

# Effects of training on respiratory gas exchange, nitrogenous waste excretion, and fuel usage during aerobic swimming in juvenile rainbow trout (*Oncorhynchus mykiss*)

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**Abstract:** Fuel utilization during aerobic exercise was determined in juvenile rainbow trout that had previously undergone 2 weeks of continuous aerobic training at 25% of their maximum sustainable speed ( $U_{crit}$ ) and was compared with that in untrained trout. Instantaneous fuel usage was calculated from simultaneous measurements of oxygen consumption ( $M_{O_2}$ ), carbon dioxide excretion ( $M_{CO_2}$ ), and nitrogenous waste excretion ( $M_N$ ). Over 58 h of sustained aerobic exercise at 55% of  $U_{crit}$ ,  $M_{O_2}$  and  $M_{CO_2}$  remained virtually constant in the trained fish, in contrast to the significant fall over time in untrained fish, but total gas exchange was similar in the two groups. Aerobic respiratory quotient remained constant in the two treatments.  $M_N$  was lower in the trained fish, resulting in a much lower (and stable) nitrogen quotient; the nitrogen quotient increased with swimming duration in the untrained fish. Lipid was the major fuel source powering aerobic exercise in both groups. Carbohydrate also played a significant role, whereas protein was of lowest quantitative importance. Training resulted in a decrease in reliance on protein and an increase in reliance on lipid metabolism. The role of protein oxidation in supporting aerobic swimming in fish, which is smaller than commonly believed, is further reduced by training.

**Résumé :** Nous avons mesuré l'utilisation de l'énergie pendant l'exercice aérobie chez des truites arc-en-ciel juvéniles qui avaient été soumises à deux semaines d'entraînement aérobie continu à 25% de la vitesse soutenable maximale ( $U_{crit}$ ), et nous avons comparé les résultats à ceux obtenus chez des truites non entraînées. L'utilisation instantanée de l'énergie a été calculée à partir de mesures simultanées de la consommation d'oxygène ( $M_{O_2}$ ), de l'excrétion de dioxyde de carbone ( $M_{CO_2}$ ) et de l'excrétion des déchets azotés ( $M_N$ ). Sur une période de 58 h d'exercice aérobie soutenu à 55% de  $U_{crit}$ ,  $M_{O_2}$  et  $M_{CO_2}$  sont demeurées pratiquement constantes chez les poissons entraînés, alors qu'elles ont nettement baissé avec le temps chez les poissons non entraînés, mais l'échange total de gaz était similaire chez les deux groupes. Le quotient respiratoire aérobie est demeuré constant chez les deux groupes.  $M_N$  était plus faible chez les poissons entraînés, ce qui donnait un quotient azote beaucoup plus bas (et stable); le quotient azote augmentait avec la durée de la nage chez les poissons non entraînés. Les lipides constituaient la principale source d'énergie pour l'exercice aérobie chez les deux groupes. Les hydrates de carbone jouaient aussi un rôle important, tandis que les protéines présentaient une moindre importance quantitative. L'entraînement provoqué une baisse de la dépendance à l'égard des protéines et une hausse de la dépendance à l'égard du métabolisme des lipides. Le rôle de l'oxydation des protéines pour soutenir la nage aérobie chez les poissons, qui est moindre qu'on ne le croyait généralement, diminue encore après entraînement.

[Traduit par la Rédaction]

## Introduction

Exercise training has been studied extensively in fish using a variety of durations (from a few days to more than a year) and swimming intensities (less than 0.5 to 3.0 body lengths per second (BL/s); reviewed in Davison 1989). Many of the studies have focused on changes in muscle characteristics such as fiber size (Davison and Goldspink 1977; Greer Walker and Emerson 1978; Johnston and Moon 1980; Davie et al. 1986; Gamperl and Stevens 1991), sequence of fiber recruitment

(Johnston and Moon 1980), as well as distribution and supply of capillaries (Davie et al. 1986). Growth rates (Greer Walker and Emerson 1978; Houlihan and Laurent 1987), body condition factor (Davie et al. 1986; Gamperl and Stevens 1991), food conversion efficiency (Davison and Goldspink 1977), and blood variables (Davie et al. 1986) have also been investigated. The fact that there have been no previous studies on how training of fish might alter fuel utilization during swimming led to the present investigation.

We employed the respirometric methods developed by Lauff and Wood (1996a) for studying instantaneous fuel usage in fish. This approach is based on simultaneous measurements of  $O_2$  consumption ( $M_{O_2}$ ),  $CO_2$  production ( $M_{CO_2}$ ), and nitrogenous waste excretion ( $M_N$ , representing ammonia-N plus urea-N), and the application of standard metabolic theory (Kleiber 1987, 1992). This differs from the traditional compositional approach in measuring the fuels actually metabolized rather than the fuels depleted over time. Using this approach with untrained juvenile rainbow trout at several aerobic

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swimming speeds, Lauff and Wood (1996b) demonstrated that lipid oxidation predominated throughout the test period, that protein oxidation was kept at minimum levels necessary for maintenance, and that carbohydrate oxidation increased with swimming speed. The results were notable inasmuch as they tended to contradict the well-established view that proteins dominate in the mix of metabolic fuels (Kutty 1972; Van den Thillart 1986; Davison 1989), that lipids are important as well (Atherton and Aitken 1970; Jezierska et al. 1982; Van Waarde 1983), and that carbohydrate is of minor importance (Black et al. 1962; Van den Thillart 1986).

The goal of the present study was to test whether the surprisingly low reliance on protein (20–36%) and high reliance on carbohydrate (up to 38%) would be altered by prior training. The results of Lauff and Wood (1997) demonstrated that relative protein usage did increase with 3 days of low-speed swimming in previously untrained fish, whereas relative carbohydrate usage decreased. Such trends might be the start of a training effect, which should be better developed after 2 weeks of continuous low-speed swimming. A training speed of 1.0 BL/s was chosen because Greer Walker and Emerson (1978) found this speed to be optimal for growth and muscle hypertrophy. In addition, Weihs (1973) predicted a cruising speed of 1.0 BL/s to be the energetically most efficient swimming speed for salmonids whereas Quinn (1987) showed that migrating sockeye salmon (*Oncorhynchus nerka*) do travel at that speed. A testing speed of 2.1 BL/s was selected on the basis of the consensus that exercise at this speed is powered mainly by aerobic red muscle (Webb 1971; Hudson 1973; Wilson and Egginton 1994; Moyes and West 1995).

## Materials and methods

### Animals and general protocol

The husbandry, test regime (save for the training, detailed below), respirometry ( $O_2$  and  $CO_2$ ), water nitrogen assays (total ammonia [ $T_{amm}$ ], urea), proximate body analyses (protein, carbohydrates, lipids, water, and ash), and calculations for fuel use were exactly as described in Lauff and Wood (1996b). The untrained fish of the present study are the low-speed swimmers from that study. Fish were held and trained in dechlorinated Hamilton tap water (see Lauff and Wood (1996a) for composition) at  $15 \pm 1^\circ C$ . Fish were fed 1% of their body mass per day. After training and prior to respirometry, the average starting mass and fork length of the trained fish ( $16.5 \pm 2.2$  g,  $112 \pm 5.8$  mm (mean  $\pm$  SE);  $n = 5$ ) was not different from that of the untrained fish ( $19.8 \pm 0.8$  g,  $119 \pm 1.8$  mm;  $t$  test,  $n = 10$ ;  $p > 0.05$  for both mass and length). The final mass of the trained fish had dropped  $5.2 \pm 0.9\%$  during respirometry (when they were not fed) whereas that for the untrained fish dropped  $4.5 \pm 1.0\%$ ; the difference between groups was not significant.

### Training

The trained fish underwent 2 weeks of swimming at 1.0 BL/s in a Beamish-style swim tunnel (Farmer and Beamish 1969). This speed represented about 25% of the maximum sustainable speed ( $U_{crit}$ ) in untrained trout (Lauff and Wood 1996b). The swim tunnel had a total capacity of approximately 200 L; fresh, dechlorinated Hamilton tap water entered, while mixed water left continuously at 4 L/min. The swim tunnel motor was turned off during feeding to ease access of the food to the fish; feeding took no longer than 5 min each day.

### Testing

The fish were quickly blotted (no anaesthesia), weighed, measured,

and placed in individual 3.2-L Bla ka-style respirometers (Blaka et al. 1960, in Beamish 1978) with a water replacement rate of 150 mL/min. The respirometers were served with decarbonated (not softened) water made from dechlorinated Hamilton tap water as described by Lauff and Wood (1996a, 1996b). These studies have shown that decarbonation does not affect respiratory gas exchange or aerobic swimming performance but does increase analytical precision for  $CO_2$  measurements. Untrained fish were transferred directly from their holding tank (containing dechlorinated tap water) to the respirometers, whereas trained fish were transferred directly from the Beamish-style swim tunnel (also containing dechlorinated tap water). The fish were allowed to adapt to the respirometers for 2 days at a current of less than 1 BL/s, to which they oriented but did not swim. A continuous swimming speed of 2.1 BL/s (55% of  $U_{crit}$  in untrained trout; Lauff and Wood 1996b) was utilized for the fuel usage tests in the Bla ka respirometers. The fish were not fed while in the respirometers.

Three respirometry periods (each 0.5–1.0 h) were run at 5-h intervals on each of 3 consecutive days (total test duration 58 h). During these periods, the respirometers were sealed, and water samples were taken over time for determination of  $M_{O_2}$ ,  $M_{CO_2}$ , and  $M_N$  and thereby calculation of respiratory quotient ( $RQ = M_{CO_2}/M_{O_2}$ ) and nitrogen quotient ( $NQ = M_N/M_{O_2}$ ). At the end of the experiment, the fish were rapidly killed by an overdose of MS-222 (1 g/L), freeze clamped in liquid nitrogen, and stored at  $-70^\circ C$  for later analysis of proximate body composition. Total body protein, lipid, inorganics (ash), water, glycogen, glucose, and lactate were measured, and the sum of the latter three has been reported as total carbohydrate.

### Calculations and statistics

The instantaneous fuel usage calculations, and the rationale behind them, have been detailed by Lauff and Wood (1996a). In brief, they used only aerobic RQ measurements ( $\leq 1.0$ ), relied on standard  $RQ_{lipid}$  (0.71) and  $RQ_{carbohydrate}$  (1.0) constants, an empirically determined  $RQ_{protein}$  calculated from the relative contributions of ammonia-N and urea-N to  $M_N$  as described by Kleiber (1987), and a theoretical maximum NQ of 0.27 (van den Thillart and Kesbeke 1978) when all aerobic metabolism is fueled by protein. These data allow calculation of fuel usage in terms of the relative contribution of lipid, carbohydrate, and protein fuels to the support of  $M_{O_2}$ . In turn, the results may be converted to absolute carbon expenditures from the three fuel types using the fuel-specific RQs and the measured values of  $M_{CO_2}$  (Fig. 1).

Data are expressed as means  $\pm$  1 SE. Regressions were fitted by the method of least squares and tested for significance using the Pearson linear correlation coefficient and the appropriate  $t$  test (Fig.P graphics package, Ferguson, Mo.). An independent  $t$  test was used to evaluate possible differences between treatment groups in gas exchange and in body composition measurements at common sampling times. For all tests,  $p < 0.05$  was considered significant.

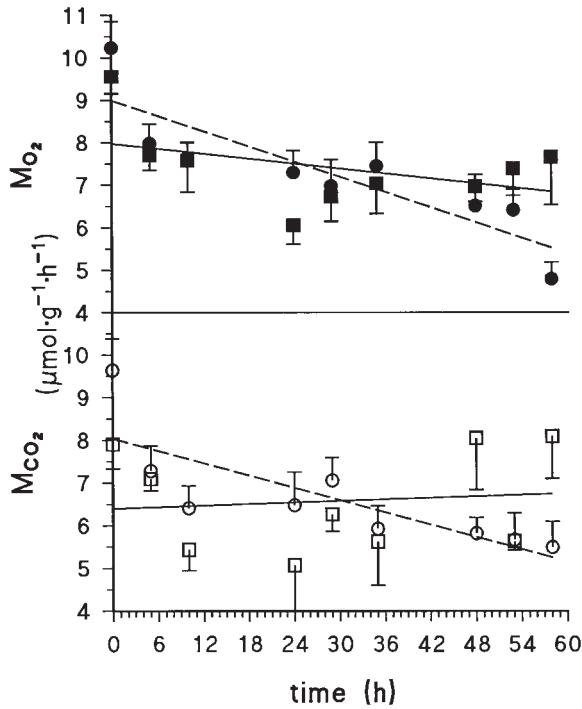
## Results

### Respirometry and instantaneous fuel use

In both groups, the initial oxygen consumption of fish swimming at 2.1 BL/s was about  $10 \mu mol \cdot g^{-1} \cdot h^{-1}$ .  $M_{O_2}$  decreased by the second period and stabilized thereafter ( $p > 0.05$ ) in the trained group but continued to decline ( $p < 0.0001$ ) in the untrained group (Fig. 1).  $M_{CO_2}$  was more variable. Overall, there was no change in  $M_{CO_2}$  over time in trained fish, whereas it decreased significantly in the untrained fish ( $p < 0.001$ ). Averaged over the entire 58-h regime, the gas exchanges were not significantly different in the two groups.

RQ was somewhat variable in both groups, although values tended to remain between 0.8 and 1.0 (Fig. 2). When anaerobic values ( $RQ > 1.0$ ) were removed, the aerobic RQ values,

**Fig. 1.** Oxygen consumption and carbon dioxide excretion of untrained (circles;  $n = 10$ ) and trained (squares;  $n = 5$ ) juvenile rainbow trout swimming at 2.1 BL/s over the 3-day test. Values are mean  $\pm$  1 SE.



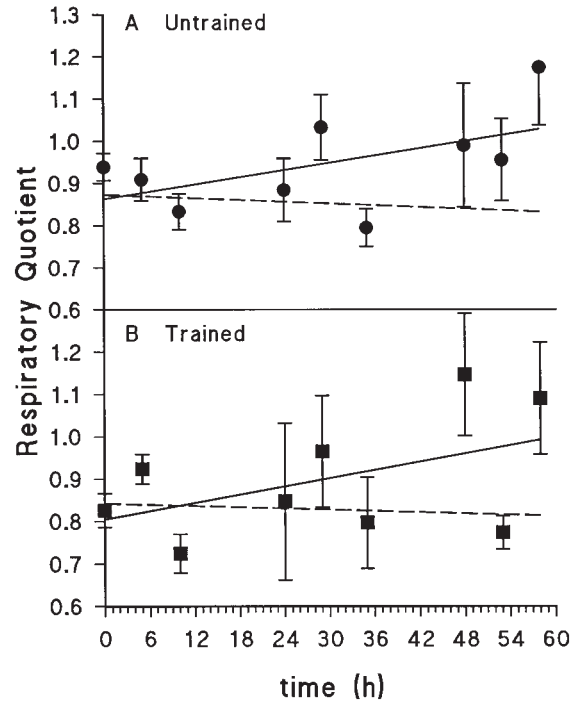
replotted as regressions, showed almost identical and stable ( $p > 0.05$ ) lines (Fig. 2).

Nitrogenous waste excretion, except for the final value of the trained group, was stable ( $p > 0.05$ ) over the 3-day test period (Fig. 3). However, the untrained group had an average excretion rate of  $0.54 \mu\text{mol N}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$  (made up of 18% urea, 82%  $T_{\text{amm}}$ ), while the trained fish showed an excretion rate 39% lower at  $0.33 \mu\text{mol N}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$  (23% urea, 77%  $T_{\text{amm}}$ ;  $p < 0.01$  for the lower rate,  $p < 0.0001$  for the difference in composition). On the basis of these urea-N:ammonia-N ratios, we calculated that the  $\text{RQ}_{\text{protein}}$  was 0.95 for the untrained group, while for the trained fish, the value was 0.94. These data permitted calculation of instantaneous fuel usage.

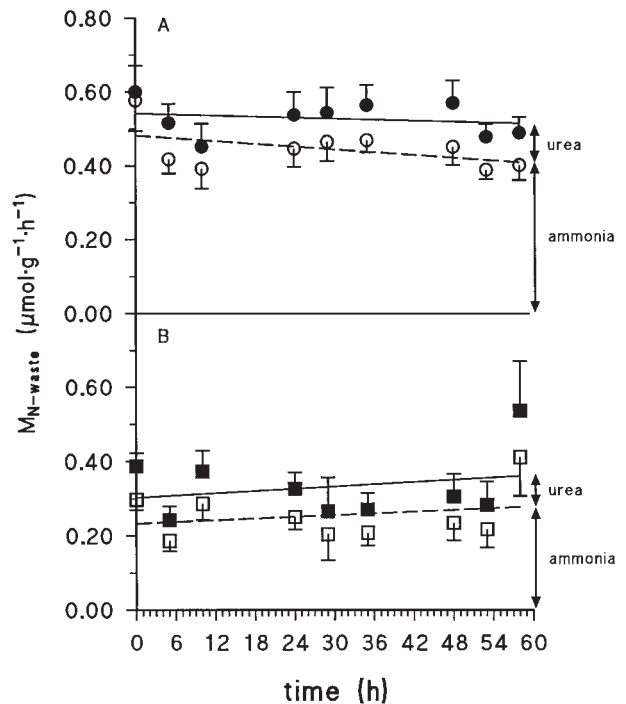
NQ remained effectively stable ( $p > 0.05$ ) at 0.04 in the trained group but increased linearly ( $p < 0.001$ ;  $r = 0.418$ ) from 0.06 to over 0.11 in the untrained group (Fig. 4). Given that aerobic protein catabolism is proportional to nitrogenous waste excretion, the right axis of Fig. 4 allows interpretation of this variable. The relatively stable NQ of the trained group arose from a protein use that represented 17% of the total fuel mixture. The protein use in the untrained group was greater than in the trained fish ( $p < 0.02$ ) and rose steadily ( $p < 0.001$ ) from 22% to greater than 35% at the end of the final day.

The patterns of lipid and carbohydrate usage were similar in the trained and untrained fish, with the contribution of the former increasing and that of the latter decreasing over time (Fig. 5). Lipid was always responsible for greater than half the fuel used in the trained group and showed a final contribution of 60%. The contribution of lipid to the total fuel mixture in the trained fish was consistently 10% higher than in the untrained group. In contrast, carbohydrate initially played a

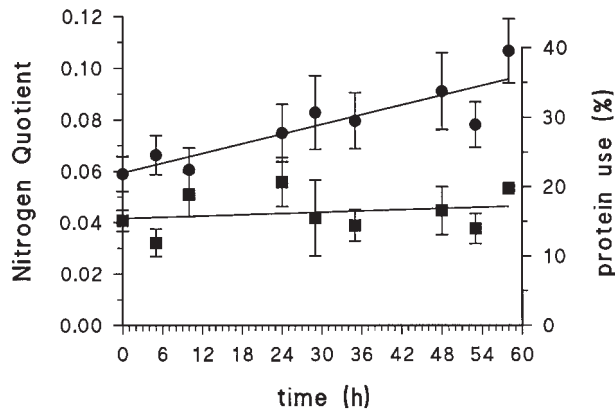
**Fig. 2.** The complete respiratory quotient (symbols and solid regression line) and the aerobic respiratory quotient (broken regression line) for (A) untrained ( $n = 10$ ) and (B) trained ( $n = 5$ ) juvenile rainbow trout swimming at 2.1 BL/s over the 3-day test. Values are mean  $\pm$  1 SE.



**Fig. 3.** Total nitrogenous waste (sum of ammonia-N and urea-N; solid symbols) and ammonia-N (open symbols) excretion for (A) untrained ( $n = 10$ ) and (B) trained ( $n = 5$ ) juvenile rainbow trout swimming at 2.1 BL/s over the 3-day test. Values are mean  $\pm$  1 SE.



**Fig. 4.** Nitrogen quotients (left axis) and protein use (right axis) for untrained (circles;  $n = 10$ ) and trained (squares;  $n = 5$ ) juvenile rainbow trout swimming at 2.1 BL/s over the 3-day test. Values are mean  $\pm 1$  SE.



stronger role in the untrained fish, representing an average of 37% on the 1st day, but the contribution decreased to 14% on the final day; in the trained group, carbohydrate usage also decreased over time but with a narrower range of 34–21%.

In both groups, the carbon use rate from protein remained relatively constant, although the average use rate in the trained fish was significantly lower at  $15 \mu\text{g C}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$  ( $p < 0.0001$ ) than the value of  $25 \mu\text{g C}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$  in the untrained fish. Carbon use rate from carbohydrate in trained trout decreased initially and then levelled off at about  $23 \mu\text{g C}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ , whereas it declined continuously in the untrained group from 49 to  $7 \mu\text{g C}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ . Finally, carbon use rate from lipid started at similar values in the two groups ( $40 \mu\text{g C}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ ) but thereafter declined and then stabilized at  $30 \mu\text{g C}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$  for the duration of the experiment in untrained fish. In contrast, the burning of lipid carbon was typically higher in the trained fish, with a slight tendency to increase on the final day.

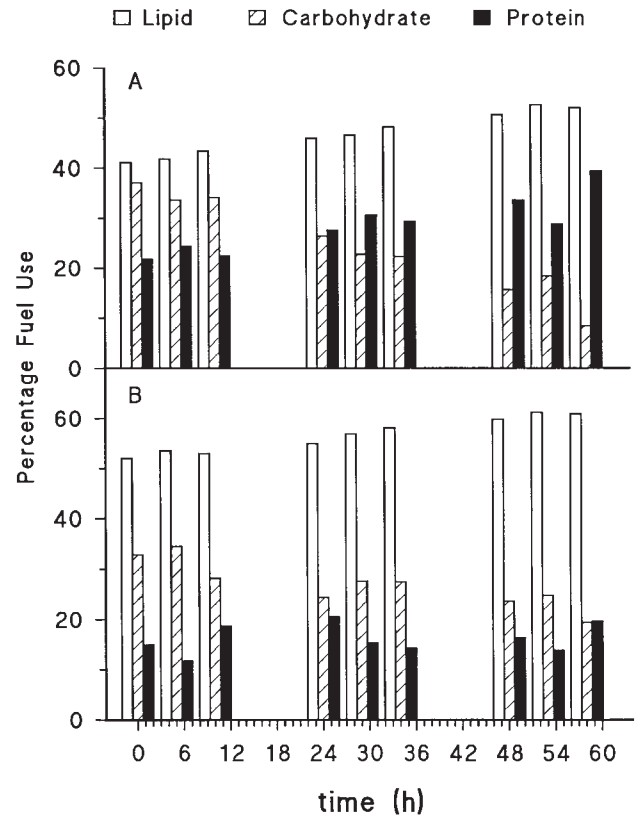
### Body composition

Terminal concentrations of lipid, inorganics (ash), and water of trained and untrained fish were similar ( $p > 0.05$ ; Table 1). Both protein and total carbohydrate levels were higher ( $p < 0.025$  and  $0.05$ , respectively) in the trained fish than in the controls.

### Discussion

In this study, some of the measured variables were strongly affected by training, whereas others were not. There was, in fact, a dichotomy between the traditional respiratory variables ( $M_{\text{O}_2}$ ,  $M_{\text{CO}_2}$ ) and N-waste excretion. For the former, even though the trained fish did not show the decline in respiratory gas exchange that was present in the untrained group, there was no difference in absolute amount of gas exchange between groups (Fig. 1). However, decreased N-waste excretion and resulting fuel use differences were obvious (Figs. 3 and 4). Because the total amount of  $\text{O}_2$  consumed and the total amount of carbon used by the trained group were not lower than that of the untrained fish, we suggest that no greater efficiency of the conversion of fuel energy to locomotory work occurred as a result of the training regime imposed. The changes that did

**Fig. 5.** Percentage use of lipid (open bars), carbohydrate (hatched bars), and protein (solid bars) in (A) untrained and (B) trained juvenile rainbow trout swimming at 2.1 BL/s over the 3-day test.



occur were the result of substantially lower protein catabolism, which was reflected in the lower N excretion (Figs. 3 and 4).

To satisfy the assumptions of the analysis (Lauff and Wood 1996a), apparent anaerobic values of RQ ( $>1.0$ ) were not used in the calculation of fuel use. If some of these bouts were due not to anaerobiosis but rather to lack of steady-state conditions in the fish, omitting these data would increase the apparent contribution of lipid while decreasing that of carbohydrate; the contribution of protein would not be affected. Therefore, no error would result in the principal conclusion of this study, that training results in a decreased reliance on protein in fueling aerobic exercise.

### Nitrogenous waste and protein use

This conclusion is opposite to the speculation of the Introduction that the gradual increase in relative protein use by the untrained fish over the 3-day test period (as seen in Fig. 4) might be the start of a training effect. Rather, it is clear that the trained fish relied to a lesser extent on protein as a fuel. In hindsight, this strategy appears entirely reasonable. Unlike lipid or carbohydrate, which can be stored in readily mobilizable deposits, protein is largely stored as the contractile material of muscle. For continuously exercising fish, it makes little sense to burn the very machinery that is powering the swimming. Instead, training reorganizes metabolism so as to spare the muscle.

In accord with this argument, terminal body protein content was significantly higher in the trained fish (Table 1), which



**Table 1.** Body compositions (mg/100 mg, wet mass; mean  $\pm$  SE) of untrained and trained juvenile rainbow trout after exercise.

	Total				
	Lipid	carbohydrate	Protein	Inorganic	Water
Untrained fish	5.1 $\pm$ 0.7	0.20 $\pm$ 0.02	13.2 $\pm$ 0.7	2.68 $\pm$ 0.17	77.8 $\pm$ 1.2
Trained fish	5.0 $\pm$ 0.1	0.25 $\pm$ 0.02*	15.3 $\pm$ 0.4**	2.42 $\pm$ 0.11	77.5 $\pm$ 0.5

**Note:** Total carbohydrate includes glucose, glycogen, and lactate. \*,  $p < 0.05$ ; \*\*,  $p < 0.025$  versus untrained fish.

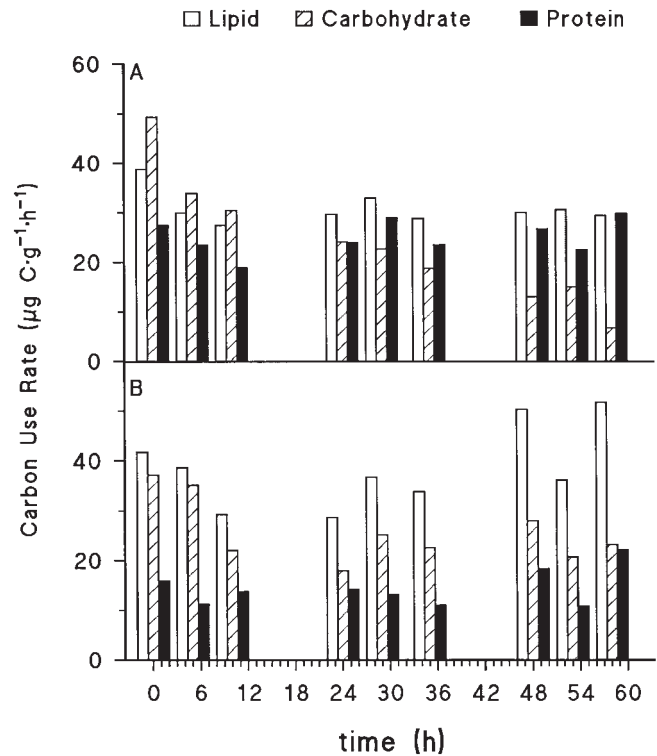
reflected the well-documented hypertrophy of one or both muscle types during training (Greer Walker and Emerson 1978; Johnston and Moon 1980; Davie et al. 1986; Houlihan et al. 1986; Houlihan and Laurent 1987; Gamperl and Stevens 1991). Interestingly, Lauff and Wood (1996b) found that high-speed swimmers (3.1 BL/s), the most exercised group in that study, used the lowest percentage of protein as a fuel. The trained group in the present study had gone directly from a 2-week training regime to the swimming test. Thus, in both cases, the fish subjected to the greatest amount of exercise, either in terms of duration or intensity, relied less on protein as a fuel than their less-exercised counterparts.

### Lipid use

Because the total amount of carbon burned was similar in the two groups (Fig. 1, CO<sub>2</sub> excretion), and the total carbon originating from protein was lower in the trained fish (Fig. 6), then the prediction would be a simple increase in the contribution of either or both of the other two fuels to make up the balance. In fact, the contribution of lipid, the most efficient fuel on a per mass basis (Kleiber 1992) was consistently higher in the trained fish. This did agree with the increasing reliance on lipid exhibited by the untrained fish during their first 3 days of low-speed swimming (Fig. 5). The conclusion also agrees with the generally accepted view that lipids, specifically free fatty acids, are important fuels for long-term aerobic swimming (Driedzic and Hochachka 1978a; Mommsen et al. 1980; Walton and Cowey 1982; Henderson and Tocher 1987; Greene and Selivonchick 1987). However, the mechanism(s) by which lipids are mobilized from muscle and other depots in fish remain(s) ill defined (Henderson and Tocher 1987; Greene and Selivonchick 1987). Even though lipid use was higher in the trained fish (Figs. 5 and 6), there was no difference between the two groups with respect to the final body content of lipid (Table 1). Either the 3-day test period was too short to detect differences in depletion, or there was more lipogenesis (or higher lipid stores at the end of the training period and prior to the test) in the trained fish. Certainly, the control of lipid metabolism during aerobic exercise is a rich field for further investigation, as are mechanisms involved in the transition of fuel use caused by training.

### Carbohydrate use

The contribution of carbohydrate in the trained fish was at or below the contribution in the untrained group seen over the 1st day of the test period. By the 3rd day, the untrained fish continued to decrease their reliance on carbohydrates such that the contribution fell below that of the trained fish. Nevertheless, the trained fish had larger carbohydrate stores than the

**Fig. 6.** The contribution of carbon from lipid (open bars), carbohydrate (hatched bars), and protein (solid bars) in (A) untrained and (B) trained juvenile rainbow trout swimming at 2.1 BL/s over the 3-day test.

untrained fish at the end of the 58-h swim test (Table 1). Earlier, Scarabello et al. (1991) showed that carbohydrate stores are very labile in untrained trout of this size, especially in the face of prolonged exercise and starvation. Furthermore, Johnston and Moon (1980) reported a twofold increase in white muscle and a fivefold increase in red muscle glycogen levels after 3 weeks of training at 2.1 BL/s in pollack (*Pollachius virens*).

The reasons for these carbohydrate patterns are unclear. Carbohydrate is typically thought of as the fuel of the white muscle (Johnston and Goldspink 1973; Driedzic and Hochachka 1978a, 1978b; Mommsen et al. 1980). The white muscle is considered by many to function primarily in burst swimming (Weihs 1973), and it is reasonable to assume that red muscle activity predominated in the present tests at 55%  $U_{crit}$  (see Introduction). Nevertheless, it has been shown electromyographically that the mosaic fibers may become active at speeds as low as 35%  $U_{crit}$  in rainbow trout (Hudson 1973). It therefore seems probable that the fish in the current study were utilizing white muscle to some degree for their swimming at 55%  $U_{crit}$ . Unfortunately, no study has investigated differential recruitment of muscle fiber types as a result of training.

### Conclusions

The main effect of training we observed was a decrease in protein catabolism during aerobic swimming (reflected in reduced N excretion), and an associated increase in lipid use, though the total amount of fuels used was unchanged. Carbohydrate usage remained appreciable. If trained trout are

representative of wild fish, then salmonids in nature may burn very little protein indeed.

## Acknowledgements

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## References

- Atherton, W.D., and Aitken, A. 1970. Growth, nitrogen metabolism and fat metabolism in *Salmo gairdneri*, Rich. Comp. Biochem. Physiol. **36**: 719–747.
- Beamish, F.W.H. 1978. Swimming capacity. In *Fish physiology*. Vol. 7. Edited by W.S. Hoar and D.J. Randall. Academic Press, New York. pp. 101–187.
- Black, E.C., Robertson, A.C., Lam, K.-C., and Chiu, W.-G. 1962. Changes in glycogen, pyruvate and lactate in rainbow trout (*Salmo gairdneri*) during and following muscular activity. J. Fish. Res. Board Can. **19**: 409–436.
- Davie, P.S., Tetens, V., and Wells, R.M.G. 1986. Effects of sustained swimming on rainbow trout muscle structure, blood oxygen transport and lactate dehydrogenase isozymes: evidence for increased aerobic capacity of white muscle. J. Exp. Zool. **237**: 159–171.
- Davison, W. 1989. Training and its effects on teleost fish. Comp. Biochem. Physiol. A Physiol. **94**: 1–10.
- Davison, W., and Goldspink, G. 1977. The effect of prolonged exercise on the lateral musculature of the brown trout (*Salmo trutta*). J. Exp. Biol. **70**: 1–12.
- Driedzic, W.R., and Hochachka, P.W. 1978a. Metabolism in fish during exercise. In *Fish physiology*. Edited by W.S. Hoar and D.J. Randall. Academic Press, New York. pp. 503–543.
- Driedzic, W.R., and Hochachka, P.W. 1978b. Control of energy metabolism in fish white muscle. Am. J. Physiol. **220**: 579–582.
- Farmer, G.J., and Beamish, F.W.H. 1969. Oxygen consumption of *Tilapia nilotica* in relation to swimming speed and salinity. J. Fish. Res. Board Can. **26**: 2807–2821.
- Gamperl, A.K., and Stevens, E.D. 1991. Sprint-training effects on trout (*Oncorhynchus mykiss*) white muscle structure. Can. J. Zool. **69**: 2786–2790.
- Greene, D.H.S., and Selivonchick, D.P. 1987. Lipid metabolism in fish. Prog. Lipid Res. **26**: 53–85.
- Greer Walker, M., and Emerson, L. 1978. Sustained swimming speeds and myotomal muscle function in the trout, *Salmo gairdneri*. J. Fish Biol. **13**: 475–481.
- Henderson, R.J., and Tocher, D.R. 1987. The lipid composition and biochemistry of freshwater fish. Prog. Lipid Res. **26**: 281–347.
- 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.
- Houlihan, D., McMillan, D., and Laurent, P. 1986. Growth rates, protein synthesis and protein degradation rates in rainbow trout: effects of body size. Physiol. Zool. **54**: 482–493.
- Hudson, R.C.L. 1973. On the function of the white muscles in teleosts at intermediate swimming speeds. J. Exp. Biol. **58**: 509–522.
- Jezierska, B., Hazel, J.R., and Gerking, S.D. 1982. Lipid mobilization during starvation in the rainbow trout, *Salmo gairdneri* Richardson, with attention to fatty acids. J. Fish Biol. **21**: 681–692.
- Johnston, I.A., and Goldspink, G. 1973. A study of glycogen and lactate in the myotomal muscles and liver of the coalfish (*Gadus virens* L.) during sustained swimming. J. Mar. Biol. Assoc. U.K. **53**: 17–26.
- Johnston, I.A., and Moon, T. 1980. Endurance exercise training in the fast and slow muscles of a teleost fish (*Pollachius virens*). J. Comp. Physiol. **135**: 147–156.
- Kleiber, M. 1987. The fire of life. Robert E. Krieger Publishing Co., Malabar.
- Kleiber, M. 1992. Respiratory exchange and metabolic rate. In *Handbook of physiology*. Edited by S.R. Geiser. American Physiological Society, Bethesda, Md. pp. 927–938.
- Kutty, M.N. 1972. Respiratory quotient and ammonia excretion in *Tilapia mossambica*. Mar. Biol. (Berlin), **16**: 126–133.
- Lauff, R.F., and Wood, C.M. 1996a. Respiratory gas exchange, nitrogenous waste excretion and fuel usage during starvation in juvenile rainbow trout, *Oncorhynchus mykiss*. J. Comp. Physiol. B, **165**: 542–551.
- Lauff, R.F., and Wood, C.M. 1996b. Respiratory gas exchange, nitrogenous waste excretion and fuel usage during aerobic swimming in juvenile rainbow trout. J. Comp. Physiol. B, **166**: 501–509.
- Mommsen, T.P., French, C.J., and Hochachka, P.W. 1980. Sites and patterns of protein and amino acid utilization during the spawning migration of salmon. Can. J. Zool. **58**: 1785–1799.
- Moyes, C.D., and West, T.G. 1995. Exercise metabolism of fish. In *Biochemistry and molecular biology of fishes*. Edited by P.W. Hochachka and T.P. Mommsen. Elsevier, Amsterdam. pp. 367–392.
- Quinn, T.P. 1987. Estimated swimming speeds of migrating adult sockeye salmon. Can. J. Zool. **66**: 2160–2163.
- Scarabello, M., Wood, C.M., and Heigenhauser, G.J.F. 1991. Glycogen depletion in juvenile rainbow trout as an experimental test of the oxygen debt hypothesis. Can. J. Zool. **69**: 2562–2568.
- Van den Thillart, G. 1986. Energy metabolism of swimming trout (*S. gairdneri*). J. Comp. Physiol. B, **156**: 511–520.
- Van den Thillart, G., and Kesbeke, F. 1978. Anaerobic production of carbon dioxide and ammonia by goldfish *Carassius auratus* (L.). Comp. Biochem. Physiol. A Physiol. **59**: 393–400.
- Van Waarde, A. 1983. Aerobic and anaerobic ammonia production by fish. Comp. Biochem. Physiol. B Biochem. Mol. Biol. **74**: 675–684.
- Walton, M.J., and Cowey, C.B. 1982. Aspects of intermediary metabolism in salmonid fish. J. Comp. Physiol. B, **73**: 59–79.
- Webb, P. 1971. The swimming energetics of trout. II. Oxygen consumption and swimming efficiency. J. Exp. Biol. **55**: 521–540.
- Weih, D. 1973. Optimal fish cruising speed. Nature (London), **245**: 48–50.
- Wilson, R.W., and Egginton, S. 1994. Assessment of maximum sustainable swimming performance in rainbow trout (*Oncorhynchus mykiss*). J. Exp. Biol. **192**: 299–305.