

Individual variation and interrelationships between swimming performance, growth rate, and feeding in juvenile rainbow trout (*Oncorhynchus mykiss*)

T. Ryan Gregory and Chris M. Wood

Abstract: Variation among individuals in specific growth rate (SGR), feeding, and two measures of swimming performance and their possible interrelationships were investigated in juvenile rainbow trout (*Oncorhynchus mykiss*) kept in groups on either satiation or half-satiation rations. Maximum sustainable velocity (U_{crit}) was measured as an index of aerobic swimming performance and stamina (fatigue time in a fixed-velocity test at 6 body lengths·s⁻¹) as an index of anaerobic performance. Individual performance in both of these tests was found to be significantly repeatable. Trout fed on half-satiation ration exhibited significantly lower mean values of SGR and body size and higher levels of aggression-related fin damage, but no significant differences in stamina, relative or absolute U_{crit} , glycogen content, or plasma cortisol. However, in these fish, there was a significant negative relationship between SGR and relative U_{crit} , a significant positive relationship between SGR and stamina, and a significant positive relationship between SGR and total daily meal. None of these relationships were seen in fish fed to satiation. Plasma cortisol and tissue glycogen stores were not related to SGR. These results indicate that under the intensified competition of restricted ration, there are trade-offs between growth, feeding, and different types of swimming performance.

Résumé : La variation entre individus du taux de croissance spécifique (TCS), de l'alimentation et de deux mesures de la performance natatoire, de même que les relations possibles entre ces paramètres, ont été étudiées chez des truites arc-en-ciel (*Oncorhynchus mykiss*) juvéniles réparties en deux groupes : un premier groupe nourri à satiété et un deuxième groupe à moitié rassasié. La vitesse soutenable maximale (U_{crit}) a été mesurée à titre d'indice de la performance natatoire aérobie, et l'endurance (temps de fatigue dans un test à vitesse fixe de 6 longueurs de corps·s⁻¹) à titre d'indice de la performance anaérobie. On a observé que la performance individuelle dans chacun de ces tests pouvait de façon significative être répétée. Chez les truites à moitié rassasiées, on a observé des valeurs moyennes de TCS et de taille corporelle significativement inférieures, et des dommages aux nageoires liés à l'agression significativement plus importants, mais aucune différence significative en ce qui a trait à l'endurance, à l' U_{crit} relative ou absolue, à la teneur en glycogène et au cortisol plasmatique. Cependant, il existait chez ces poissons une relation négative significative entre le TCS et l' U_{crit} relative, une relation positive significative entre le TCS et l'endurance, et une relation positive significative entre le TCS et la ration alimentaire totale quotidienne. Aucune de ces relations n'a été observée chez les poissons nourris à satiété. Il n'y avait pas non plus de relation entre, d'une part, le cortisol plasmatique et le glycogène tissulaire et, d'autre part, le TCS. Ces résultats montrent que l'intensification de la compétition liée à la limitation de la ration alimentaire induit des compromis entre la croissance, l'alimentation et différents types de performance natatoire.

[Traduit par la Rédaction]

Introduction

When groups of fish are raised under continuous swimming conditions, they show both faster growth and improved swimming performance (Davison 1997). The faster growth is thought to be due to an increase in the ratio of protein synthesis to protein degradation (Houlihan and Laurent 1987) and a

reduction of nonspecific aggressive activity associated with continuous exercise, as well as the implementation of energy-efficient "ram ventilation" (Christiansen and Jobling 1990). However, in themselves, growth rate and swimming ability had been viewed as unrelated until very recently, and very few studies have been conducted that investigate any possible interactions between them within individual animals. Furthermore, many physiologists have traditionally viewed individual variation as no more than "statistical noise," which could be avoided or masked with the use of a sufficiently large number of animals. More recently, individual variation in swimming performance has been shown to be repeatable in largemouth bass (*Micropterus salmoides*) (Kolok 1992), altering its status from a mere statistical annoyance to something of real importance worthy of study. By experimentally exploiting, rather than suppressing, the existence of individual differences in growth rate and swimming ability, it is possible to investigate

Received June 4, 1997. Accepted February 11, 1998.
J14046

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potential trade-offs between these two aspects of trout life history. A pioneering recent study on fathead minnow (*Pimephales promelas*) suggests that there may indeed be a trade-off between growth rate and aerobic swimming ability (Kolok and Oris 1995), but the mechanistic basis of the trade-off was not investigated, nor was the possibility of a similar trade-off with anaerobic swimming ability. To date, there have been no studies of this nature on rainbow trout (*Oncorhynchus mykiss*).

Individual variation in feeding may be an important causal element in the interaction between growth rate and exercise ability. Recent developments in X-ray technology have greatly facilitated the study of individual feeding with a minimum of disturbance to the fish (e.g., Carter et al. 1993; McCarthy et al. 1993). With this approach, it has been shown that position in the feeding hierarchy affects growth, with subordinate individuals receiving less food than dominant ones (McCarthy et al. 1992, 1993). Subordinate fish also have significantly lower food conversion efficiencies and grow more slowly even if fed the same ration as dominant fish (Abbott and Dill 1989). Slower growth rates are almost certainly exacerbated by the increased levels of stress and physical activity among subordinate fish, but this may not represent a complete explanation (Abbott and Dill 1989).

The present study employed these approaches, together with swim tunnel tests (Hammer 1995), to examine individual variation in swimming ability, growth rate, and feeding in juvenile rainbow trout. The maximum sustainable swimming speed, or U_{crit} (critical velocity), was used to measure aerobic capacity (Brett 1964) and the fixed-velocity test of fatigue to measure stamina (Brett 1967; Beamish 1978). This latter test has recently been evaluated by McDonald et al. (1998), who concluded that it provided a nondestructive approximation (as opposed to destructive tissue metabolite analysis) of anaerobic capacity. The first specific objective was to examine the relationships between specific growth rate and these two ecologically relevant measures of swimming performance, and a second objective was to relate the relationships between swimming performance and growth rate to feeding and to examine the effects of different rations on individual growth rates.

Materials and methods

Juvenile rainbow trout (series 1: 11–25 g; series 2 and 3: 4–11 g) were obtained from Humber Springs Trout Hatchery in Orangeville, Ont. The fish were kept at $15 \pm 1^\circ\text{C}$ in dechlorinated Hamilton, Ont., tap water (see Alsop and Wood 1997) with a photoperiod of 12.5 h light : 11.5 h dark and constant flow-through at a rate of $\sim 1 \text{ L}\cdot\text{min}^{-1}$. Holding tanks consisted of 60-L tubs covered by fabric mesh and shaded by opaque plastic lids. Three pieces of ABS piping were added to each tank to act as shelters after preliminary experiments showed a high degree of aggression-related mortality.

Series 1: Repeatability of swim performance

Eight fish (mean initial mass $18.70 \pm 1.04 \text{ g}$) were anaesthetized individually in 0.1 g tricaine methanesulfonate (MS 222)·L⁻¹ set to a pH of 8.0 with 3.0 M NaOH, weighed (to 0.01 g), measured for fork length (to the nearest 0.1 cm), and marked for individual identification using a PanJet ink injector and Alcian Blue 8GX dye. The fish were then placed in a 60-L holding tank and allowed to recover for 48 h. The fish were offered food 2 days after marking and were swum for the first time 2 days after feeding (and therefore had been fasted for 48 h prior to swimming). On the day of swimming, all eight fish

were identified, weighed, measured for fork length, maximum height, and maximum width, and placed in the 50-cm (20-L) swimming chamber of a modified 100-L Beamish-type respirometer calibrated prior to use with a Kent Microflo type 265 propeller-style flowmeter. The fish were allowed to habituate to the tunnel at 1 body length (BL)·s⁻¹ (all increments were based on the mean length of the group) for 2 h. After this initial period, the velocity of the water was increased by 0.75 BL·s⁻¹ every 40 min. Fish that became impinged against the grating at the rear of the swim chamber were prompted to resume swimming by manual removal from the grating and reintroduction into the current. When a fish could no longer be prompted to swim in this manner, it was judged exhausted and removed. The relative U_{crit} (BL per second) of each fish was then calculated as in Brett (1964). Following this initial trial, the fish were given 8 days to recover and were offered food every 48 h. A second identical U_{crit} trial was carried out at the end of this recovery period (with a 48-h fasting period prior to swimming). The U_{crit} values were not corrected for blocking effects, since the total cross-sectional area of the fish (as calculated in Kolok and Oris 1995) did not occupy more than 10% of the area of the swim tunnel. A shocking grid was not used, in accordance with animal care regulations.

A test of the repeatability of stamina was also conducted. Ten fish of similar size (mean initial mass $13.44 \pm 0.34 \text{ g}$) were chosen from a larger tank of fish, measured for fork length (to the nearest 0.1 cm), and swum immediately (one at a time) in the 100-L Beamish-type respirometer described above. Each fish was allowed to habituate to the swim tunnel for 5 min, followed by an increase in velocity of 1 BL·s⁻¹ every 30 s until a speed of 6 BL·s⁻¹ was reached, at which time a stopwatch was started. When the fish became impinged against the rear grating, the timing clock was stopped, and was restarted only if the fish resumed swimming following manual reintroduction into the current. When the fish could no longer be prompted to swim in this way, it was judged exhausted and removed from the tunnel and the total time swum at 6 BL·s⁻¹ recorded. After swimming, each fish was weighed, measured for maximum height and width, marked for individual identification, and then allowed to recover for 48 h before being offered food. Thereafter, the fish were fed on three consecutive days to promote replenishment of glycolytic substrates. The fish were then fasted for 48 h before a second identical trial was conducted. In this trial, the individual trout were swum in a different order from the first trial.

Series 2: Growth rate and swim performance

Fish were weighed to the nearest 0.01 g, measured for fork length (to the nearest 0.1 cm), marked for individual identification as above, and then placed alternately in each of the four tanks to avoid any "ease-of-capture" biases in any given tank. Twenty fish were placed in each tank, with no significant differences in mean initial mass between any of the tanks (tank 1, $7.67 \pm 0.37 \text{ g}$; tank 2, $7.43 \pm 0.38 \text{ g}$; tank 3, $7.75 \pm 0.66 \text{ g}$; tank 4, $7.47 \pm 0.39 \text{ g}$; all $p > 0.60$). Fish in tanks 2 and 3 were fed to satiation three times per day (10:00, 13:00, 16:00; all times $\pm 0.5 \text{ h}$) using commercial feed (Ziegler Bros., Inc., Gardeners, Pa.). This process involved providing ~ 5 –10 pellets at a time until the fish stopped eating, a process that typically took 10–15 min. The total percent body mass of food consumed was then measured and used to calculate a half-satiation diet for the other two tanks (1 and 4), such that these tanks received one half of the food given to the satiation tanks, in terms of percent body mass. These fish were also fed three times per day, but since the amount to be delivered was predetermined and the fish ate quickly, feeding was typically complete in less than 5 min.

The fish were grown for 3 weeks and were weighed and measured weekly (anaesthesia was deemed unnecessarily stressful and was not used). After the initial growing period, the fish were challenged with one of two types of swimming trial. Fish from two tanks (one satiation, one half-satiation) were tested for U_{crit} whereas the other two were tested for stamina using the methods described in series 1. After

a 1-week recovery period, during which the feeding regime was maintained, the trials were reversed such that each fish had eventually been tested for both types of swimming performance. In all cases, the fish were fasted for at least 18 h prior to swimming. The U_{crit} was evaluated by swimming fish in groups of 10 or less, with groups formed on the basis of body length (with a maximum range of 1.5 cm). Relative U_{crit} (BL per second) was calculated separately for each fish as in Brett (1964) and was multiplied by the individual body length to give absolute U_{crit} (centimetres per second).

The specific growth rate (SGR) of each fish (percent per day) was calculated as in Kolok and Oris (1995) at the time of swimming based on growth over the total growth period. Days on which the fish were swum were not counted as growing days, since the fish were not fed on these days. In addition to mass and length, the fish were measured for maximum height and width prior to swimming, which permitted calculation of both maximum cross-sectional area ($\pi[(0.5 \times \text{maximum height}) \times (0.5 \times \text{maximum width})]$) and condition factor ($100 \times \text{mass} \times \text{length}^{-3}$).

Series 3: Feeding and growth rate

Fish were kept in two of the same tanks as used in series 2, under the same conditions, except that the temperature was $14 \pm 1^\circ\text{C}$ and the flow-through rate was $\sim 0.4 \text{ L}\cdot\text{min}^{-1}$. These small differences were dictated by the need to heat the inflowing water during midwinter. Twenty-five fish were placed in each tank, with no significant differences in mean initial mass between the two (tank 1: $5.55 \pm 0.18 \text{ g}$, tank 2: $5.34 \pm 0.11 \text{ g}$; $p > 0.32$).

The fish were fed three times per day, with one tank fed to satiation and the other fed a half-satiation ration exactly as in series 2. However, the diet was altered. Commercial fish feed (Ziegler Bros., Inc., Gardners, Pa.) was powdered in a standard kitchen blender, mixed with water, and repelleted using a pasta maker. The food was cut into pellets and dried overnight at 60°C . A second diet was prepared in the same manner, but with the incorporation of 8.5-grade (0.400–0.455 mm) lead glass ballotini beads (Jencons USA, Inc., Bridgeville, Pa.) into the food (6% by mass of dry powdered food).

The fish were grown for 3 weeks and weighed and measured weekly. During this time, they were fed the repelleted food without beads. After this initial growing period, the fish were then fed a single meal consisting of the repelleted food containing the ballotini beads (Carter et al. 1993; McCarthy et al. 1993). The ballotini beads did not affect the palatability of the food, as judged from the total meal size. After at least 1 h, the fish were anaesthetized individually as above and X-rayed using a Faxitron 805 portable X-ray machine (3- to 4-s exposure at 70 kVP) to visualize the number of ballotini beads. All X-raying was completed within 3 h of feeding, and the fish were air exposed for no more than 1 min. The condition of the dorsal and caudal fins was also noted at this time, and each was assigned a numerical score between 1 (worst) and 4 (best). This process was repeated three times, with 1-week recovery periods, such that each fish had been X-rayed once after each of the three daily meals. A sample of 180 food pellets was also X-rayed, and <4% of the pellets were found to be devoid of beads.

The beads located in the digestive tracts of the fish were counted from the X-ray image, and the total number of beads found in all of the fish within each tank was used to calculate the percent meal obtained by each individual fish. The amount of food in grams (wet weight) obtained by each fish for each of the three daily meals was calculated by determining the percentage of beads found within each fish and multiplying this by the known amount of food given to the tank. In only three cases were individual fish seen to regurgitate food, and none of the X-rays showed movement of beads further than one third of the way along the digestive tract, suggesting that none of the beads had been evacuated prior to X-raying.

Coefficient of variation (CV) was calculated for each fish based on the three recorded meals (McCarthy et al. 1992). The total daily meal of each fish was also calculated and was corrected for body

mass, since it consisted of values obtained over a 3-week period, during which the mass of the fish changed:

(1) Total daily meal =

$$\sum_{n=1}^3 \left(\frac{(\% \text{ meal obtained})_n \times (\text{total meal size})_n}{(\text{body mass at time of meal})_n} \right) \times 100\%.$$

After the completion of all three X-ray exposures, the fish were sacrificed in groups of five or six using $0.6 \text{ g MS } 222\cdot\text{L}^{-1}$, a concentration that is lethal within 30 s of immersion, thereby preventing the induction of a cortisol response (Beitinger and McCauley 1990). Individuals were identified and blood samples were taken following caudal severance using standard haematocrit tubes. Bodies were freeze-clamped in liquid nitrogen, and the blood was spun for 2 min at $5000 \times g$. Haematocrits were measured, and then blood plasma was withdrawn and frozen in liquid nitrogen. Whole carcasses and blood plasma were stored at -70°C for several days. Whole-body glycogen was analyzed enzymatically as outlined in Bergmeyer (1965), and plasma cortisol was measured using an ImmunoChem Coated Tube Cortisol ^{125}I radioimmunoassay kit (ICN Biomedicals, Inc., Costa Mesa, Calif.).

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.). In all cases, differences in means between groups were evaluated using two-sample *t*-tests, and all differences in variance between groups were evaluated using *F*-tests. Single, multiple, and forward stepwise linear regressions were performed with Statistix v1.0 using least-squares regression, and the repeatability of performance was determined using the Spearman rank correlation test as in Kolok (1992). All averages are reported as mean \pm SE (*n*).

Results

Series 1

The mean U_{crit} of the fish was $5.23 \pm 0.09 \text{ BL}\cdot\text{s}^{-1}$ in the first trial and $5.64 \pm 0.10 \text{ BL}\cdot\text{s}^{-1}$ in the second trial, indicating a significant improvement in performance ($p = 0.0079$, $n = 8$). More importantly, the relative performance of these individual fish was repeatable when swum in groups (Spearman rank correlation coefficient, $\rho = 0.8571$, $p = 0.0065$) (Fig. 1A).

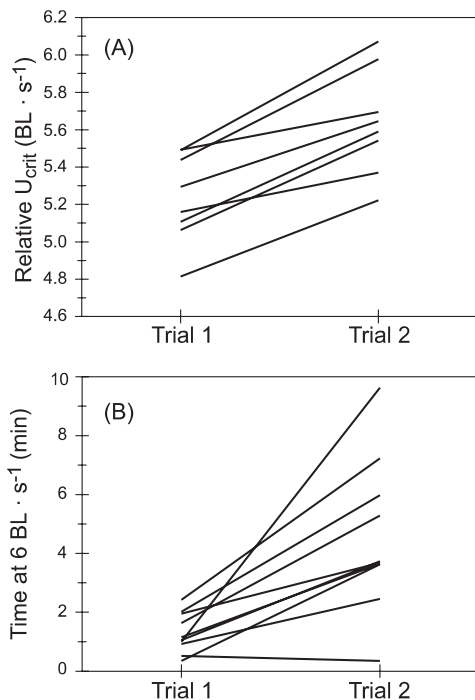
The fish used in the stamina tests also showed a significant increase in performance between trials (mean time at $6 \text{ BL}\cdot\text{s}^{-1}$; trial 1, $1.30 \pm 0.21 \text{ min}$; trial 2, $4.56 \pm 0.82 \text{ min}$; $p = 0.0031$, $n = 10$). As for U_{crit} , the stamina of individual fish was repeatable during the two trials ($\rho = 0.6485$, $p = 0.0425$) (Fig. 1B).

Series 2

A significant *negative* regression was found between SGR and relative U_{crit} in the half-satiation group ($r^2 = 0.2004$, $p = 0.0131$) (Fig. 2A). Relative U_{crit} was also found to be significantly negatively correlated with body mass, fork length, and maximum cross-sectional area (all $p < 0.05$) but not with condition factor ($p > 0.27$). A forward stepwise linear regression including all of these variables showed SGR to be the most explanatory model (explaining roughly 20% of the variance in U_{crit} observed). Mass, cross-sectional area, length, and SGR were found to be positively correlated with one another in the half-satiation group (all $p < 0.05$).

Linear regressions were performed using the regression residuals of relative U_{crit} versus SGR. No significant regressions

Fig. 1. Repeatability of two different types of individual swimming performance, (A) relative critical swimming velocity (U_{crit}) ($\rho = 0.8571$, $p < 0.01$) and (B) stamina (swimming duration at a fixed velocity) ($\rho = 0.6485$, $p < 0.05$). Both types of swimming showed repeatability and an improvement in performance over the two trials.



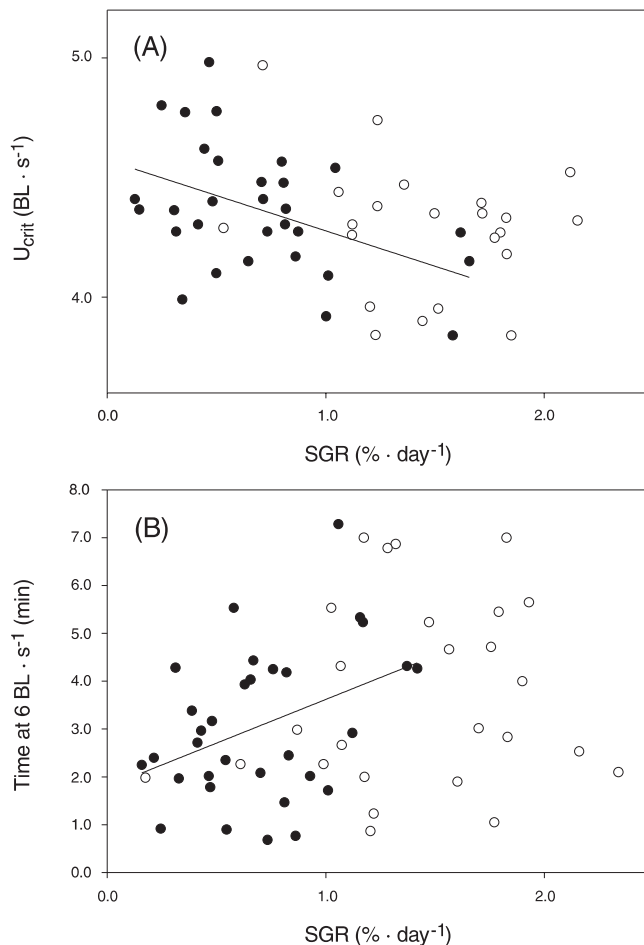
were found between these residuals and mass, length, or cross-sectional area (all $p > 0.19$). A significant regression was found between the regression residuals from the relationship between mass and SGR and those from the relationship between mass and relative U_{crit} ($r^2 = 0.172$, $p < 0.02$).

The fish fed to satiation did not show any significant correlation between relative U_{crit} and SGR or between relative U_{crit} and mass, length, cross-sectional area, or condition factor (all $p > 0.10$). When the data from both diet groups were pooled together, a similar relationship to that found in the half-satiation group alone was observed, with significant negative correlations between relative U_{crit} and SGR, mass, length, and cross-sectional area (all $p < 0.05$).

The fish were also evaluated in terms of absolute U_{crit} (centimetres per second). In both diet groups, significant positive regressions were found between absolute U_{crit} and mass, length, and cross-sectional area (all $p < 0.05$) but not with SGR or condition factor (all $p > 0.43$). No significant differences in mean absolute U_{crit} ($p > 0.50$) or variance ($p > 0.13$) were found between the two diet groups (Table 1).

In contrast with the relationship with relative U_{crit} , a significant *positive* correlation was found between SGR and stamina in the half-satiation group ($r = 0.3848$, $p < 0.03$) (Fig. 2B). No significant correlations were found between stamina and mass, length, cross-sectional area, or condition factor (all $p > 0.25$). In the satiation group, stamina was not significantly correlated with SGR or with any of the other variables examined (all $p > 0.74$). When the data for both diet groups were pooled, stamina and SGR were not significantly correlated ($r = 0.2554$, $p =$

Fig. 2. Relationship between (A) critical swimming velocity (U_{crit}) and specific growth rate (SGR) and (B) stamina (swimming duration at a fixed velocity) and SGR among fish fed on satiation (open circles) and half-satiation (solid circles) rations. A significant negative regression ($r^2 = 0.2004$, $p < 0.02$, $n = 30$) was found between U_{crit} and SGR, and a significant positive regression ($r^2 = 0.1481$, $p < 0.03$, $n = 32$) was found between stamina and SGR in the half-satiation group, but not among fish fed to satiation. The regression lines $y = -0.3x + 4.57$ (Fig. 2A) and $y = 1.83x + 1.79$ (Fig. 2B) represent the relationships found in the half-satiation group only.



0.0530). Furthermore, no significant correlations were found between stamina and mass, length, cross-sectional area, or condition factor (all $p > 0.15$).

The mean values of swimming performance and growth rates were also compared between the two diet groups (Table 1). While the fish fed to satiation exhibited a significantly higher mean SGR than the fish fed to half-satiation ($p < 0.0001$), there was no significant difference in relative U_{crit} or fatigue time between the two treatments (all $p > 0.14$).

Series 3

A significant *positive* regression was found between SGR and total daily meal (percent body mass) in the half-satiation group ($r^2 = 0.5413$, $p < 0.0001$). No significant regressions were found between SGR and total daily meal among fish fed a satiation diet ($p > 0.44$) (Fig. 3). As in series 2, fish fed to

Table 1. Mean values \pm SE (*n*) of mass, length, condition factor, cross-sectional area, specific growth rate (SGR), and swimming performance in the satiation and half-satiation diet groups of series 2.

Variable	Half-satiation	Satiation	<i>p</i>
Initial mass (g)	7.38 \pm 0.24 (40)	7.34 \pm 0.25 (40)	>0.99
Final mass (g)	9.91 \pm 0.39 (33)	13.24 \pm 0.63 (29)	<0.0001*
Initial length (cm)	8.7 \pm 0.1 (40)	8.7 \pm 0.1 (40)	>0.87
Final length (cm)	9.4 \pm 0.1 (33)	9.8 \pm 0.1 (29)	<0.04*
Condition factor ($100 \times \text{g}\cdot\text{cm}^{-3}$)	1.11 \pm 0.01 (34)	1.16 \pm 0.02 (29)	<0.02*
Cross-sectional area (cm ²)	1.6 \pm 0.1 (34)	1.9 \pm 0.1 (29)	<0.01*
Final SGR (%·day ⁻¹)	0.76 \pm 0.05 (33)	1.61 \pm 0.08 (29)	<0.0001*
Relative U_{crit} (BL·s ⁻¹)	4.37 \pm 0.05 (30)	4.25 \pm 0.05 (25)	>0.14
Absolute U_{crit} (cm·s ⁻¹)	40.69 \pm 0.52 (30)	41.26 \pm 0.71 (25)	>0.50
Time at 6 BL·s ⁻¹ (min)	3.06 \pm 0.28 (32)	3.73 \pm 0.39 (26)	>0.15

Note: Condition factor and cross-sectional area are calculated as the means of measurements taken on both swimming days. Differences in sample size are due primarily to mortality, although some fish that did not swim during the ramp-up phase or that escaped from the swim tunnel have been omitted from the data set.

*Significant difference ($p < 0.05$).

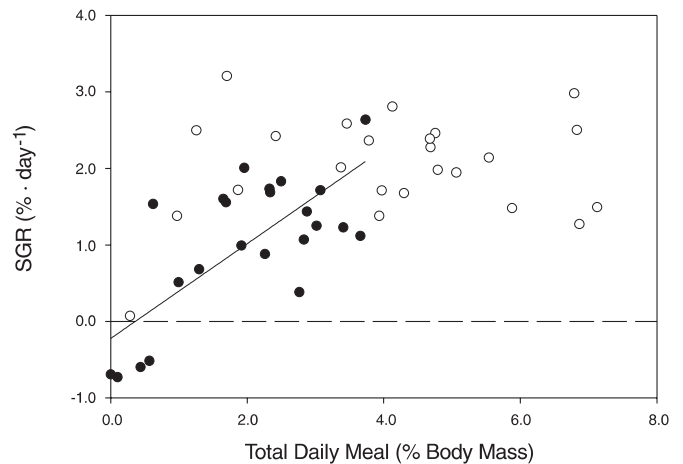
satiation showed significantly higher mean final mass and SGR than those fed a half-satiation ration (all $p < 0.0001$) (Table 2). However, there was no significant difference in mean CV between the two diet groups ($p > 0.80$) (Table 2). Neither of these diet groups showed significant regressions between CV and SGR (all $p > 0.48$) or CV and initial mass (all $p > 0.09$). Fin conditions were evaluated by tabulating the total fin score of each fish using the results of all three evaluation periods and adding the separate scores assigned to the dorsal and caudal fins. No significant correlations were found between SGR and fin score in either of the diet groups (all $p > 0.27$). However, fish in the satiation group showed significantly higher mean fin scores (i.e., less damage) than those in the half-satiation group ($p < 0.006$). No significant correlations were found between either SGR or CV and plasma cortisol level in either diet group (all $p > 0.68$), and no significant differences in mean plasma cortisol levels were found between the two diet groups ($p > 0.34$) (Table 2). Plasma cortisol levels did not increase with sampling order in either of the tanks, indicating that the sampling procedures did not induce a cortisol response.

There were no significant correlations between SGR and whole-body glycogen levels in either diet group, or when the data from both groups were pooled (all $p > 0.23$). In addition, there was no significant difference in mean glycogen levels between the fish kept in the two groups ($p > 0.76$) (Table 2).

When the data from both diet groups were pooled, a weak but significant negative regression was found between haematocrit and SGR ($r^2 = 0.1105$, $p < 0.04$), but this was not seen in the individual groups. Fish in the half-satiation diet group showed a higher mean haematocrit value than those in the satiation group, although this difference was not quite significant ($p = 0.056$) (Table 2). Fish that had lost weight (i.e., $\text{SGR} < 0$, $n = 3$) were not included in this data set.

Fish from both tanks were divided into three groups of equal size ($n = 8$) according to SGR (fast, medium, and slow growers), and the mean percentage of each meal obtained by the members of each of these groups was calculated. The feeding patterns of the fish in these groups for each of the daily meals are shown in Fig. 4. In the half-satiation group, fish that showed the fastest growth rates were also found to be those that consumed the largest portion of each of the three daily

Fig. 3. Relationship between specific growth rate (SGR) and total daily meal among fish fed on satiation (open circles) and half-satiation (solid circles) rations. A significant positive regression was found between growth rate and meal size in the half-satiation diet group ($r^2 = 0.5413$, $p < 0.01$, $n = 24$), but not among fish fed to satiation. The regression line $y = 0.62x - 0.22$ represents the relationship found in the half-satiation group only.



meals. In addition, the slowest growing fish were those that received the smallest portion of the meals. There was negligible variation in this relationship over the three daily meals (Fig. 4A). However, among satiation-fed fish, those who grew the fastest were not necessarily the same fish that obtained the largest portion of each meal, and there appeared to be much more variability in the group feeding patterns at different times (Fig. 4B).

Discussion

Swimming performance and growth rate

Individual rainbow trout raised together under food restriction show a significant negative relationship between SGR and relative U_{crit} ($r^2 = 0.2004$) and a significant positive relationship between SGR and stamina ($r = 0.3848$). These relationships occur at the level of individual variation and are not

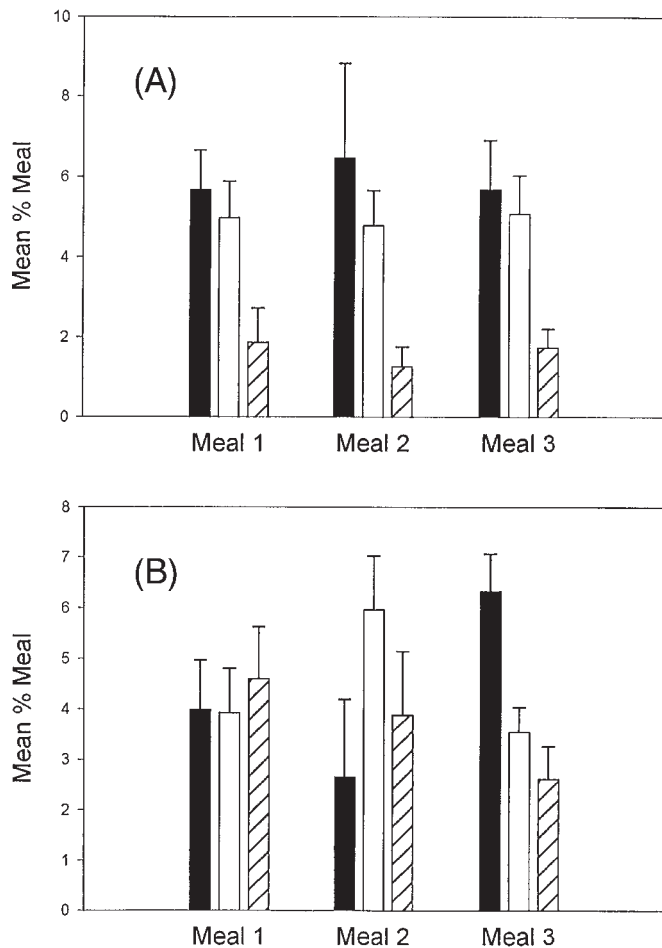
Table 2. Mean values \pm SE (*n*) of mass, specific growth rate (SGR), coefficient of variation (CV), fin score, plasma cortisol levels, glycogen content, and haematocrit in the satiation and half-satiation diet groups of series 3.

Variable	Half-satiation	Satiation	<i>p</i>
Initial mass (g)	5.34 \pm 0.11 (25)	5.55 \pm 0.18 (25)	>0.32
Final mass (g)	7.85 \pm 0.46 (24)	11.05 \pm 0.54 (24)	<0.0001*
Final SGR (% \cdot day ⁻¹)	1.04 \pm 0.19 (24)	2.03 \pm 0.14 (24)	<0.0001*
CV (%)	62.51 \pm 9.85 (24)	65.90 \pm 9.21 (24)	>0.80
Fin score	19.38 \pm 0.38 (24)	20.71 \pm 0.25 (24)	<0.006*
Plasma cortisol (μ g \cdot dL ⁻¹)	15.88 \pm 0.80 (22)	14.69 \pm 0.95 (22)	>0.34
Glycogen content (μ mol glycosyl U \cdot g wet weight ⁻¹)	10.84 \pm 1.37 (23)	10.24 \pm 1.39 (23)	>0.76
Haematocrit (% vol.)	41.48 \pm 0.61 (23)	39.55 \pm 0.78 (22)	>0.055

Note: CV is a measure of the variability in the food intake of individual fish from meal to meal. Differences in sample size are due to mortality and (or) problems with chemical analysis (such as an insufficient plasma sample in very small fish).

*Significant difference ($p < 0.05$).

Fig. 4. Mean percentage of each meal acquired by fish in fast- (solid bars), medium- (open bars), and slow-growing (hatched bars) groups (eight fish per group) for each of the three daily meals among fish fed (A) a half-satiation diet and (B) a satiation diet. Error bars represent standard error.



apparent when SGR is increased by feeding a greater ration or in the comparison of group means. They are seen most clearly under the intensified competition of a restricted ration.

It is important to consider whether these relationships could be spurious because of the observed intercorrelations between

body size and growth rate and the well-known effects of size itself on swimming performance. In general, a *reduction* in relative U_{crit} is associated with greater size (e.g., Brett 1964; Hawkins and Quinn 1996) whereas an *increase* in fatigue time in fixed-velocity trials is associated with greater size (e.g., Brett 1967; Beamish 1978; McDonald et al. 1998). However, since there was no significant relationship between fatigue time and mass or other indices of body size in the present data, this was clearly not a complication in the positive SGR versus stamina relationship found among fish fed to half-satiation.

The situation is more complex for the negative relationship between SGR and relative U_{crit} present in the trout on the half-satiation diet because relative U_{crit} was also negatively correlated with body mass, fork length, and maximum cross-sectional area. However, forward stepwise linear regression analysis showed SGR to provide the most powerful explanatory model, and no significant relationships were found between the regression residuals (of U_{crit} versus SGR) and these other factors. More importantly, there was a significant regression between the residuals of the relationship between mass versus SGR and those of mass versus relative U_{crit} , indicating a nonspurious relationship between SGR and relative U_{crit} . In addition, absolute U_{crit} showed a significant positive relationship with body size, but not with SGR. These findings suggest that there is an association between relative U_{crit} and SGR independent of body size. This conclusion is supported by a recent study using transgenic coho salmon (*Oncorhynchus kisutch*) that showed an inordinate increase in growth rate and an associated reduction in aerobic swimming performance that could not be explained by differences in body size (Farrell et al. 1997). Kolok and Oris (1995) reported a negative correlation between SGR and *absolute* U_{crit} in fathead minnow (compared with the relationship between SGR and *relative* U_{crit} reported in the present study). These authors did not evaluate relative swimming performance, and the use of different swimming protocols is believed to be responsible for any discrepancies in the relationships between SGR and absolute U_{crit} reported in the two studies (T.R. Gregory and C.M. Wood, unpublished results).

There are several possible, and in no way mutually exclusive, explanations for this antagonistic relationship between SGR and relative U_{crit} . These include changes in morphology (Taylor and McPhail 1985) associated with rapid growth, excessive energetic inputs required for white muscle synthesis in fast-growing fish (Loughna and Goldspink 1984), the

metabolic cost of specific dynamic action (SDA) associated with feeding (e.g., Jobling and Davis 1980; Alsop and Wood 1997), the effects of lower haematocrit on swimming performance (e.g., Gallagher et al. 1995), and insufficient aerobic enzyme activity in fast-growing fish (Somero and Childress 1980; Pelletier et al. 1993a).

The explanation for the positive relationship between SGR and stamina may be more straightforward, considering that the stamina test provides a measure of anaerobic capacity (McDonald et al. 1998). As a general paradigm, the activities of glycolytic enzymes tend to be greater in larger fish (Somero and Childress 1980), although there was no relationship between stamina and body size in the present study (only between stamina and SGR). In accord with this finding, Pelletier et al. (1993b) have shown that the activities of several key glycolytic enzymes are positively correlated with growth rate but not with body size in Atlantic cod (*Gadus morhua*). As such, faster growing fish may have more efficient anaerobic metabolisms than slower growing individuals. The absence of a significant relationship between growth rate and glycogen levels in the present study suggests that the efficiency with which an individual carries out glycolysis, and not the concentration of anaerobic substrates, may be the more important determinant of anaerobic swimming performance. It is also possible that the positive relationship between SGR and stamina in the half-satiation diet is directly "causative." The capacity for rapid, short-term activity measured by the fixed-velocity fatigue test may be related to the abilities needed to acquire food more effectively, and therefore grow more rapidly, in a highly competitive, limited-ration situation (Fig. 3).

Feeding and growth rate

In both series 2 and 3, fish that were fed a satiation diet showed significantly higher mean growth rates than fish fed a half-satiation diet. Obviously, the availability of food is an important determinant of growth rate, since the energy required for growth is acquired in the diet. At high levels of feeding, however, growth efficiency declines with increases in ration, due primarily to an increase in SDA (Wurtsbaugh and Davis 1977). There may be a phenomenon of "diminishing returns" associated with high levels of feeding, whereby fish that consume large amounts of food do not grow as efficiently as fish fed a smaller ration.

The significant difference in fin score between the two groups suggests that fish fed a half-satiation diet experienced more aggression than fish fed to satiation (Abbott and Dill 1989), probably as a result of more intense competition for food. However, mean plasma cortisol levels were not significantly different and SGR was not directly correlated with fin score in either group.

In addition to ration, feeding schedule may affect the feeding patterns of fish. Other researchers have reported significant differences in CV among fish fed different rations, with low rations resulting in more variable individual feeding patterns (McCarthy et al. 1992). However, no significant differences in CV were found between the two diet groups in this study. This difference appears to be due to the use of three daily meals rather than a single large daily meal (T.R. Gregory and C.M. Wood, unpublished results). As is evident from Fig. 4, the feeding patterns of the diet groups were quite different. The fastest growing fish were not always those who acquired the

most food in each of the three daily meals in the satiation group whereas in the half-satiation group, the fastest growing fish received the largest portion of the meal in all three cases. This difference probably results from the more strict enforcement of a feeding hierarchy in the half-satiation group, with the same individuals acquiring most of the food each time.

Limits to fish growth

In addition to the well-known advantages inherent in rapid growth, such as earlier reproduction (Metcalfe et al. 1989), improved access to preferred sites (Fausch 1984), and more flexible food sources (Webb et al. 1984), the present results indicate another potential benefit: greater stamina. Nevertheless, the growth of fish is ultimately limited by several important aspects of physiology and ecology, including increased predation risk associated with the heightened appetite and foraging behaviour stimulated by high levels of growth hormone, increased occurrence of developmental errors associated with rapid growth, and the investment in growth occurring at the expense of somatic maintenance and repair (Johnsson and Björnsson 1994). Rapid growth may also be limited by the energetic cost associated with high levels of feeding, digestion, and food conversion. The results of the present study offer yet another explanation: that rapid growth occurs to the detriment of another key element of fitness, aerobic swimming performance.

Acknowledgments

This study was supported by a Natural Sciences and Engineering Research Council of Canada research grant to C.M.W. Sincere thanks to Dr. Ian McCarthy for information on X-ray techniques, Dr. D.G. McDonald for access to unpublished data, and to all in the laboratory who helped, and especially to Julianne Partridge who participated in almost every aspect of the research.

References

- 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 performance, and protein usage in juvenile rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* **200**: 2337–2346.
- 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.
- Beitinger, T.L., and McCauley, R.W. 1990. Whole-animal physiological processes for the assessment of stress in fishes. *J. Great Lakes Res.* **16**: 542–575.
- Bergmeyer, H.V. 1965. *Methods in enzymatic analysis*. Academic Press, New York.
- Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can.* **21**: 1183–1225.
- Brett, J.R. 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. *J. Fish. Res. Board Can.* **24**: 1731–1741.
- Carter, C.G., McCarthy, I.D., Houlihan, D.F., Fonseca, M., Perera, W.M.K., and Sillan, A.B.S. 1993. The application of radiography to the study of fish nutrition. *J. Appl. Ichthyol.* **11**: 231–239.

- Christiansen, J.S., and Jobling, M. 1990. The behaviour and the relationship between food intake and growth of juvenile Arctic charr, *Salvelinus alpinus* L., subjected to sustained exercise. *Can. J. Zool.* **68**: 2185–2191.
- Davison, W. 1997. The effects of exercise training on teleost fish, a review of recent literature. *Comp. Biochem. Physiol. A Comp. Physiol.* **117**: 67–75.
- Farrell, A.P., Bennett, W., and Devlin, R.H. 1997. Growth-enhanced transgenic salmon can be inferior swimmers. *Can. J. Zool.* **75**: 335–337.
- Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Can. J. Zool.* **62**: 441–451.
- Gallaughan, P., Thorarensen, H., and Farrell, A.P. 1995. Hematocrit in oxygen transport and swimming in rainbow trout (*Oncorhynchus mykiss*). *Resp. Physiol.* **102**: 279–292.
- Hammer, C. 1995. Fatigue and exercise tests with fish. *Comp. Biochem. Physiol. B Comp. Biochem.* **135**: 147–156.
- Hawkins, D.K., and Quinn, T.P. 1996. Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. *Can. J. Fish. Aquat. Sci.* **53**: 1487–1496.
- Houlihan, D.F., and Laurent, P. 1987. Effects of exercise training on the performance, growth, and protein turnover of rainbow trout (*Salmo gairdneri*). *Can. J. Fish. Aquat. Sci.* **44**: 1614–1621.
- Jobling, M., and Davis, P.S. 1980. Effects of feeding on metabolic rate and the specific dynamic action in plaice, *Pleuronectes platessa*. *J. Fish Biol.* **16**: 629–638.
- Johnsson, J.L., and Björnsson, G.Th. 1994. Growth hormone increases growth rate, appetite and dominance in juvenile rainbow trout, *Oncorhynchus mykiss*. *Anim. Behav.* **48**: 177–186.
- Kolok, A.S. 1992. The swimming performances of individual large-mouth bass (*Micropterus salmoides*) are repeatable. *J. Exp. Biol.* **170**: 265–270.
- 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.
- Loughna, P.T., and Goldspink, G. 1984. The effects of starvation upon protein turnover in red and white myotomal muscle of rainbow trout, *Salmo gairdneri* Richardson. *J. Fish Biol.* **25**: 223–230.
- 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.
- McDonald, D.G., McFarlane, W.J., and Milligan, C.L. 1998. Anaerobic capacity and swim performance of juvenile salmonids. *Can. J. Fish. Aquat. Sci.* **55**: 1198–2007.
- Metcalfe, N.B., Huntingford, F.A., Graham, W.D., and Thorpe, J.E. 1989. Early social status and the development of life-history strategies in Atlantic salmon. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **236**: 7–19.
- Pelletier, D., Guderley, H., and Dutil, J.-D. 1993a. Does the aerobic capacity of fish muscle change with growth rates? *Fish Physiol. Biochem.* **12**: 83–93.
- Pelletier, D., Guderley, H., and Dutil, J.-D. 1993b. Effects of growth rate, temperature, season, and body size on glycolytic enzyme activities in the white muscle of Atlantic cod (*Gadus morhua*). *J. Exp. Zool.* **265**: 477–487.
- Somero, G.N., and Childress, J.J. 1980. A violation of the metabolism size scaling paradigm: activities of glycolytic enzymes in muscle increase in larger-sized fish. *Physiol. Zool.* **53**: 322–337.
- 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.
- Webb, P.W., Kostecki, P.T., and Stevens, E.D. 1984. The effect of size and swimming speed on locomotor kinematics of rainbow trout. *J. Exp. Biol.* **109**: 77–95.
- Wurtsbaugh, W.A., and Davis, G.E. 1977. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri*, Richardson. *J. Fish Biol.* **11**: 87–98.