

Anaerobic exercise in teleost fish

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In teleost fish, high speed ("burst") swimming is performed anaerobically while sustained performance is aerobic. The degree to which anaerobic energy production contributes to swimming performance in the steady exercise zone (swimming maintained for 2 to 200 min) is unknown. The relationship between oxygen consumption or scope for activity and swimming speed (U), the repayment of an oxygen debt during recovery from fatigue, and the reduction in maximum sustained speed (critical velocity, U_{crit}) by reduced environmental oxygen or lowered blood haemoglobin suggest that steady performance in salmonids is aerobic. In salmonids, sufficient power is provided from the oxygen consumed to swim steadily at least at 80% of U_{crit} . On the other hand, depending on the temperature, aerobic power output in cyprinids is only sufficient to reach 30–50% of U_{crit} . Aerobic relationships holding for salmonids do not apply to cyprinids. In fact, high respiratory quotients early in exercise along with glycogen depletion and lactate accumulation rates in muscle during vigorous swimming suggest that steady performance in cyprinids is worthy of further examination.

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Chez les téléostéens, la nage soudaine à haute vitesse est anaérobie, alors que la nage constante est aérobie. Jusqu'à quel point la production d'énergie anaérobie contribue à la performance de nage au cours d'un exercice constant (nage de 2 à 200 min) demeure une question sans réponse. La relation entre la consommation d'oxygène ou la quantité utilisée pour l'activité et la vitesse de nage (U), le paiement de la dette d'oxygène pendant la récupération après la fatigue et la réduction de la vitesse maximale de nage (vitesse critique, U_{crit}) lorsque l'oxygène du milieu diminue ou que la concentration d'hémoglobine baisse permettent de croire que la nage constante chez les salmonidés est un phénomène aérobie. Chez les salmonidés, la consommation d'oxygène fournit suffisamment d'énergie pour permettre au poisson de nager longtemps à 80% de sa vitesse U_{crit} . Par ailleurs, chez les cyprinidés, selon la température, le rendement énergétique aérobie ne permet pas au poisson d'atteindre plus de 30–50% de sa vitesse U_{crit} . Les relations aérobiques en vigueur chez les salmonidés ne s'appliquent pas aux cyprinidés. En fait, les quotients respiratoires élevés au début de l'exercice et les taux de baisse de glycogène et d'accumulation de lactates dans les muscles au cours d'un exercice vigoureux permettent de croire à l'intérêt d'une investigation plus poussée du phénomène de nage constante chez les cyprinidés.

[Traduit par le journal]

In fish, as in all vertebrates, the highest levels of exercise performance are achieved anaerobically. This "burst-type" activity can only be maintained for brief periods (up to 30 s), being terminated by exhaustion of intracellular energy supplies or by accumulation of waste products (Bainbridge 1960, 1962; Brett 1964). On the other hand fish are also capable of "marathon-type" performance in which activity can be sustained for hours or even days (Brett 1964, 1972). Sustained performance is aerobic and metabolic demand matches supply while waste production is balanced by disposal. Between these two extremes is a zone of steady performance (Brett 1964) in which exercise is kept up for periods from 2 to 200 min, terminated by fatigue. Two protocols are used to study steady performance. In one, fish are forced to swim at a constant speed until exhaustion (fatigue or fixed velocity tests), while in the other protocol, fish are forced to increase swimming speed in steps, each speed being held for a fixed time period, until fatigue (incremental velocity test; fatigue speed = critical velocity, U_{crit}). The aetiology of fatigue with the two protocols

may be quite different. In the former fatigue probably results from exhaustion of metabolite supply whereas, in the latter, it is more probably caused by inability to supply metabolites. Once initiated, the progression to exhaustion is probably similar in both protocols. Just before fatigue, anaerobic metabolism will predominate but whether anaerobiosis contributes significantly to performance below U_{crit} is unknown.

The myotomal muscle of fishes consists of three main fibre types. A superficial layer of red muscle (slow, oxidative) is separated from white fibres (fast fatiguing, glycolytic), making up the bulk of the myotome, by a layer of pink fibres (fatigue resistant, oxidative or glycolytic) (Johnston *et al.* 1977; Johnston and Moon 1980b). Various subpopulations of these types of fibres have been identified histochemically (Bone 1978; Johnston 1977). Red muscle is utilized for sustained swimming and white for "burst" swimming, whereas in steady performance pink and white fibres are involved, in addition to red muscle, particularly at speeds approaching U_{crit} (Greer-Walker and Pull 1973; Hudson

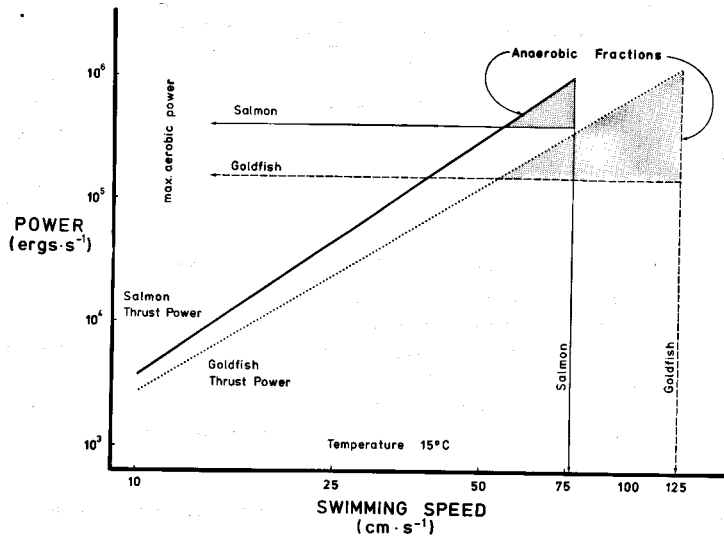


FIG. 1. Calculated thrust power (ergs per second (1 erg = 0.1 μ J)) generated by salmon (—) and goldfish (····), of similar mass (63.1 and 57.4 g, respectively), to swim at velocities (centimetres per second) up to U_{crit} . Horizontal arrows show the maximum power output that can be derived aerobically at 15°C for salmon (—) and goldfish (---). These values were obtained from measurements of oxygen consumed by assuming that the calorific equivalent of 1 mL of oxygen is 0.44×10^8 ergs·s⁻¹ when muscle efficiency is 20%. Vertical arrows indicate U_{crit} at 15°C (Brett 1964; Smit *et al.* 1971). Shading shows the anaerobic energy contribution to the thrust power at 15°C in salmon and goldfish. Data from Webb (1973) and Hunter and Zweifel (1971) after Webb (1978).

1973; Johnston and Goldspink 1973a, 1973b; Johnston *et al.* 1977; Bone *et al.* 1978; Johnston and Moon 1980a, 1980b). However, this is not convincing evidence for anaerobiosis in steady swimming, except approaching U_{crit} , for in some teleosts the white fibres may have significant vascularization and aerobic capacity (Johnston and Moon 1980b). Also, aerobic red fibres in the mosaic muscle of salmonids may contribute to the electromyogram from this portion of the myotome (Hudson 1973; Johnston *et al.* 1975; Bone 1978; Bone *et al.* 1978).

Anaerobiosis may contribute to salmonid energy budgets at the start of swimming or when swimming speed changes, and even during swimming at the highest sustained speeds (Kutty 1968; Webb 1971b; Wokoma and Johnston 1981). Yet much indirect evidence suggests that, at least up to 70–80% of U_{crit} , aerobic metabolism predominates in salmonids. Oxygen uptake increases exponentially with speed and any reduction in oxygen delivery to exercising muscle, either by lowering environmental oxygen or reducing blood haemoglobin, reduces U_{crit} (Davis *et al.* 1963; Dahlberg *et al.* 1968; Jones 1971). Furthermore, in salmon (*Oncorhynchus nerka*) acclimated to and exercised at a range of temperatures from 5 to 25°C, the highest U_{crit} occurs at 15°C, when scope for activity (maximum minus resting oxygen consumption) is greatest (Brett 1964). Also, up to about 80% of U_{crit} , no electrical activity is recorded from mosaic muscle (Webb 1971a, 1971b; Hudson

1973; Bone *et al.* 1978). In fact, it is activity in this muscle mass which probably leads to buildup of anaerobic end products causing repayment of an oxygen debt in the postexercise recovery period (Brett 1964, 1972; Webb 1971b; Driedzig and Kiceniuk 1976). Finally, maximum aerobic power output is sufficient to provide the thrust power to swim at all speeds up to about 80% of U_{crit} (Fig. 1).

On the other hand, cyprinids can swim faster than salmonids of the same length (compare Brett 1964 and Smit *et al.* 1971) yet aerobic power output is only sufficient to provide thrust power to achieve about 50% of U_{crit} at 15°C (Fig. 1). At a temperature of 30°C, only one-third of the thrust power required to reach U_{crit} is provided from oxygen consumed in cyprinids. The discrepancy between calculated and observed values is so large that it is unlikely to be caused by experimental error. Furthermore, both salmonids and cyprinids swim in the subcarangiform mode at similar mechanical efficiencies (Fig. 1) although extremely high aerobic muscular efficiencies in cyprinids could explain the discrepancy. Again, this is unlikely, and a more plausible explanation is that anaerobic metabolism makes a significant contribution to steady performance in cyprinids. Some indirect evidence supports the latter possibility. Cyprinids do not show a smooth exponential relation between oxygen uptake and swimming velocity; in fact in individual goldfish (*Carassius auratus*), increase in swimming speed may be accompanied by a

reduction in oxygen uptake (Smit *et al.* 1971). Furthermore, the maximum scope for activity and maximum sustained swimming speed do not correspond in cyprinids (Fry and Hart 1948; Fry and Hochachka 1970). Also, even at very low speeds, electromyographical activity can be recorded from white muscle (Johnston *et al.* 1977; Bone *et al.* 1978) while, after fatigue in incremental velocity tests, there is no repayment of an oxygen debt during recovery (Smit *et al.* 1971).

An anaerobic contribution to steady performance in cyprinids is not a new concept although the precise metabolic pathways involved are unknown (Smit *et al.* 1971; Johnston 1977; Johnston *et al.* 1977; Bone 1978). In goldfish a respiratory quotient over 2 can exist during the 1st h of exercise (Kutty 1968) while the fall in muscle glycogen concentration in carp (*C. carassius*) is 10 times larger than lactate increase during 15 min of "vigorous" swimming (Johnston and Goldspink 1973a). Furthermore, muscles in cyprinids have a low glycolytic potential and a low rate of lactate accumulation during steady exercise (Johnston and Goldspink 1973a; Johnston 1977). These observations indicate either that unusual physiological mechanisms (novel nonvascular transport phenomena or acid-base relations (Auvergnat and Secondat 1942; Wittenberger 1973; Jones and Randall 1978)) or unusual biochemical pathways are utilized during steady swimming. Certainly, there is more to steady swimming metabolism in cyprinids than is generally considered.

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- AUVERGNAT, R., and M. SECONDAT. 1942. Retentissement plasmatique de l'exercice musculaire chez la carpe (*Cyprinus carpio* L.). C.R. Hebd. Seances Acad. Sci. **215**: 92.
- BAINBRIDGE, R. 1960. Speed and stamina in three fish. J. Exp. Biol. **37**: 129-153.
- . 1962. Training, speed and stamina in trout. J. Exp. Biol. **39**: 537-555.
- BONE, Q. 1978. Locomotor muscle. In Fish physiology. Vol. VII. Locomotion. Edited by W. S. Hoar and D. J. Randall. Academic Press, New York. pp. 361-424.
- BONE, Q., J. KICENIUK, and D. R. JONES. 1978. On the role of the different fibre types in fish myotomes at intermediate swimming speeds. U.S. Fish Wildl. Serv. Fish. Bull. **76**: 691-699.
- BRETT, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can. **21**: 1183-1226.
- . 1972. The metabolic demand for oxygen in fish, particularly salmonids, and a comparison with other vertebrates. Respir. Physiol. **14**: 151-170.
- DAHLBERG, M. L., D. L. SHUMWAY, and P. DOUDOROFF. 1968. Influence of dissolved oxygen and carbon dioxide on swimming performance of largemouth bass and coho salmon. J. Fish. Res. Board Can. **25**: 49-70.
- DAVIS, G. E., J. FOSTER, C. E. WARREN, and P. DOUDOROFF. 1963. The influence of oxygen concentration on swimming performance of juvenile Pacific salmon at various temperatures. Trans. Am. Fish. Soc. **92**: 111-124.
- DRIEDZIC, W. R., and J. W. KICENIUK. 1976. Blood lactate levels in free-swimming rainbow trout (*Salmo gairdneri*) before and after strenuous exercise resulting in fatigue. J. Fish. Res. Board Can. **33**: 173.
- FRY, F. E. J., and J. S. HART. 1948. Cruising speed of goldfish in relation to water temperature. J. Fish. Res. Board Can. **7**: 169-175.
- FRY, F. E. J., and P. W. HOCHACHKA. 1970. Fish. In Comparative physiology of thermoregulation. Vol. 1. Invertebrates and nonmammalian vertebrates. Edited by G. C. Whittow. Academic Press, New York. pp. 79-134.
- GREER-WALKER, M., and G. PULL. 1973. Skeletal muscle function and sustained swimming speeds in the coalfish (*Gadus virens* L.). Comp. Biochem. Physiol. **44A**: 495-501.
- HUDSON, R. C. L. 1973. On the function of the white muscles in teleosts at intermediate swimming speeds. J. Exp. Biol. **58**: 509-522.
- HUNTER, J. R., and J. R. ZWEIFEL. 1971. Swimming speed, tail beat frequency, tail beat amplitude and size in jack mackerel, *Trachurus symmetricus*, and other fishes. U.S. Fish Wildl. Serv. Fish. Bull. **69**: 253-266.
- JOHNSTON, I. A. 1977. A comparative study of glycolysis in red and white muscles of the trout (*Salmo gairdneri*) and mirror carp (*Cyprinus carpio*). J. Fish. Biol. **11**: 575-588.
- JOHNSTON, I. A., W. DAVISON, and G. GOLDSPIK. 1977. Energy metabolism of carp swimming muscles. J. Comp. Physiol. **114B**: 203-216.
- JOHNSTON, I. A., and G. GOLDSPIK. 1973a. A study of the swimming performance of the crucian carp *Carassius carassius* (L.) in relation to the effects of exercise and recovery on biochemical changes in the myotomal muscles and liver. J. Fish Biol. **5**: 249-260.
- . 1973b. 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 T. W. MOON. 1980a. Endurance exercise training in the fast and slow muscles of a teleost fish (*Pollachius virens*). J. Comp. Physiol. **135**: 147-156.
- . 1980b. Exercise training in skeletal muscle of brook trout (*Salvelinus fontinalis*). J. Exp. Biol. **87**: 177-194.
- JOHNSTON, I. A., P. S. WARD, and G. GOLDSPIK. 1975. Studies on the swimming musculature of the rainbow trout. I. Fibre types. J. Fish Biol. **7**: 451-458.
- JONES, D. R. 1971. The effect of hypoxia and anemia on the swimming performance of rainbow trout (*Salmo gairdneri*). J. Exp. Biol. **55**: 541-551.
- JONES, D. R., and D. J. RANDALL. 1978. The respiratory and circulatory systems during exercise. In Fish physiology. Vol. VII. Locomotion. Edited by W. S. Hoar and D. J. Randall. Academic Press, New York. pp. 425-501.

- KUTTY, M. N. 1968. Respiratory quotients in goldfish and rainbow trout. *J. Fish. Res. Board Can.* **25**: 1689-1728.
- SMIT, H., J. M. AMELINK-KOUTSTAAL, J. VIJUERBERG, and J. C. VON VAUPEL-KLEIN. 1971. Oxygen consumption and efficiency of swimming goldfish. *Comp. Biochem. Physiol.* **39A**: 1-28.
- WEBB, P. W. 1971*a*. The swimming energetics of trout. I. Thrust and power output at cruising speeds. *J. Exp. Biol.* **55**: 489-520.
- 1971*b*. The swimming energetics of trout. II. Oxygen consumption and swimming efficiency. *J. Exp. Biol.* **55**: 521-540.
- 1973. Effects of partial caudal fin amputation on the kinematics and metabolic rate of under yearling sockeye salmon (*Oncorhynchus nerka*) at steady swimming speeds. *J. Exp. Biol.* **59**: 565-581.
- 1978. Hydrodynamics: nonscombroid fish. *In* Fish physiology. Vol. VII. Locomotion. Edited by W. S. Hoar and D. J. Randall. Academic Press, New York. pp. 190-239.
- WITTENBERGER, C. 1973. Metabolic interaction between isolated white and red muscles. *Rev. Roum. Biol. Ser. Zool.* **18**: 71-76.
- WOKOMA, A., and I. A. JOHNSTON. 1981. Lactate production at high sustainable cruising speeds in rainbow trout (*Salmo gairdneri*, Richardson). *J. Exp. Biol.* **90**: 361-364.