

# Interactions between individual feeding behaviour, growth, and swimming performance in juvenile rainbow trout (*Oncorhynchus mykiss*) fed different rations

T. Ryan Gregory and Chris M. Wood

**Abstract:** Aerobic swimming performance (critical swimming speed,  $U_{crit}$ ), food consumption per meal (by X-ray radiography), specific growth rate (SGR), haematocrit, and fin condition were monitored in individual juvenile rainbow trout (*Oncorhynchus mykiss*). The fish were held in groups over a 9-week period and fed daily group rations (dry food) of 2.0, 1.5, 1.0, and 0.5% wet body mass (BM)·day<sup>-1</sup>. SGR declined and competition increased at lower ration levels, as reflected by greater fin damage, reduced haematocrits and condition factors, and, at 0.5% BM·day<sup>-1</sup>, a substantial increase in the coefficient of variation among individual meals. Absolute  $U_{crit}$  also declined at lower ration levels. However, there was no relationship between  $U_{crit}$  and haematocrit, fin damage, or condition factor in any of the ration groups. A negative correlation was found between  $U_{crit}$  and SGR in individual trout fed a group ration of 2.0% BM·day<sup>-1</sup>, but a positive correlation was seen at 0.5% BM·day<sup>-1</sup> and no relationship at 1.0 and 1.5% BM·day<sup>-1</sup>. There was a positive relationship between individual SGR and food consumption only among fish fed a ration of 2.0% BM·day<sup>-1</sup>. A significant negative relationship between  $U_{crit}$  and individual food consumption was also found among fish in this ration group.

**Résumé :** On a surveillé la performance natatoire aérobie (vitesse de nage critique,  $U_{crit}$ ), la consommation de nourriture par repas (par radiographie aux rayons X), le taux de croissance spécifique, l'hématocrite et l'état de nageoires chez des truites arc-en-ciel (*Oncorhynchus mykiss*) juvéniles. Les poissons étaient gardés en groupes durant 9 semaines et on les nourrissait avec des rations de groupe quotidiennes (nourriture sèche) de 2,0, 1,5, 1,0 et 0,5% de la masse corporelle fraîche (MC)·jour<sup>-1</sup>. Le taux de croissance spécifique a diminué et la compétition s'est accrue aux plus faibles rations, comme en ont témoigné les dommages accrus aux nageoires, la réduction des hématocrites et des coefficients de condition et, à la ration de 0,5% MC·jour<sup>-1</sup>, l'accroissement substantiel du coefficient de variation entre les repas des individus. L' $U_{crit}$  absolue a aussi diminué aux rations inférieures. Cependant, on n'a pas observé de relation entre l' $U_{crit}$  et l'hématocrite, les dommages aux nageoires ou le coefficient de condition dans l'ensemble des groupes, quelle que soit la ration. On a observé entre l' $U_{crit}$  et le taux de croissance spécifique une corrélation négative chez les truites ayant reçu une ration de groupe de 2,0% MC·jour<sup>-1</sup>, une corrélation positive chez les truites ayant reçu une ration de 0,5% MC·jour<sup>-1</sup> et aucune relation chez celles ayant reçu une ration de 1,0 et de 1,5% MC·jour<sup>-1</sup>. Il y avait une relation positive entre les taux de croissance spécifiques individuels et la consommation de nourriture seulement chez les poissons ayant reçu une ration de 2,0% MC·jour<sup>-1</sup>. Enfin, dans ce même groupe de poissons, on a observé une relation négative significative entre l' $U_{crit}$  et la consommation individuelle de nourriture.

[Traduit par la Rédaction]

## Introduction

It is becoming increasingly clear that in fish, there exist complex relationships among feeding, growth, and other key elements of fitness such as swimming performance. For example, trade-offs between growth rate and aerobic swimming capacity have now been reported in several fish species (Kolok and Oris 1995; Farrell et al. 1997; Gregory and Wood

1998). Thus, under certain conditions, individual fish may be able to maximize either growth rate or swimming performance, but not both. This trade-off is potentially puzzling, since the activities of key muscle enzymes are known to correlate positively with aerobic swimming performance (Farrell et al. 1991; Kolok 1992b) and growth rate (Goolish and Adelman 1987).

Several possible explanations exist, including differences in body size (Beamish 1978), morphology (Taylor and McPhail 1985), and haematocrit (Gregory and Wood 1998) associated with growth. It has also been suggested that energetic costs associated with the digestion and conversion of food could have deleterious effects on aerobic swimming performance (Alsop and Wood 1997; Gregory and Wood 1998), but to date, the effect of feeding level on swimming performance has not been examined directly. The results of a previous study using juvenile rainbow trout (*Oncorhynchus*

Received May 7, 1998. Accepted October 30, 1998.  
J14574

T.R. Gregory<sup>1</sup> and C.M. Wood. Department of Biology, McMaster University, Hamilton, ON L8S 4K1, Canada.

<sup>1</sup>Author to whom all correspondence should be addressed.  
Present address: Department of Zoology, University of Guelph, Guelph, ON N1G 2W1, Canada.  
e-mail: rgregory@uoguelph.ca

**Table 1.** Mean values  $\pm$  SE (*n*) of the various parameters measured for fish in the 2.0, 1.5, 1.0, and 0.5% BM·day<sup>-1</sup> ration groups.

Variable	2.0% BM·day <sup>-1</sup>	1.5% BM·day <sup>-1</sup>	1.0% BM·day <sup>-1</sup>	0.5% BM·day <sup>-1</sup>
Initial mass (g)	5.54 $\pm$ 0.18 (25) <i>a</i>	5.57 $\pm$ 0.16 (25) <i>a</i>	5.40 $\pm$ 0.17 (25) <i>a</i>	5.52 $\pm$ 0.18 (25) <i>a</i>
Food consumption (%BM·day <sup>-1</sup> )	2.05 $\pm$ 0.10 (25) <i>a</i>	1.57 $\pm$ 0.06 (23) <i>b</i>	1.11 $\pm$ 0.04 (23) <i>c</i>	0.56 $\pm$ 0.06 (22) <i>d</i>
Overall SGR (%·day <sup>-1</sup> )	1.79 $\pm$ 0.07 (25) <i>a</i>	1.43 $\pm$ 0.07 (23) <i>b</i>	0.81 $\pm$ 0.06 (23) <i>c</i>	0.11 $\pm$ 0.03 (22) <i>d</i>
Condition factor (100 $\times$ g $\times$ cm <sup>-3</sup> )	1.29 $\pm$ 0.02 (25) <i>a</i>	1.24 $\pm$ 0.02 (23) <i>a</i>	1.16 $\pm$ 0.01 (23) <i>b</i>	1.06 $\pm$ 0.02 (22) <i>c</i>
Haematocrit (% volume)	45.70 $\pm$ 0.88 (20) <i>a</i>	46.84 $\pm$ 0.73 (19) <i>a</i>	42.20 $\pm$ 0.90 (20) <i>b</i>	38.52 $\pm$ 0.93 (21) <i>c</i>
CV (%)	31.52 $\pm$ 2.43 (25) <i>a</i>	28.83 $\pm$ 2.64 (23) <i>a</i>	34.65 $\pm$ 2.69 (23) <i>a</i>	59.75 $\pm$ 4.39 (22) <i>b</i>
Fin score	35.56 $\pm$ 0.51 (25) <i>a</i>	33.83 $\pm$ 0.58 (23) <i>ab</i>	31.61 $\pm$ 0.83 (23) <i>b</i>	26.83 $\pm$ 0.90 (22) <i>c</i>
Swim length (cm)	10.50 $\pm$ 0.16 (24) <i>a</i>	9.77 $\pm$ 0.16 (22) <i>b</i>	9.07 $\pm$ 0.18 (18) <i>c</i>	8.27 $\pm$ 0.09 (20) <i>d</i>
Swim SGR (%·day <sup>-1</sup> )	2.20 $\pm$ 0.11 (24) <i>a</i>	1.70 $\pm$ 0.08 (22) <i>b</i>	1.02 $\pm$ 0.10 (18) <i>c</i>	0.15 $\pm$ 0.11 (20) <i>d</i>
Relative $U_{crit}$ (BL·s <sup>-1</sup> )	4.23 $\pm$ 0.14 (24) <i>a</i>	3.82 $\pm$ 0.11 (22) <i>ab</i>	4.16 $\pm$ 0.19 (18) <i>a</i>	3.42 $\pm$ 0.10 (20) <i>b</i>
Absolute $U_{crit}$ (cm·s <sup>-1</sup> )	44.21 $\pm$ 1.26 (24) <i>a</i>	37.35 $\pm$ 1.32 (22) <i>b</i>	37.72 $\pm$ 1.86 (18) <i>b</i>	28.37 $\pm$ 1.08 (20) <i>c</i>

**Note:** Differences in sample size reflect mortality or problems with blood sampling in small fish. In addition, fish that refused to swim or escaped from the swim tunnels were omitted from the data set. Different letters represent significant differences ( $p < 0.05$ ).

*mykiss*) suggested that the trade-off occurred only below a certain ration level (Gregory and Wood 1998), but the precise range of food intakes over which this relationship occurs was not investigated in detail. As such, the primary goal of the present study was to evaluate the roles of body size, morphology, haematocrit, and feeding in the development of this trade-off and to determine the range of rations over which it occurs. By beginning at the level where trade-offs were seen previously (~2% body mass (BM)·day<sup>-1</sup>, Gregory and Wood 1998) and decreasing to roughly one quarter of this amount (to ~0.5% BM·day<sup>-1</sup>), and by measuring the feeding behaviours, growth characteristics, and swimming performances of the same individual trout, many questions raised by the results of previous studies can be addressed directly.

Before any relationships involving swimming performance can be considered biologically relevant, the repeatability of individual swimming ability must be demonstrated. Individual swimming performance has been found to be significantly repeatable among largemouth bass (*Micropterus salmoides*) (Kolok 1992a) and among juvenile rainbow trout swum in small groups (Gregory and Wood 1998), but the repeatability of swim performance among trout swum individually remains to be shown. In addition, it is desirable to determine whether the trade-off between aerobic swimming performance and growth rate reported previously (Gregory and Wood 1998) was simply an artefact of the social interactions present among fish swimming in groups. The resolution of these issues represents the second goal of the present study.

In addition to the processes associated with the ingestion and assimilation of food, social interactions may play an important role in determining the growth rates of individual fish. Recent studies employing X-ray radiography have shown that feeding rank can have a significant impact on the amount of food obtained by individuals and therefore affect growth (McCarthy et al. 1992; Gregory and Wood 1998). Moreover, as ration decreases and competition for food increases, there may be further impacts on growth resulting from heightened levels of stress and energetic expenditure as aggressive interactions become intensified (Moutou et al. 1998). In this regard, the third goal of the present study was to examine the effects of group ration on the strength of the

feeding hierarchy formed and the possible consequences of aggressive interactions between individual fish.

## Materials and methods

### Experimental animals and design

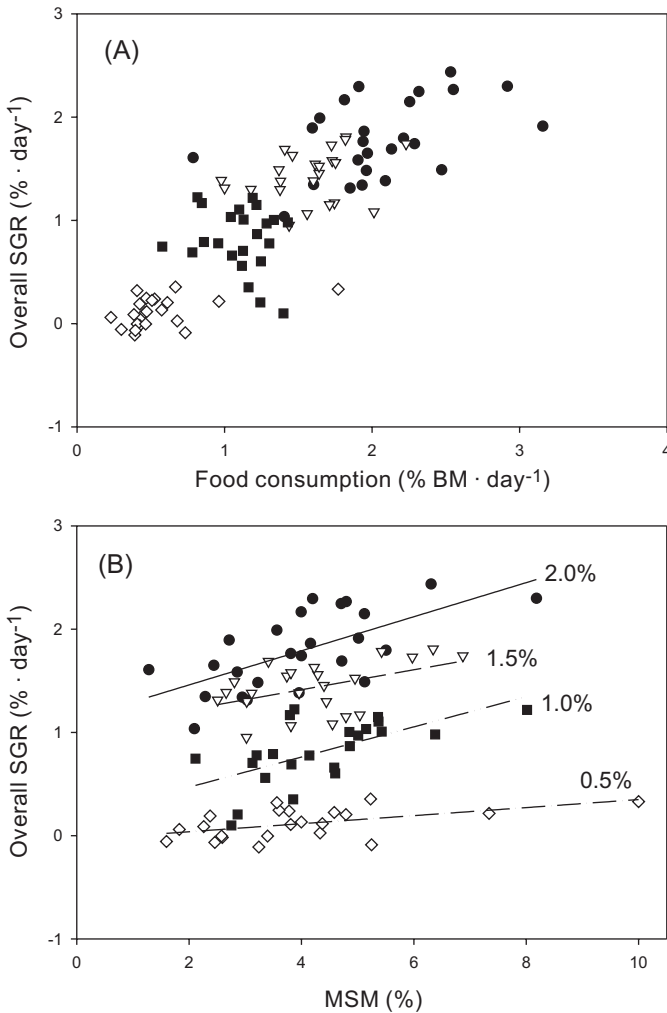
Juvenile rainbow trout (4–8 g) were obtained from Humber Springs Trout Hatchery in Orangeville, Ontario. The fish were kept at 15  $\pm$  1°C in dechlorinated Hamilton, Ontario, tapwater (composition reported in Alsop and Wood 1997) with a photoperiod of 12.5 h light : 11.5 h dark. Fish were screened for healthy dorsal and caudal fins, weighed to the nearest 0.01 g, measured for fork length to the nearest 0.1 cm, and marked for identification using a PanJet ink injector and Alcian Blue dye. The fish were re-marked again every 4 weeks to ensure accurate identification of individuals. Twenty-five fish were placed in each of four square 60-L tanks (flow-through rate ~1.0 L·min<sup>-1</sup>), with no significant differences in mean initial mass among tanks ( $p > 0.91$ ) (Table 1). The fish in the four tanks were fed once per day (between 10:00 and 11:00) on one of four rations, 2.0, 1.5, 1.0, or 0.5% BM·day<sup>-1</sup>, using commercial trout food (Ziegler Bros., Inc., Gardners, Pa.) that was powdered in a standard kitchen blender, mixed with water, and then repelleted using a pasta maker.

The fish were allowed to grow for 3 weeks and were weighed and measured weekly (without anaesthesia). After this initial growing period, swim trials were initiated, a process that lasted a further 6 weeks. During this period, weekly measurements of mass and length were continued, together with repetitive X-ray analyses of individual food consumption (see below). No fish were swum on the day immediately following X-raying.

### Swimming performance

On swimming days, a single fish was selected from each tank and placed into one of four 3.23-L Blazka-type swimming respirometers. The respirometers were calibrated prior to use with a Kent Microflo type 265 propeller-style flowmeter and kept in a temperature-controlled water bath at 16  $\pm$  1°C. Individuals were allowed to habituate to the swim tunnels at 1 body length (BL)·s<sup>-1</sup> for at least 2.5 h and were fasted for a minimum of 27 h prior to swimming. The velocity of the water was increased by 0.75 BL·s<sup>-1</sup> every 40 min until the fish could no longer be prompted to swim by temporarily lowering or raising the velocity or by gently shaking the tunnel, at which time the fish was judged exhausted. A shocking grid was not employed, in accord with animal care regulations. Each fish was weighed and measured after exhaustion and then returned to its holding tank until the end of the 9-week period (with the exception of weekly weighing and X-raying). Relative critical

**Fig. 1.** Relationships between individual (A) mean daily food consumption and (B) MSM and overall SGR and for fish in the 2.0% (●), 1.5% (▽), 1.0% (■), and 0.5% (◇) BM·day<sup>-1</sup> ration groups. In Fig. 1A, there was a significant positive regression between food consumption and overall SGR among fish in the 2.0% BM·day<sup>-1</sup> group ( $r^2 = 0.2896$ ,  $p < 0.03$ ) and when the data were pooled ( $r^2 = 0.7022$ ,  $p < 0.0001$ ) but not within any of the other ration groups (all  $p > 0.11$ ). Regressions in Fig. 1B were as follows: 2.0%,  $r^2 = 0.4261$ ,  $p < 0.001$ ,  $n = 25$ ,  $y = 0.17x + 1.13$ ; 1.5%,  $r^2 = 0.2182$ ,  $p < 0.03$ ,  $n = 23$ ,  $y = 0.10x + 1.03$ ; 1.0%,  $r^2 = 0.3859$ ,  $p < 0.002$ ,  $n = 23$ ,  $y = 0.15x + 0.18$ ; 0.5%,  $r^2 = 0.2141$ ,  $p < 0.04$ ,  $n = 22$ ,  $y = 0.03x + 0.02$ . There were no significant differences in slopes among these regressions ( $p > 0.30$ ), although the elevations of the lines were significantly different from one another (all  $p < 0.001$ ).



swimming speed ( $U_{crit}$ , body lengths per second) and absolute  $U_{crit}$  (centimetres per second) were calculated for each fish as in Brett (1964). Each fish was swum only once.

The specific growth rate (SGR, percent per day) of each fish was calculated as in Kolok and Oris (1995) over two different time periods: “overall SGR” (initial mass to final mass, a period of roughly 9 weeks) and “swim SGR” (initial mass to mass at time of swimming, the same as “SGR” used in Gregory and Wood (1998)). Condition factor ( $100 \times \text{mass} \times \text{length}^{-3}$ ) and maximum cross-sectional area ( $\pi [(0.5 \times \text{maximum height})(0.5 \times \text{maximum width})]$ ,

Kolok and Oris 1995) were also calculated for each fish at the time of swimming. In addition, a group of eight fish (10–25 g) was tested for repeatability of swimming performance exactly as described in Gregory and Wood (1998), except that the fish were swum individually in one of the 3.23-L Blazka-type respirometers rather than communally in a single 100-L Beamish-type respirometer.

**X-ray radiography**

In order to evaluate the feeding patterns of individuals, the fish were X-rayed on four separate occasions beginning at the start of week 6, with 1 week recovery periods during which the feeding regime was maintained (see McCarthy et al. 1992, 1993; Gregory and Wood 1998). On these days, the fish were fed food that was repelleted in the same manner as the regular diet but that contained 8.5-grade (0.400- to 0.455-mm) lead glass ballotini beads at fixed density (6% by dry mass of food) (Jencons USA, Inc., Bridgeville, Pa.). The ballotini beads did not affect the palatability of the food, which was completely consumed as in regular feeding. In order to prevent regurgitation caused by anaesthesia, the fish were allowed to settle for at least 1 h prior to X-raying. After this time, groups of 10 fish were identified and placed into a 10-part glass grid filled with water, which was then drained and filled with 0.1 g tricaine methanesulfonate (MS 222)-L<sup>-1</sup> and set to a pH of ~8.0 with 3 M NaOH. X-raying was carried out using a General Electric AMX-110 mobile X-ray machine with a 70 kVP (kilovolts peak), 150 mAs (milliamperere seconds) exposure at 61 cm. The fish were returned to the holding tanks immediately following X-ray exposure and the process repeated until all fish had been X-rayed. The X-ray films were then developed and the number of beads located in the digestive tract counted for each fish. No regurgitation or clearance of beads was observed, and all X-raying was completed within 2 h of feeding. The total number of beads found within all of the fish in a tank was used to calculate the mean share of meal (MSM) obtained by each individual fish (McCarthy et al. 1992). In addition, coefficient of variation (CV, a measure of the day-to-day variability in food consumption of each individual fish) was calculated as in McCarthy et al. (1992).

The conditions of the dorsal and caudal fins were evaluated prior to the commencement of swimming trials at the start of week 4 and again at each X-ray period (weeks 6–9) and assigned a numerical value between 1 (poor) and 4 (excellent) according to the absolute amount of damage present. These values were then added together to give a final “fin score” that served as an indication of the total amount of damage sustained by each individual during the experimental period (i.e., maximum possible score = 40) (Gregory and Wood 1998). An index of fin condition was also tabulated for each ration group using the equation given in Moutou et al. (1998) and used to assess the relationship between fin condition and ration at various times throughout the experiment.

After the completion of the X-raying and swim trials, the fish were sacrificed individually in 1.0 g MS 222-L<sup>-1</sup>, weighed, and measured and a blood sample taken by caudal severance. Haematocrits were measured following 5 min of centrifugation at 5000 g.

**Statistical analysis**

Statistical analyses were performed using Statistix v1.0 for Windows (© 1996 Analytical Software), SigmaPlot v4.0 for Windows 95 (© 1997 SPSS, Inc.), and Quattro Pro v7.0 for Windows 95 (© 1996 Corel Corporation Ltd.). Correlations and regressions consisted of Pearson correlation analyses and least-squares regression, and comparisons of regression slopes and elevations were carried out using ANCOVA and the Tukey test of multiple comparison (Zar 1996). The repeatability of swim performance was assessed using Spearman rank correlation analysis. Differences in group

means were evaluated using two-sample *t* tests or one-way ANOVA followed by Tukey tests. All averages are reported as mean  $\pm$  SE (*n*).

## Results

### Growth

The mean individual food consumptions in the four tanks, based on four separate X-ray analyses over the 9-week experiment, corresponded almost exactly to the group rations of 2.0, 1.5, 1.0, and 0.5% BM·day<sup>-1</sup> (Table 1). There were significant differences in mean overall SGR (i.e., over the entire experimental period) among these tanks, with the 0.5% ration group showing a mean SGR somewhat lower than would be predicted based on ration alone (Table 1). Not surprisingly, when the data from all four groups were considered together, there was a strong positive correlation between overall SGR and individual food consumption ( $r = 0.838$ ,  $p < 0.0001$ ) (Fig. 1). Overall SGR showed a positive correlation with individual food consumption only among fish fed a 2.0% BM·day<sup>-1</sup> ration ( $r = 0.538$ ,  $p < 0.03$ ; others,  $p > 0.11$ ).

Fish in the 0.5% BM·day<sup>-1</sup> group showed significantly lower condition factors than those in the 1.0% BM·day<sup>-1</sup> group. There were no significant differences in condition factor between fish in the 2.0 and 1.5% BM·day<sup>-1</sup> tanks, but these fish had significantly higher condition factors than fish in the other two tanks (Table 1). In all tanks, condition factor was unrelated to both food consumption (all  $p > 0.05$ ) and SGR (all  $p > 0.28$ ). Haematocrit followed qualitatively similar relationships as those for condition factor (Table 1). In addition, haematocrit was unrelated to both individual food consumption (all  $p > 0.05$ ) and overall SGR (all  $p > 0.11$ ) in all ration groups. Significant correlations between haematocrit and fin score were found only in the 1.5% ( $r = -0.644$ ,  $p < 0.004$ ) and 1.0% BM·day<sup>-1</sup> groups ( $r = 0.691$ ,  $p < 0.009$ ; note the difference in sign between these groups; others,  $p > 0.15$ ), indicating that haematocrits were not affected by blood loss associated with fin damage.

### Feeding rank

Fish in the 0.5% BM·day<sup>-1</sup> group showed a significantly higher mean CV than fish in all other tanks ( $p < 0.0001$ ), indicating higher variability among the four separate meals recorded by X-ray radiography for each fish. There were no differences in mean CV among any of the other diet groups, however (Table 1). CV was not significantly correlated with overall SGR (all  $p > 0.32$ ) or MSM in any of the tanks, although overall SGR was positively correlated with MSM in all tanks (all  $r \geq 0.463$ , all  $p < 0.03$ ) (Fig. 1B). The slopes of the regression lines were not significantly different from one another, but there were significant differences in the elevations of the regression lines between all diet groups (all  $p < 0.001$ ).

In general, fish fed lower rations showed higher levels of fin damage, as reflected by significantly lower mean fin scores (Table 1). Individual fin score was positively correlated with MSM in the 1.0% BM·day<sup>-1</sup> group ( $r = 0.571$ ,  $p < 0.005$ ) and showed a similar but nonsignificant trend in the 0.5% BM·day<sup>-1</sup> group ( $r = 0.378$ ,  $p < 0.076$ ), but was unrelated to both MSM and CV in all other cases (all  $p > 0.11$ ). Similarly, individual fin score showed positive relationships

with initial mass in the 1.0% ( $r = 0.515$ ,  $p < 0.012$ ) and 0.5% BM·day<sup>-1</sup> ration groups ( $r = 0.546$ ,  $p < 0.007$ ), suggesting that smaller fish received more fin damage in these low-ration tanks. There were no such relationships in the two higher ration tanks (all  $p > 0.31$ ). Fin condition indices (as calculated in Moutou et al. 1998) for the caudal fin and total fin measurements were positively correlated with ration at weeks 7, 8, and 9 (all  $r > 0.94$ , all  $p < 0.05$ ) but not for the first two measurement periods (weeks 4 and 6). Dorsal fin condition index was not significantly correlated with ration at any of the measurement periods (all  $p > 0.06$ ) but followed a qualitatively similar pattern as that for the caudal and total fin condition indices (Fig. 2). Dorsal fins typically received more damage than caudal fins, as reflected by their lower fin condition indices (Figs. 2A and 2B).

### Swimming performance

Individual swimming performance was significantly repeatable when the fish were swum individually (Spearman rank correlation coefficient, one-tailed,  $\rho = 0.735$ ,  $p < 0.05$ ) and very comparable with earlier results where fish were swum communally in a much larger swim tunnel (Gregory and Wood 1998). There were no significant differences in mean relative  $U_{crit}$  between the two trials ( $p > 0.52$ ), indicating no improvement or reduction in performance from one trial to the next.

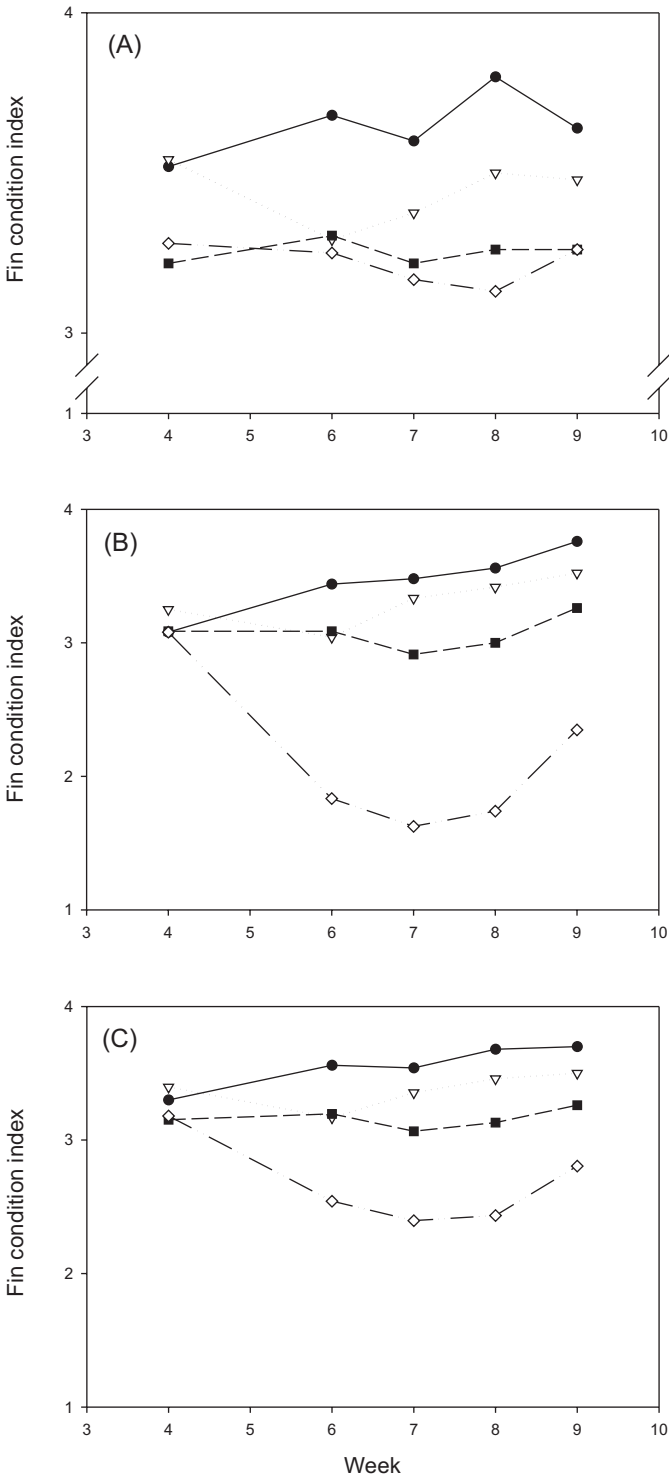
Fish in the 0.5% BM·day<sup>-1</sup> group showed the poorest aerobic swimming performance, both in terms of relative  $U_{crit}$  (body lengths per second) and absolute  $U_{crit}$  (centimetres per second) (Table 1). The relative  $U_{crit}$  values of fish in the 2.0% BM·day<sup>-1</sup> group were not significantly different from those in the 1.5 and 1.0% BM·day<sup>-1</sup> groups (Table 1), but these fish showed a significantly higher mean absolute  $U_{crit}$  than fish in the other tanks, reflecting their greater length (Table 1).

There was a significant negative correlation between relative  $U_{crit}$  and swim SGR among fish in the 2.0% BM·day<sup>-1</sup> tank ( $r = -0.477$ ,  $p < 0.02$ ) (Fig. 3A). A similar relationship was found between absolute  $U_{crit}$  and swim SGR in this group ( $r = -0.446$ ,  $p < 0.03$ ) (Fig. 3B). Significant positive correlations were found between both relative ( $r = 0.576$ ,  $p < 0.008$ ) and absolute  $U_{crit}$  ( $r = 0.610$ ,  $p < 0.005$ ) and swim SGR in the 0.5% BM·day<sup>-1</sup> fish (Fig. 3). No such relationships were found in either the 1.5 or 1.0% BM·day<sup>-1</sup> group (all  $p > 0.26$ ).

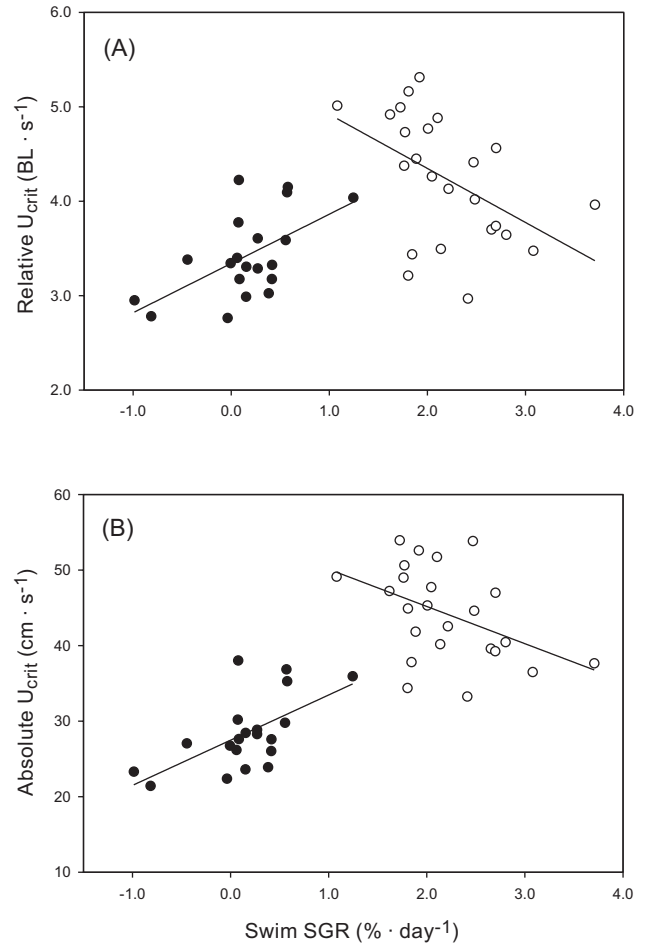
In the 2.0% BM·day<sup>-1</sup> group, there was a negative relationship between  $U_{crit}$  and food consumption ( $r = -0.460$ ,  $p < 0.03$ ) (Fig. 4). There were no significant relationships between  $U_{crit}$  and food consumption in the other ration groups (all  $p > 0.12$ ). Similarly, there was a negative relationship between  $U_{crit}$  and MSM in the 2.0% BM·day<sup>-1</sup> group ( $r = -0.658$ ,  $p < 0.001$ ) but not among any of the other groups (all  $p > 0.09$ ). None of the tanks showed a relationship between either relative (all  $p > 0.27$ ) or absolute  $U_{crit}$  (all  $p > 0.07$ ) and number of growing days prior to swimming, indicating that differences in swimming performance between individuals were not greatly affected by the swimming schedule used.

The possibility of spurious relationships among  $U_{crit}$ , SGR, and body size was also investigated. Both relative and absolute  $U_{crit}$  showed significant positive correlations with indi-

**Fig. 2.** (A) Caudal fin condition index, (B) dorsal fin condition index, and (C) total fin condition index calculated at weeks 4, 6, 7, 8, and 9 for fish in the 2.0% (●), 1.5% (▽), 1.0% (■), and 0.5% (◇) BM-day<sup>-1</sup> ration groups. Higher condition index values indicate less fin damage. All fish were screened for a minimum level of fin quality prior to placement in the holding tanks such that all fish began the experiment with similar fin conditions. Relationships between ration and fin condition are discussed in the text. Note the axis break in Fig. 2A.



**Fig. 3.** Relationship between (A) relative  $U_{crit}$  and swim SGR and (B) absolute  $U_{crit}$  and swim SGR among fish fed on 2.0% (○) and 0.5% (●) BM-day<sup>-1</sup> rations. Significant *negative* regressions were found between relative  $U_{crit}$  and SGR ( $r^2 = 0.2300$ ,  $p < 0.02$ ,  $n = 24$ ,  $y = -0.57x + 5.49$ ) and absolute  $U_{crit}$  and SGR ( $r^2 = 0.1987$ ,  $p < 0.03$ ,  $n = 24$ ,  $y = -4.93x + 55.03$ ) in the 2.0% BM-day<sup>-1</sup> group. Significant *positive* regressions were found between relative  $U_{crit}$  and SGR ( $r^2 = 0.3319$ ,  $p < 0.008$ ,  $n = 20$ ,  $y = 0.52x + 3.34$ ) and between absolute  $U_{crit}$  and SGR ( $r^2 = 0.3716$ ,  $p < 0.005$ ,  $n = 20$ ,  $y = 5.98x + 27.48$ ) in the 0.5% BM-day<sup>-1</sup> group. No such relationships were found in the 1.5 and 1.0% BM-day<sup>-1</sup> ration groups (all  $p > 0.26$ ).



icators of body size (mass, length, and cross-sectional area) in the 0.5% BM-day<sup>-1</sup> group (all  $r \geq 0.536$ , all  $p < 0.02$ ). These relationships were absent in the 1.0% BM-day<sup>-1</sup> group (all  $p > 0.08$ ). In the 1.5% BM-day<sup>-1</sup> group, there were significant positive correlations between body size and absolute  $U_{crit}$  only (all  $r \geq 0.471$ , all  $p < 0.03$ ), while in the 2.0% BM-day<sup>-1</sup> group, there were significant negative correlations between body size and relative  $U_{crit}$  only (all  $r \leq -0.491$ , all  $p < 0.02$ ). More importantly, swim SGR was found to be unrelated to indicators of body size in both the 2.0 and 1.5% BM-day<sup>-1</sup> groups (all  $p > 0.08$ ) but was significantly positively correlated with body size in the 1.0 and 0.5% BM-day<sup>-1</sup> groups (all  $r \geq 0.459$ , all  $p < 0.03$ ). Neither relative nor absolute  $U_{crit}$  was significantly correlated with haematocrit, condition factor, or fin score in any of the tanks (all  $p > 0.05$ ).

## Discussion

### Growth

Since the energy required for growth is obtained in the diet, food intake necessarily affects the growth rates of fish. However, at lower rations, where there is intensified competition for food and a more strictly enforced hierarchy (McCarthy et al. 1993), there is a disproportionate decrease in mean growth rate (Table 1). This depression of growth at low rations is most likely the result of increased energy expenditure and stress levels as individuals compete for food (Metcalf 1986; Abbott and Dill 1989).

It is important to note that the positive relationship between overall SGR and food consumption was significant only among fish fed a 2.0% BM-day<sup>-1</sup> ration but not when rations were higher (Gregory and Wood 1998) or lower (present study). At high rations, the costs associated with the digestion and conversion of food (i.e., specific dynamic action, Alsop and Wood 1997), the reduction of growth efficiency as fish become larger (Wurtsbaugh and Davis 1977), and the increase in gastric evacuation rate (and associated decrease in absorptive efficiency) that occurs with increasing ration (Wurtsbaugh and Davis 1977; Jobling 1994) may contribute to a system of "diminishing returns" whereby beyond a certain maximum food intake, there is no further benefit to growth rate as ration increases (Fig. 1; also see Gregory and Wood 1998). At very low rations, the relationship between food intake and SGR is presumably not significant, simply because there is little difference in the actual food consumptions of individual fish. This lack of separation of the data therefore makes the resolution of any relationships very difficult. In the case of MSM, where there was a more profound separation of the data, significant positive relationships between SGR and MSM were found under all rations (Fig. 1B).

Fish in the low-ration tanks also showed lower condition factors and haematocrits (Table 1). The first of these suggests a higher level of protein and lipid catabolism among these fish (Barton et al. 1987). Although morphological differences may influence the relative swimming performances of fish from fast- versus slow-growing strains (Taylor and McPhail 1985), the lack of association between morphological characteristics (i.e., condition factor, a measure of the "bulkiness" of a fish) and either growth rate or swimming performance in the present study suggests that changes in body shape of this type are not responsible for the relationships between SGR and  $U_{crit}$  observed among individual fish.

Differences in haematocrit probably did not result from blood loss associated with higher levels of fin damage (see below) in the fish, since there was no correlation between haematocrit and fin score. Instead, the lower haematocrits probably resulted from the insufficient energy and nutrient intake among these fish, limiting their ability to produce somatic tissues of various types (including red blood cells). More importantly, haematocrit was found to be unrelated to both growth rate and swimming performance in the present study. Experimental manipulations of haematocrit over a larger range have been shown to affect swimming performance, with increased haematocrit resulting in increased performance (Gallaughan et al. 1995). However, this rela-

tionship may be of limited biological significance and certainly does not explain the SGR versus swimming performance trade-off, thereby discounting the earlier suggestion of Gregory and Wood (1998).

### Feeding rank

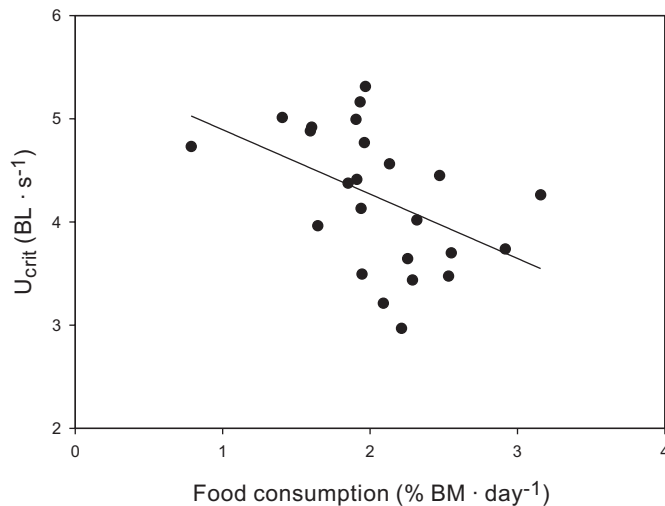
In accordance with previous studies using one daily feeding (McCarthy et al. 1992), and in contrast with a previous study that employed three daily meals (Gregory and Wood 1998), fish fed on the lowest ration in the present study showed a significantly higher mean CV than the fish in all other ration groups (Table 1). This result indicates more variable individual feeding patterns from day to day in a situation where competition for food is intensified. However, CV was not related to any other potential indicators of social rank, such as MSM, fin score, or individual food consumption. In addition, CV has been shown to be altered significantly by elevations in plasma cortisol levels independent of social interactions (Gregory and Wood 1999). Although CV has previously been found to correlate with MSM (McCarthy et al. 1992), which in turn has been correlated with indicators of social rank such as brain serotonin activity (Winberg et al. 1993), the results of the present study suggest that CV may not always provide a reliable index of feeding rank in fish (cf. McCarthy et al. 1992, 1993; Winberg et al. 1993; Jobling 1994).

The dorsal and caudal fins are the primary sites of aggressive attack among juvenile rainbow trout (Abbott and Dill 1985), with the dorsal fin typically receiving more damage than the caudal fin (Abbott and Dill 1985, 1989; Moutou et al. 1998; present study). Under low-ration conditions (1.0 and 0.5% BM-day<sup>-1</sup>), MSM and initial mass were positively related to fin score, suggesting that there were higher levels of aggression in these tanks as a result of more intense competition for food or the enforcement of a more strict dominance hierarchy (Davis and Olla 1987; Olla et al. 1992; Moutou et al. 1998). In addition, caudal and total fin condition indices were positively correlated with ration level at weeks 7, 8, and 9 (but not at the earlier measurements), suggesting that there were higher levels of aggressive attacks in the low-ration tanks whose effects became apparent after a few weeks. It is also possible that the intensified competition for food leads to higher stress levels among low-ration fish, resulting in decreased fin conditions arising in part from the reduced immunity and tissue repair associated with plasma cortisol elevation (Pickering and Pottinger 1989; Gregory and Wood 1999).

### Swimming performance

The swimming performances of rainbow trout swum individually were repeatable in this study, similar to the repeatability when fish are swum communally in small groups (Gregory and Wood 1998). This result suggests that either swimming fish in groups or swimming them individually is an acceptable approach for studies of this sort. This consistency further supports the view expressed by several researchers (Bennett 1987; Kolok 1992a; Gregory and Wood 1998, 1999) that variation among individuals should be seen as a valuable experimental resource rather than a statistical annoyance.

**Fig. 4.** Relationship between relative  $U_{crit}$  and individual food consumption for fish in the 2.0% BM·day<sup>-1</sup> ration group ( $r^2 = 0.2111$ ,  $p < 0.03$ ,  $n = 24$ ,  $y = -0.62x + 5.52$ ). No such relationships were found in any of the other ration groups (all  $p > 0.12$ ).



More importantly, the negative relationships between SGR and relative  $U_{crit}$  reported in Gregory and Wood (1998) have been confirmed and occurred over a similar range of food intakes as in that study (Fig. 3A). Thus, even when the possibility of social interactions is removed by swimming the fish individually rather than communally, the relationships persist. In addition, there was a negative relationship between SGR and absolute  $U_{crit}$  among fish in the appropriate ration group (Fig. 3B), which confirms the results reported by Kolok and Oris (1995) using fathead minnows (*Pimephales promelas*).

The results of the present study have also clarified the issue of possible spurious correlations between SGR and  $U_{crit}$  resulting from the well-established relationships between  $U_{crit}$  and body size. In the present study, both swim SGR and indicators of body size were negatively correlated with  $U_{crit}$ , but because the swimming schedule used resulted in differences in the lengths of growth periods for individual fish, there were no correlations between body size and swim SGR in the relevant ration group. Thus, growth rate itself, independent of effects on body size, significantly affects the swimming performance of individual fish. This is consistent with the findings of Farrell et al. (1997) who found that growth-enhanced transgenic salmon showed a reduction in swimming performance that could not be explained on the basis of differences in body size alone.

This negative relationship between swim SGR and  $U_{crit}$  is seen only among fish fed a 2.0% BM·day<sup>-1</sup> ration and is not apparent at higher rations (~4% BM·day<sup>-1</sup>, which represents satiation, Gregory and Wood 1998) or lower rations ( $\leq 1.5\%$  BM·day<sup>-1</sup>). Moreover, the significant negative relationship between  $U_{crit}$  and individual food consumption (Fig. 4) clearly indicates that the costs associated with feeding, digestion, and conversion of food to somatic tissue are largely responsible for the emergence of this trade-off. At a very low ration (0.5% BM·day<sup>-1</sup>), on the other hand, the relationship reverses sign and becomes positive, with higher growth rates

resulting in heightened swimming performance. It is therefore apparent that below a certain threshold, there is insufficient energetic intake to invest in either growth or swimming performance and that under conditions of very low rations, only those fish that receive a certain amount of food are able to both grow and swim effectively. Thus, the observed trade-off between SGR and  $U_{crit}$  may occur only over a range of food intakes from roughly 2.0 to 4.0% BM·day<sup>-1</sup>, disappearing above and below this level and switching to a positive relationship below a certain threshold around 0.5% BM·day<sup>-1</sup> where many fish exhibit negative growth rates.

Our findings are of potential importance in programs of captive breeding and reintroduction into the wild, since the range (i.e., 2.0–4.0% BM·day<sup>-1</sup>) for which the potential trade-off occurs precisely is that recommended in aquaculture for the size of fish and water temperatures used in the present study (Cho 1990). The relevance of this trade-off to fish in the wild is much more difficult to assess because the daily rations of wild fish can only be estimated based on measurements of instantaneous stomach content and approximate rates of gut clearance (e.g., Boisclair and Marchand 1993) and because these studies typically involve various fish sizes and water temperatures. However, the few available estimates of daily ration among wild juvenile salmonids suggest that the 2.0–4.0% BM·day<sup>-1</sup> range of rations (and higher, which is important, since naturally occurring food sources would be of lower digestive quality than commercial fish feed) occurs naturally in the wild (Doble and Eggers 1978; Brodeur and Pearcy 1987; Angradi and Griffith 1990), suggesting that this trade-off applies to juvenile trout swimming and growing in the wild as well.

The results of the present study make it clear that individual feeding, growth, and swimming performance are interrelated in a highly complex fashion. Specifically, there is a trade-off between aerobic swimming performance and growth rate that occurs only over a narrow but biologically relevant range of food intakes. In addition, this trade-off appears to result from costs associated with feeding and digestion and cannot be explained simply as a result of the differences in body size or haematocrit associated with rapid growth.

## Acknowledgments

This research was supported by a Natural Sciences and Engineering Research Council of Canada grant to C.M.W. Sincere thanks are given to Michelle Cottreau of the Radiology Department at the McMaster University Medical Centre for her generous assistance. Thanks also to the anonymous reviewers who provided helpful comments.

## References

- Abbott, J.C., and Dill, L.M. 1985. Patterns of aggressive attack in juvenile steelhead trout (*Salmo gairdneri*). *Can. J. Fish. Aquat. Sci.* **42**: 1702–1706.
- Abbott, J.C., and Dill, L.M. 1989. The relative growth of dominant and subordinate juvenile steelhead trout (*Salmo gairdneri*) fed equal rations. *Behaviour*, **108**: 104–113.
- Alsop, D.H., and Wood, C.M. 1997. The interactive effects of feeding and exercise on oxygen consumption, swimming perfor-

- mance, and protein usage in juvenile rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* **200**: 2337–2346.
- Angradi, T.R., and Griffith, J.S. 1990. Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho. *Can. J. Fish. Aquat. Sci.* **47**: 199–209.
- Barton, B.A., Schreck, C.B., and Barton, L.D. 1987. Effects of chronic plasma cortisol administration and daily acute stress on growth, physiological conditions, and stress responses in juvenile rainbow trout. *Dis. Aquat. Org.* **2**: 173–185.
- Beamish, F.W.H. 1978. Swimming capacity. *In* Fish physiology. Vol. VII. Locomotion. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, New York. pp. 101–187.
- Bennett, A.E. 1987. Interindividual variability: an underutilized resource. *In* New directions in ecological physiology. *Edited by* M.E. Feder, A.E. Bennett, W.W. Burggren, and R.B. Huey. Cambridge University Press, Cambridge, U.K. pp. 147–166.
- Boisclair, D., and Marchand, F. 1993. The guts to estimate fish daily ration. *Can. J. Fish. Aquat. Sci.* **50**: 1969–1975.
- Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can.* **21**: 1183–1225.
- Brodeur, R.D., and Percy, W.G. 1987. Diel feeding chronology, gastric evacuation and estimated daily ration of juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum), in the coastal marine environment. *J. Fish Biol.* **31**: 465–477.
- Cho, C.Y. 1990. Fish nutrition, feeds, and feeding: with special emphasis on salmonid aquaculture. *Food Rev. Int.* **6**: 333–357.
- Davis, M.W., and Olla, B.L. 1987. Aggression and variation in growth of chum salmon (*Oncorhynchus keta*) juveniles in seawater: effects of limited rations. *Can. J. Fish. Aquat. Sci.* **44**: 192–197.
- Doble, B.D., and Eggers, D.M. 1978. Diel feeding chronology, rate of gastric evacuation, daily ration, and prey selectivity in Lake Washington juvenile sockeye salmon (*Oncorhynchus nerka*). *Trans. Am. Fish. Soc.* **107**: 36–45.
- Farrell, A.P., Johansen, J.A., and Suarez, R.K. 1991. Effects of exercise-training on cardiac performance and muscle enzymes in rainbow trout, *Oncorhynchus mykiss*. *Fish Physiol. Biochem.* **4**: 303–312.
- Farrell, A.P., Bennett, W., and Devlin, R.H. 1997. Growth-enhanced transgenic salmon can be inferior swimmers. *Can. J. Zool.* **75**: 335–337.
- Gallaugh, P., Thorarensen, H., and Farrell, A.P. 1995. Hematocrit in oxygen transport and swimming in rainbow trout (*Oncorhynchus mykiss*). *Resp. Physiol.* **102**: 279–292.
- Goolish, E.M., and Adelman, I.R. 1987. Tissue-specific cytochrome oxidase activity in largemouth bass: the metabolic costs of feeding and growth. *Physiol. Zool.* **60**: 454–464.
- Gregory, T.R., and Wood, C.M. 1998. Individual variation and interrelationships between swimming performance, growth rate, and feeding in juvenile rainbow trout (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* **55**: 1583–1590.
- Gregory, T.R., and Wood, C.M. 1999. The effects of chronic plasma cortisol elevation on the feeding behaviour, growth, competitive ability, and swimming performance of juvenile rainbow trout. *Physiol. Zool.* **72**. In press.
- Jobling, M. 1994. Fish bioenergetics. Chapman and Hall, London, U.K. pp. 101–109.
- Kolok, A.S. 1992a. The swimming performances of individual largemouth bass (*Micropterus salmoides*) are repeatable. *J. Exp. Biol.* **170**: 265–270.
- Kolok, A.S. 1992b. Morphological and physiological correlates with swimming performance in juvenile largemouth bass acclimatized to winter and summer conditions. *Am. J. Physiol.* **263**: R1042–R1048.
- Kolok, A.S., and Oris, J.T. 1995. The relationship between specific growth rate and swimming performance in male fathead minnows (*Pimephales promelas*). *Can. J. Zool.* **73**: 2165–2167.
- McCarthy, I.D., Carter, C.G., and Houlihan, D.F. 1992. The effect of hierarchy on individual variability in daily feeding of rainbow trout, *Oncorhynchus mykiss* (Walbaum). *J. Fish Biol.* **41**: 257–263.
- McCarthy, I.D., Houlihan, D.F., Carter, C.G., and Moutou, K. 1993. Variation in individual food consumption rates of fish and its implications for the study of fish nutrition and physiology. *Proc. Nutr. Soc.* **52**: 427–436.
- Metcalf, N.B. 1986. Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. *J. Fish Biol.* **28**: 525–531.
- Moutou, K.A., McCarthy, I.D., and Houlihan, D.F. 1998. The effect of ration level and social rank on the development of fin damage in juvenile rainbow trout. *J. Fish Biol.* **52**: 756–770.
- Olla, B.L., Davis, M.W., and Ryer, C.H. 1992. Foraging and predator avoidance in hatchery-reared Pacific salmon: achievement of behavioural potential. *In* The importance of feeding behavior for the efficient culture of salmonid fishes. *Edited by* J.E. Thorpe and F.A. Huntingford. The World Aquaculture Society, Baton Rouge, La. pp. 156–168.
- Pickering, A.D., and Pottinger, T.G. 1989. Stress responses and disease resistance in salmonid fishes: effects of chronic elevation of plasma cortisol. *Fish Physiol. Biochem.* **7**: 253–258.
- Taylor, E.B., and McPhail, J.D. 1985. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. *Can. J. Fish. Aquat. Sci.* **42**: 2029–2033.
- Winberg, S., Carter, C.G., McCarthy, I.D., He, Z.-Y., Nilsson, G.E., and Houlihan, D.F. 1993. Feeding rank and brain serotonergic activity in rainbow trout *Oncorhynchus mykiss*. *J. Exp. Biol.* **179**: 197–211.
- Wurtsbaugh, W.A., and Davis, G.E. 1977. Effects of fish size and ration level on the growth and food conversion efficiency of rainbow trout, *Salmo gairdneri* Richardson. *J. Fish Biol.* **11**: 99–104.
- Zar, J.H. 1996. Biostatistical analysis. 3rd ed. Simon & Schuster, Upper Saddle River, N.J. pp. 362–367.