on five occasions in 1988 to obtain estimates of the swimming speeds used during periods of movement. The videocamera was mounted on a tripod at the edge of the stream and fish within a field of view approximately 1 m^2 were recorded for 49 to 86 min. At the end of each session we videotaped a ruler placed in horizontal and vertical directions within the field of view to provide a scale for measurement. Nine to 15 measurements of swimming speed during periods of movement lasting 10 to 43 s in duration were made from each tape.

Data on morphology and stomach contents were obtained from fish collected between 1 April and 3 May 1988, and 13 and 25 April 1989. Fish were collected in both years to increase sample size and hence statistical power (Arnold & Bennett 1988). Fish collected in 1988 were captured at the end of an observation period (see above) as were those collected in still water during 1989. To collect fish from current in 1989, we used the same protocol described above, but did not collect behavioural data.

Captured fish were preserved in 10% formalin and later transferred to 37.5% isopropyl alcohol. For each fish we measured 23 morphometric characters (see Appendix 1). Fifteen fish were later remeasured to evaluate the repeatability of the measurements (Appendix 1). Prey items found in the oesophagus and stomach of each fish were identified to order, counted, and their lengths measured. Dry weights of prey items were estimated from prey length using published equations (Rogers et al. 1977, Smock 1980, McCauley 1984).

Statistical analysis

The relationship between current speed and morphology was examined using multiple regression analysis. Values for each variable were standardized to mean zero within each site-year cohort prior to analysis to minimize any potential confounding effects due to differences among site-year cohorts (see Strauss 1990). Analysis of the unadjusted values provided results very similar to those presented here indicating that site and year differences were negligible (unpublished data). The regression analysis presented here relates the current speed at a fish's foraging location to the fish's standard length, the maximum height of its caudal fin, the maximum depth of its body, and the depth of its caudal peduncle. This regression provided the highest R^2 of all possible regressions considering four mensural characters, and considering any other character in addition to these four did not provide any significant increase in R^2.

Diet was related to current speed using a multiple logistic regression (Hosmer & Lemeshow 1989). Stomach contents were divided into three prey categories: copepods and ostracods (benthic prey), Diptera larvae (midwater prey), and insect pupae and adults (surface prey). The logistic regression examined the log-odds ratios of copepods and ostracods vs. Diptera larvae, and insect pupae and adults vs. Diptera larvae, in relation to current speed, standard length, and sampling date. Standardized partial regression coefficients are presented to indicate the sign and relative magnitude of the relationships examined.

Prior to analysis, several variables were transformed to normalize their distributions as closely as possible. The morphological variables, current speed, prey length, and the dry weight of stomach contents were $\log_{10}$ transformed. The number of foraging attempts made per min and the number of prey items in the oesophagus and stomach were square-root transformed.

The distribution of current speeds remained skewed even after $\log_{10}$ transformation. This occurred because we sampled still-water habitats more heavily than running-water habitats because of the broad behavioural variation that occurs in the former (Grant & Noakes 1988, McLaughlin et al. 1992). Rather than categorizing foraging locations as still vs. running water, which would obscure the variation in current speed within running-water habitats, we verified the probabilities from our regressions using randomization tests (see Manley 1991: Chapter 6). The randomization probabilities are based on the observed data and 4999 random permutations of the data. Randomization was not conducted for the logistic regressions since this type of analysis does not require the variables to be distributed normally (Press & Wilson 1978).

Results

Swimming behaviour and morphology vs. current speed

In still water, swimming behaviour was unsteady and slow. None of the fish spent 100% of their time moving and half (48/96) spent less than 54% of their time moving (Fig. 1). Based on measurements from videotape, fish in these habitats swam at speeds of 2.4 $\text{cm}\cdot\text{s}^{-1}$ on average when they did move (95% confidence limits: 2.2–2.6 $\text{cm}\cdot\text{s}^{-1}$, N = 55 measurements). In current, on the other hand, swimming was steady and fast. Individuals spent less time moving relative to the stream bottom as they held station in the water column by swimming steadily against currents as high as 13 $\text{cm}\cdot\text{s}^{-1}$ (Fig. 1). The search movements observed for fish in current usually involved individuals returning to their station after attempting to capture a prey item, or slight changes in the location of their station. Only 1 of the 145 individuals we observed foraged in both still- (0 $\text{cm}\cdot\text{s}^{-1}$) and fast-running (3.5 $\text{cm}\cdot\text{s}^{-1}$) water. One other individual moved between locations where current speed ranged from 0 and 1 $\text{cm}\cdot\text{s}^{-1}$.

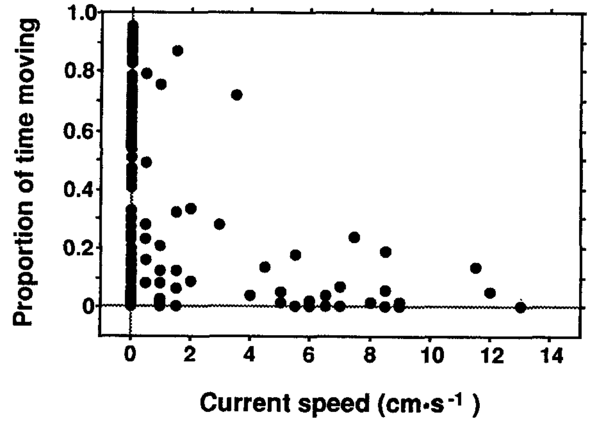

Fig. 1. The proportion of search time spent moving relative to the stream bottom by recently-emerged brook charr sampled from locations differing in current speed. N = 145 individuals.

Despite a narrow range of fish lengths (16.1 and 27.3 mm standard length), individuals in faster current were larger, on average, than those in slower current (standard length vs. current speed: $r = 0.28$, $p < 0.001$, N = 137 individuals). The current speed where individuals were located was also related significantly to the maximum height of the caudal fin, the maximum depth of the body, and the depth of the caudal peduncle. Overall these mensural characters accounted for 21% of the variation in the current speed where individuals were observed foraging, and the latter three accounted for 13% more of the variation than just standard length alone (overall $F = 8.77$, $p < 0.0001$, df = 4, 132). After adjusting for the other morphological variables, individuals in faster current had larger caudal fin heights than those in slower currents (Fig. 2a). Moreover, the simple correlation between caudal fin height and current speed ($r = 0.33$, $p < 0.0001$) was slightly larger than that found between standard length and current speed (see above). After adjusting for other morphological variables, fish in faster currents also had smaller maximum body depths and smaller caudal peduncle depths (Fig. 2b, c). Absolute differences expected for fish in 0 and 10 $\text{cm}\cdot\text{s}^{-1}$ currents are summarized in Table 1.

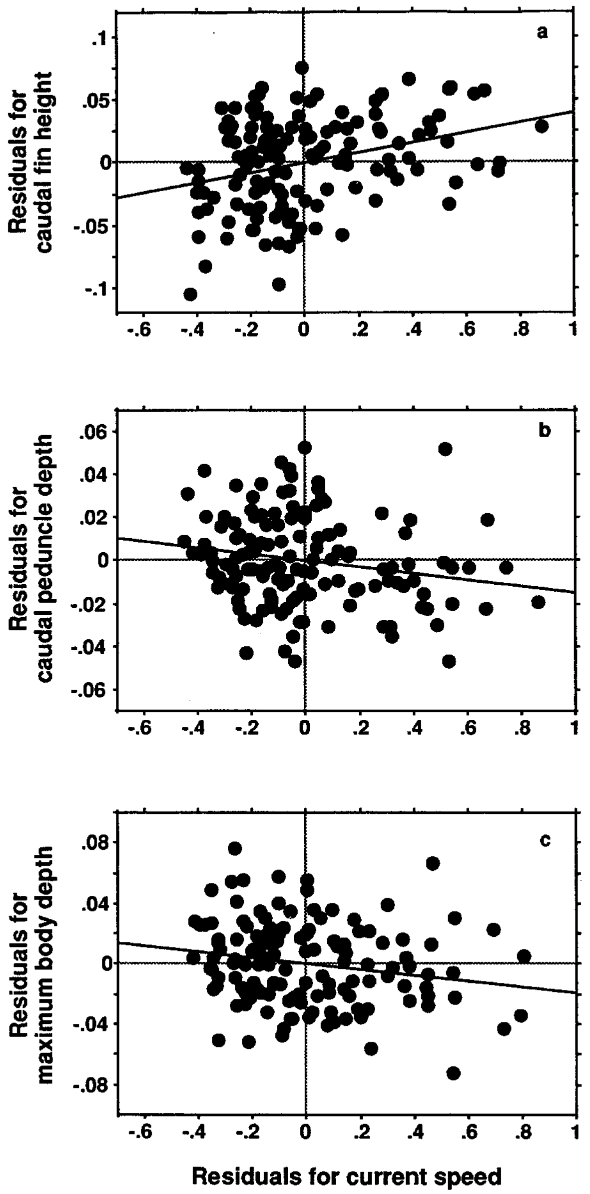

Fig. 2. Leverage plots from a multiple regression relating the current speed where individual brook charr were located to their standard length, maximum caudal fin height, caudal peduncle depth, and maximum body depth. a – Maximum caudal fin height vs. current speed; partial r = 0.31, $p < 0.001$. b – Caudal peduncle depth vs. current speed; partial r = 0.19, $p < 0.05$. c – Maximum body depth vs. current speed, partial r = 0.20, $p < 0.05$. N = 137 individuals.

Table 1. Predicted sizes of maximum caudal fin height, maximum body depth, and caudal peduncle depth for an individual brook charr of mean standard length (18.60 mm) in currents of 0 vs. 10 cm·s^{-1}. Values in parentheses represent lower and upper 95% confidence limits of the sizes predicted for each attribute.

Current speed	Morphometric character		
	Maximum caudal fin height (mm)	Maximum body depth (mm)	Caudal peduncle depth (mm)
0 cm·s^{-1}	4.19	3.63	1.47
	(4.12–4.26)	(3.58–3.68)	(1.45–1.48)
10 cm·s^{-1}	4.61	3.46	1.41
	(4.41–4.81)	(3.35–3.58)	(1.38–1.45)

Types and amounts of prey consumed vs. current speed

The proportion of midwater foraging attempts was highly variable among fish observed in still water but increased toward 1.0 as current speed increased (Fig. 3). Conversely, proportions of benthic and surface attempts both declined with increasing current speed (r_s's = – 0.37 and – 0.37, N = 137, respectively).

Between 0 and 17 prey items (median = 4) were found in the stomachs of the captured fish. Ten individuals had no prey in their stomachs but 7 of these had prey in their intestine indicating that they had eaten before. By number, stomach contents were comprised of 42.7% Diptera larvae (mainly chironomids), 32.3% copepods, 11.1% Diptera pupae, 5.8% ostracods, 2.9% Diptera adults, 2.0% Collembolla spp., 1.5% nematode worms, 0.2% isopods,

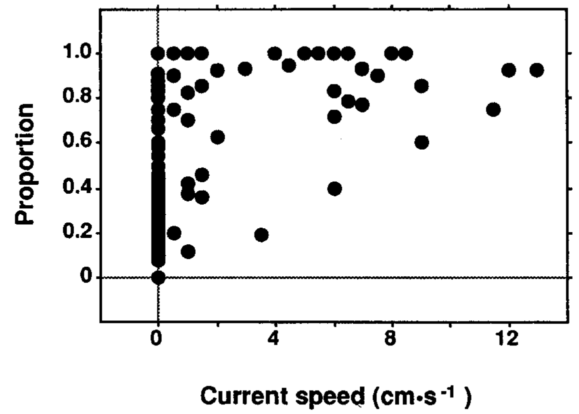

Fig. 3. Proportion of midwater foraging attempts made by individual brook charr sampled from locations differing in current speed. N = 143 individuals.

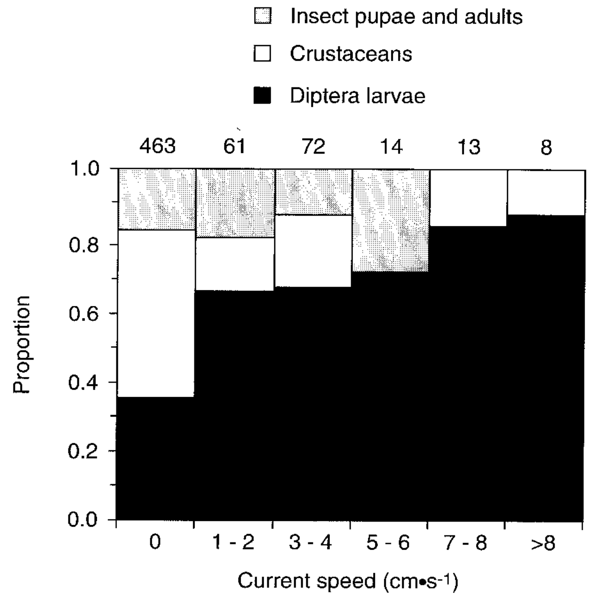

Fig. 4. Diet composition for recently-emerged brook charr sampled from locations differing in current speed. Values above the figure indicate the number of prey items eaten by the fish sampled from each category of current speed. Standardized regression coefficients: $b_s = -1.32$, df = 1, $p < 0.0001$ and $b_s = -0.61$, df = 1, $p < 0.01$; for crustaceans vs. Diptera larvae, and insect pupae and adults vs. Diptera larvae, respectively.

0.2% Plecoptera larvae, 0.2% Trichoptera larvae, and 1.1% unidentifiable parts, respectively.

Individuals in faster current had lower proportions of insect adults and pupae, lower proportions of crustaceans, and higher proportions of Diptera larvae in their stomachs than did individuals in slower current (Fig. 4). This trend remained significant after statistically adjusting for variation in standard length, to control for any predator size – prey size effect (see below), and for variation in sampling date, to control for any day to day changes in the relative abundances of the prey categories (Table 2).

Table 2. Partial standardized regression coefficients from a logistic regression relating the stomach contents of individual brook charr to current speed, standard length, and date.

Predictor	Relative proportions of prey categories	
	Crustaceans vs. Diptera larvae	Insect adults and pupae vs. Diptera larvae
Current speed	– 1.21**	– 0.49*
Standard length	– 0.30**	0.43**
Date	0.27**	1.04**

* $p < 0.05$
** $p < 0.01$

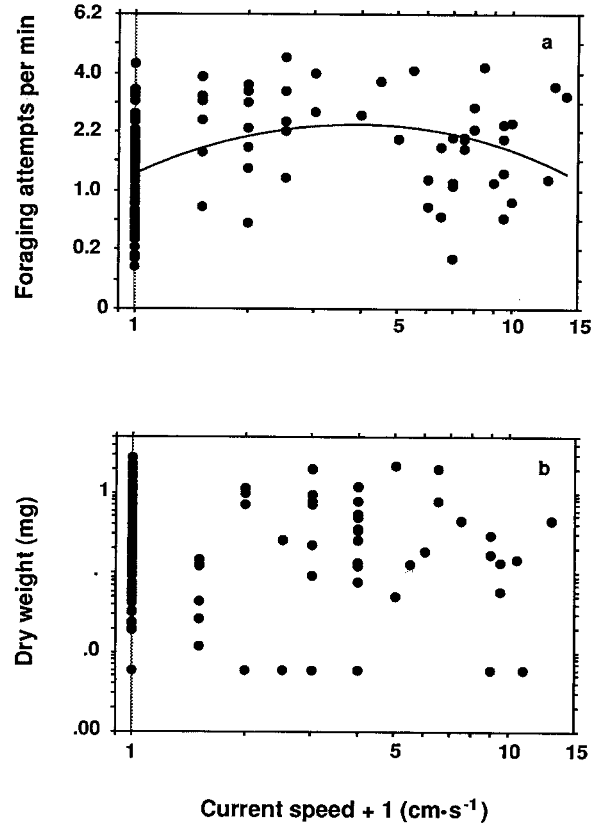

Fig. 5. Foraging attempts made per min (a) and dry weight of stomach contents (b) for recently-emerged brook charr sampled from locations differing in current speed. N = 145 and 137 individuals, respectively.

The number of foraging attempts per min initially increased with increasing current speed, reached a maximum at about 2.7 cm·s^{-1}, and then declined at faster current speeds (Fig. 5, Table 3). Independent of that, the number of foraging attempts per min was also positively correlated with water temperature, but not significantly correlated with fork length. Water temperature and body size are known to influence the amount of food juvenile salmonids will consume in a day under laboratory conditions (Elliott 1975).

The dry weight of stomach contents was not significantly correlated with current speed (Fig. 5). However, larger fish did have greater weights of food in their stomachs than did smaller fish (Table 3). This arose because on average, larger fish consumed larger prey than smaller fish (mean prey length vs. standard length: $r = 0.27$, $p < 0.005$, $N = 123$). However, they did not consume more prey items than smaller fish (number of prey in stomach vs. standard length: $r = 0.09$, $p > 0.25$, $N = 137$). The dry weight of stomach contents could vary with the time-of-day, however, no significant statistical relationship was found when time-of-day was added to the analysis summarized in Table 3 (partial $r = 0.14$, $p > 0.10$).

Discussion

Swimming behaviour and morphology vs. current speed

Brook charr located where current speed was high were slightly larger, and had more fusiform bodies and larger caudal fin heights, than those located where current speed was low. This relationship may reflect adaptive variation in morphology and behaviour. Based on hydrodynamic theory, a more fusiform body shape is thought to reduce drag and thus the energy expended while swimming at a given speed (Webb 1984). A caudal fin of large span connected to the body by a narrow caudal preduncle is expected to increase thrust and reduce energy losses during recoil (Webb 1984, 1988). For salmonids in particular, studies comparing species or different populations within species have found that fish experiencing more stressful hydrodynamic conditions have more fusiform body shapes than those experiencing less stressful hydrodynamic conditions (see Introduction; also Bisson et al. 1988, Taylor & Foote 1991). The noteworthy feature of our study is that we have statistically related individual differences in body form directly with current speed, an index of swimming effort in the field. Such relationships are rarely observed at the individual level, but they are a necessary prerequisite if adaptive explanations for the patterns reported at higher taxonomic levels are correct. Finally, while the correlation coefficients we observed were small they are comparable in magnitude to those reported in laboratory studies relating morphology to locomotor performance at the individual level (e.g. Arnold & Bennett 1988).

Table 3. Partial correlations relating foraging attempts per min and total dry weight of stomach contents to current speed, water temperature, and body length for recently-emerged brook charr.

Predictor	Measure of food intake	
	Foraging attempts per min	Dry weight of stomach contents
Current speed	0.34**	0.10
Current speed^2	– 0.27**	– 0.11
Water temperature	0.26**	0.17
Body length	0.03	0.35**
R^2	0.19**	0.16**
No. of individuals	130	132

* $p < 0.05$
** $p < 0.005$

Whether the body form – current speed relationship represents adaptive phenotypic plasticity or fixed genetic differences is unknown. On one hand, a fish's location may be relatively fixed, and fish in habitats differing in current speed may develop different morphologies (e.g. Caswell 1983, Meyer 1987). Bams (1967), for example, found that swimming performance varied among sockeye salmon (*Oncorhynchus nerka*) juveniles reared on natural vs. artificial substrates. Bams (1967) concluded this variation was related to variation in size and suggested it was also related to variation in condition factor, an index of body shape.

On the other hand, a fish's morphology may be relatively fixed, and fish with different morphologies may either select different habitats, or experience different selection pressures in different habitats. This could occur in several ways. First, current speed could act as a filter on maximal swimming ability, with areas of slow current being suitable to both weak and strong swimmers, but areas of fast current being suitable to strong swimmers only. Second, the energetic cost ($J \cdot s^{-1}$) of swimming at a particular speed could vary for individuals differing in body form, thus leading to variation in the current speed where individuals would maximize their net rate of energy gain. Third, body shape could be related to aggressiveness (Swain & Holtby 1989), with more aggressive individuals influencing the foraging locations of less aggressive individuals (Fausch 1984, Gotceitas & Godin 1992). At our study sites aggression is more prevalent in running water than in still water (Grant & Noakes 1988). Consequently, the direction of the relationship between aggressiveness and body form appears to be the opposite of that observed for juvenile coho salmon, *Oncorhynchus kisutch*, by Swain & Holtby (1989).

We believe the body form – current speed relationship reflects variation in sustained swimming ability rather than the speed maximizing an individual's net rate of energy gain. Morphological limits on swimming ability should be most apparent as fish approach their maximum sustained swimming speeds, and may not be detectable at slower speeds. Conversely, individual variation in the speed maximizing the net rate of energy gain should be apparent at relatively slow speeds, because values of the speed maximizing this currency are expected to be well below a fish's maximum sustained speed (Ware 1978). In contrast to the findings presented here, the broad variation in activity observed among fish within still-water pools is not significantly related to standard length, caudal fin height, maximum body depth, or caudal peduncle depth (McLaughlin et al. 1994). Fish in current swim more continuously than those in still water. Further, only fish in running-water habitats maintain speeds approaching the 13–23 $cm \cdot s^{-1}$ estimated for the maximum sustained swimming speeds of brook charr at this stage of development (Heggenes & Traaen 1988).

Types and amounts of prey consumed vs. current speed

Relative to fish in slower currents, those in faster currents directed more foraging attempts toward the midwater portion of the water column and fewer toward the benthos and water surface, and they ate more Diptera larvae, fewer crustaceans, and fewer insect pupae and adults. These findings are consistent with two earlier studies comparing the use of the water column and the diets of juvenile salmonids from areas of slow- and fast-running water (Irvine & Northcote 1982, Rondorf et al. 1990). Our findings, however, are for fish sampled from locations tens of metres apart within our study sites while these other studies compared fish sampled from sites 3 to 20 km apart. We have also attempted more strongly than these previous studies to control for other factors that could influence diet, such as day to day variation in the types of prey available, and potential ontogenetic shifts from crustaceans to insect prey (e.g. Luecke 1986).

The variation in diet across current speeds probably reflects, in part, small-scale variation in prey availability, because the distributions of aquatic invertebrates are related to flow conditions (Statzner 1981). This may account for the lack of benthic foraging in running-water. Grant & Noakes (1987a), for example, found that abundances of benthic invertebrates were lower in substrates of sand than in substrates of gravel or silt. Twenty nine percent of the fish we observed in running-water habitats were foraging over substrates of sand as compared with only four percent of the fish observed in still-water habitats. The variation in diet may also reflect increased selectivity by the fish feeding in fast currents, since the time and energy costs of capturing prey will be higher there (Grant & Noakes 1987a, Godin & Rangeley 1989). Surface prey, in particular, would be eaten less often in fast currents if the fish reduced their capture radius in response to the higher swimming costs (Godin & Rangeley 1989). Moreover, the water was deeper in areas of fast current, and the charr held station closer to the bottom (personal observation). The increased depth could reduce the chance of successfully detecting and capturing surface prey.

On average, the number of foraging attempts per min was highest for fish in currents of intermediate magnitude, and lowest for the fish in the slowest and fastest currents. Similar patterns have been observed before for charr at our study sites (Grant & Noakes 1988), as well as for young-of-the-year from stream-dwelling populations of smallmouth bass, *Micropterus dolomieui* (Simonson & Swenson 1990). The current speed where the rate of foraging attempts was maximal is lower here than the 7.5 cm·s^{-1} reported by Grant & Noakes, however, we measured current speed at the position where a fish was holding station, whereas Grant & Noakes' analysis considered the current speed in the fish's foraging zone. These two measurements are highly correlated but the former is about half the magnitude of the latter (Grant & Noakes 1988).

Under optimal viewing conditions we often saw individuals miss or reject potential prey, and foraging attempts do not incorporate capture success. It is noteworthy therefore that dry weights of stomach contents did not vary significantly with current speed. While the amount of food in the stomach is not equivalent to intake rate (dry weight per unit time), the relationship between the dry weight of stomach contents and current speed at least suggests that intake rates of fish foraging in different current speeds were not as disparate as analyses of foraging attempts alone would suggest. Considering how indices of growth, such as RNA-DNA ratios (Bulow 1987), vary with current speed would be valuable in future field studies.

Our findings suggest that variation in foraging location could account for the individual variation in water-column use and diet often reported for salmonids (Ringler 1983, McNicol et al. 1985, Ringler 1985). In at least one instance, this variation reflected specializations that were stable for weeks in the field (Bryan & Larkin 1972). Yet the factors promoting such variation are not well understood, presumably because studies tend to focus on the diet of the 'average individual' rather than the variation among individuals (Ringler 1983). With small-scale patchiness in food availability an individual may encounter the same prey type several times in succession. This can lead to changes in attack latency and capture efficiency, and thus a tendency for an individual to prefer the portion of the water column or prey type it has exploited most recently, i.e. a training bias (Bryan 1973, Dill 1983). Individuals foraging at locations differing in current speed could therefore develop different patterns of water-column use and diet, and even develop biases for different parts of the water column and different types of prey.

Variation in the location of foraging sites may also involve a trade-off between prey quality and swimming effort. The prey taxa eaten by the charr are comparable in energetic content (kJ·g^{-1}) (Cummins & Wuychek 1971), but the crustaceans and terrestrial insects could take longer to digest because they possess more chitin in their exoskeletons (Kionka & Windell 1972, Jobling 1987). Therefore, fish foraging in still water may incur lower swimming costs, but also consume lower quality prey, while fish foraging in running water incur higher swimming costs, but consume higher quality prey. Such a trade-off would be important for understanding the costs and benefits of foraging-site selection since growth rate can be influenced by the type of prey consumed as well as the amount (Brett 1979). Earlier theoretical and empirical studies of site selection did not consider the potential for differences in diet across habitats differing in current speed (Puckett & Dill 1985, Grant & Noakes 1987a, 1988, Mangel & Clark 1988, Hughes & Dill 1990, Simonson & Swenson 1990).

We do not know the level of fidelity that individuals exhibit for particular foraging locations because the durations of our observation periods were short, and because of the technical difficulties with marking and handling fish this small in the field. There is laboratory and field evidence indicating that stream salmonids will leave preferred sites to feed at atypical sites in response to new foraging opportunities (Gotceitas & Godin 1992). Nevertheless, our impression from field observations is that at least some fish do use the same site repeatedly. Individuals of the same relative size and exhibiting the same qualitative behaviour were observed at the same location over successive days. In addition, the patterns observed in morphology and diet would not be expected if individuals were moving frequently between still- and running-water habitats, and spending comparable proportions of time in each habitat.

To conclude, our comparisons have identified differences in the morphology and resource use of brook charr sampled from locations differing in current speed. While the patterns are subtle, they have important ecological and evolutionary implications when considered in light of earlier studies comparing the morphology and resource use of salmonids at broader taxonomic and spatial scales.

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Appendix 1. Univariate statistics for the 23 morphological measurements (in mm) made for the 137 captured brook charr.

Character	$\bar{x}$	SD	Repeatability
Fork length[a]	21.74	2.38	0.99
Standard length	18.60	1.94	0.99
Head length	4.86	0.61	0.98
Head width	2.82	0.36	0.99
Eye width	1.82	0.18	0.97
Jaw length	2.08	0.34	0.97
Snout to pectoral fin	4.52	0.47	0.99
Snout to anterior of dorsal fin	9.13	1.00	0.99
Snout to pelvic fin	9.56	1.12	0.99
Maximum body depth	3.64	0.60	0.99
Position of maximum body depth	7.35	1.08	0.98
Maximum caudal fin depth	4.32	0.75	0.99
Minimum caudal fin depth			
without fin fold	1.77	0.26	0.98
with fin fold	3.02	0.31	0.97
Caudal fin length	3.17	0.42	0.97
Caudal peduncle depth			
without fin fold	1.47	0.20	0.99
with fin fold	2.82	0.29	0.99
Dorsal fin length	1.96	0.27	0.99
Dorsal fin height	2.56	0.49	0.96
Anal fin length	1.68	0.23	0.98
Anal fin depth	2.34	0.43	0.99
Pelvic fin length	1.88	0.37	0.99
Pectoral fin length	2.65	0.42	0.99

[a] For preserved specimens. Fork lengths of live specimens (LFL) were longer than those of preserved specimens (PFL) due to effects of preservation. $LFL = 1.09 \star PFL$, $r = 0.99$, $p < 0.001$.