

AEROBIC AND ANAEROBIC SWIMMING PERFORMANCE OF INDIVIDUAL ATLANTIC COD

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Summary

Individual Atlantic cod (*Gadus morhua*) were exercised using three different measures of swimming performance. (1) An endurance test (critical swimming speed, U_{crit} , protocol) designed to assess predominantly aerobic endurance swimming (duration hours). (2) An acceleration test (U_{burst}), in which the fish were required to swim against a rapidly increasing current until exhausted (duration minutes). This test was designed to assess predominantly glycolytic-based swimming capacity. (3) A sprint test that examined the animals' ability to swim away from a sudden stimulus (duration seconds). Rates of oxygen consumption (\dot{M}_{O_2}) during the endurance test and various morphological variables of the individual fish were also measured. Both aerobic and anaerobic swimming performance of individual cod were found to be significantly repeatable over a 3 month period. \dot{M}_{O_2} during the U_{crit} protocol was also significantly repeatable at intermediate to high swimming speeds, but not at low speeds. Our results support extrapolation from metabolic rates at incremented

swimming speeds to zero activity as the best way to measure standard metabolic rate in cod. While performance in the U_{crit} test and the sprint test were positively correlated, there was a negative correlation between performance in the U_{crit} test and performance in the U_{burst} test. This implies a potential trade-off in individual cod between stamina and the ability to use glycolytic-based locomotion. Inter-individual variation in swimming performance during these protocols, while substantial, was not correlated with individual variation in fin surface areas, age or morphology. However, U_{burst} performance was dependent upon the sex of the animals, while performance during the U_{crit} protocol was significantly correlated with their aerobic scope for activity.

Key words: Atlantic cod, *Gadus morhua*, metabolic rate, oxygen consumption, fish, locomotion, morphology, critical swimming speed, swimming.

Introduction

The ability to move is a fundamental property by which we often define animal life. Although rarely proven, logic dictates that the ability to move factors into the Darwinian fitness of most animals. Accordingly, the study of locomotor performance in populations of feral vertebrates has undergone explosive growth over the past 20 years as investigators attempt (1) to partition a polygenic trait such as locomotor performance into key component processes (Bennett et al., 1984, 1989; Johnson et al., 1993); (2) to establish the heritability of measures of locomotor performance (Laurie-Ahlberg et al., 1985; Garland and Bennett, 1990); (3) to demonstrate selection for locomotor performance in the field (Huey et al., 1990; Jayne and Bennett, 1990); and (4) to establish the efficacy of laboratory measures of locomotor performance (van Berkum et al., 1989; Huey et al., 1990). For a variety of reasons, the fishes have largely been left out of this arena of experimentation. Although the study of locomotor capacity in fishes has a long history (for reviews, see Beamish, 1978; Randall and Brauner, 1991), most of this work has

focused on the mechanism of propulsion by fish and the use of exercise performance as a gauge of fish health or stress level, while little attention has been given to the raw material of natural selection: variation in performance among individual fish.

Large variations in swimming ability exist among teleosts. Scombroids have been recorded swimming at over 10 m s^{-1} (Magnuson, 1978), while males of the Ceratioidei suffer complete atrophy of their axial musculature and become parasitic appendages of the female (Pietsch, 1976). Morphological and physiological specialization are considered to be the main determinants of this diversity of locomotor capacities. Many fish species, depending upon prey type and habitat, have evolved specialist locomotor strategies, often at the expense of another type of locomotion (Webb, 1978, 1984). For example, a generalist swimmer, such as rainbow trout (*Oncorhynchus mykiss*), specializes in neither endurance nor acceleration swimming, yet performs both reasonably well (Webb, 1978, 1984), while an acceleration specialist, such as

northern pike (*Esox lucius*), has much higher swimming velocities during acceleration tests than do rainbow trout (Harper and Blake, 1990) yet is a poor endurance swimmer. The Atlantic cod (*Gadus morhua*) is another example of a species that employs a generalist locomotor strategy. This species participates in seasonal migrations of over 1000 km (Harden-Jones, 1968), spawns in currents (Rose et al., 1995; Rose, 1993), as a juvenile can capture prey in currents flowing at 8 body length s^{-1} (Lough et al., 1989) and avoids trawls.

Variation in swimming capacity is also manifest within a fish species. Kolok has demonstrated that the inter-individual variation in critical swimming speed (U_{crit}) exceeds individual performance variability for two species: largemouth bass (*Micropterus salmoides*; Kolok, 1992a) and northern squawfish (*Ptchocheillus oregonensis*; Kolok and Farrell, 1994). Nelson et al. (1992) found that inter-individual variation in U_{crit} also exceeded individual performance variability in Atlantic cod. They presented evidence that individual cod were relying on anaerobic metabolism to different degrees while reaching U_{crit} (Nelson et al., 1994, 1996). In general, it is poorly understood how inter-individual variation in critical swimming performance is related to the physiological variables that might determine locomotor prowess in fish. Kolok and Farrell (1994) provide strong evidence that individual variation in cardiac output does not account for individual variation in critical swimming performance of squawfish, and Kolok (1992b) was unable to relate several morphological characters and enzyme V_{max} measurements to performance in a hatchery-reared stock of largemouth bass (*Micropterus salmoides*). This is in contrast to the state of knowledge for a number of other ectotherms (e.g. Garland, 1984; Laurie-Ahlberg et al., 1985) and for animals whose exercise performance is of direct interest to humans (e.g. Thoroughbred racehorses; Gaffney and Cunningham, 1988), in which the determinants of exercise performance have been heavily studied. In addition to our poor state of knowledge concerning what accounts for intraspecific differences in swimming performance in fish, it is also poorly understood how the most commonly measured type of swimming performance (critical swimming speed, U_{crit}) is related to other types of swimming performance in the same individual. Because fish under different environmental conditions can use varying degrees of anaerobic metabolism in reaching U_{crit} (Nelson, 1990; Nelson et al., 1996), more than one performance test is needed to characterize the swimming potential of an individual fish adequately.

The present study was designed to examine the possible relationships among primarily aerobically fuelled swimming performance, primarily anaerobically fuelled swimming performance and the ability to sprint in a generalist fish species. The swimming performance of a group of Atlantic cod was measured using three different exercise protocols designed to assess these capacities. To identify some possible underlying sources of variation in the swimming performance of fish, we also investigated the relationship between each swimming performance capacity and morphology, fin surface areas and

rates of oxygen consumption. In addition, to determine whether swimming performance and metabolic rate are stable over time, we measured the repeatability of individual swimming performances and rates of oxygen consumption of the cod over a 3 month period.

Materials and methods

Animals

Twenty-five adult Atlantic cod (*Gadus morhua* L.) were selected from our laboratory stock of wild-captured Scotian Shelf cod, individually tagged and held in 6 m³ insulated circular holding tanks. These tanks were continuously supplied with temperature-regulated (5 ± 0.5 °C), air-saturated and filtered sea water. The tanks contained submersible pumps which maintained a water current of approximately 15 cm s^{-1} . The fish were exposed to their natural photoperiod (adjusted monthly) and fed a diet of chopped mackerel (*Scomber scombrus* L.) and chopped squid (*Illex illecebrosus* L.) on 3 days each week. The fish did not receive food for 4 days prior to an experimental trial. All swimming performance tests were conducted without investigator knowledge of that particular individual's performance in any previous test.

Aerobic swimming performance

Swimming performance of cod in a critical swimming speed (U_{crit}) protocol (Brett, 1964) has previously been shown to depend largely upon aerobic capacity, even though anaerobic metabolism is recruited during the swim (Nelson et al., 1996). Two days before a fish was to begin swimming, it was placed in a 1 m long opaque tube of identical cross-sectional area to the Brett-type swim-tunnel/respirometer used to determine U_{crit} . The conditioning tube was supplied with a continuous 15 cm s^{-1} flow of sea water at 5 °C and had a light suspended above its downstream end, which contained a transparent window. This apparatus required the fish to swim against the current to remain in their preferred low light levels. This pre-conditioning to swimming against a current while inside a tube had produced more robust swimming trials with earlier groups of cod. After 24 h in this tube, the fish were gently slid from the tube without handling into the swim-tunnel/respirometer, where they remained for an additional 24 h at a flow speed of 15 cm s^{-1} and at 5 °C. The respirometer was designed by the Department of Engineering at Guelph University, Canada, had a total volume of 84.5 l, a swimming section of 110.0 cm length and 19.2 cm in diameter, and was powered by an adjustable-speed hydraulic drive.

The U_{crit} protocol began with an increase in the water velocity to 20 cm s^{-1} from the 15 cm s^{-1} acclimation velocity; water velocity was subsequently raised in 10 cm s^{-1} increments every 30 min until the fish was exhausted. A 12 V, manually activated, electronic grid was located at the rear of the swimming section to prevent the fish from resting. This was usually used only at high speeds and was only activated as a brief pulse when the fish was actually resting at the back of the

section. The grid provided a way to exhaust each fish uniformly by considering the experiment finished when the fish did not move away from the grid after receiving a shock. Subsequently, the water velocity was reduced to 15 cm s^{-1} ; after 0.5 h of recovery, the fish was returned to its holding tank. The critical swimming velocities (U_{crit} , cm s^{-1}) of the fish were calculated as described by Brett (1964). Three months later, this protocol was repeated on a subgroup of the cod ($N=12$) to test for individual performance repeatability over an extended period. For these cod, the highest U_{crit} from the two trials was used for comparison with other swimming tests.

Metabolic rate

The respirometer was sealed during the middle 20 min of each velocity increment of the U_{crit} test and for 10 min immediately following exhaustion to measure oxygen tension in the water with a Radiometer 5046 P_{O_2} electrode. Output from this electrode, which was maintained at 5°C and calibrated daily for both zero and saturated oxygen levels, was recorded both on a chart recorder and on an IBM-compatible computer. The computer collected P_{O_2} data at a rate of 50 measurements s^{-1} . The average of 20 P_{O_2} measurements was written to disk every 2 s (modified from Webber and O'Dor, 1986). The temperature in the respirometer was regulated by the computer at $5 \pm 0.1^\circ\text{C}$ throughout the experiments.

The rate of oxygen consumption (\dot{M}_{O_2} ; $\mu\text{mol kg}^{-1} \text{min}^{-1}$) was calculated according to the following equation:

$$\dot{M}_{\text{O}_2} = [(\Delta P_{\text{O}_2}/\Delta T)(V - M)\alpha_{\text{O}_2}]/M, \quad (1)$$

where ΔP_{O_2} is the change in the partial pressure of oxygen in the water (mmHg), ΔT is the time interval (min), V is the respirometer volume (l), M is the mass of the fish (kg) and α_{O_2} is the solubility coefficient of oxygen at the experimental temperature and salinity taken from Boutilier et al. (1984). Salinity was measured daily using a refractometer. To account for variations in oxygen consumption rate due to size differences among the fish, \dot{M}_{O_2} was adjusted to a standard body mass of 1 kg using a mass exponent of 0.8 (Saunders, 1963; Reidy et al., 1995):

$$X_s = (1/M)^{0.8} \times X_m, \quad (2)$$

where X_s is the standardized value and X_m is the measured value. When \dot{M}_{O_2} was not being measured (first 5 min and last 5 min of each velocity increment), the respirometer was continuously flushed with air-saturated sea water (5°C). Oxygen levels in the water never fell below 85 % of saturation during any of the experiments. A measured 'scope for activity' was calculated by subtracting the maximal rates of oxygen consumption measured for each individual cod from their lowest rates of oxygen consumption.

Burst swimming performance (U_{burst})

Individual cod were placed in the swim-tunnel/respirometer 24 h prior to this swimming performance test. The following day, the water velocity was increased from 15 to 20 cm s^{-1} to initiate the swimming test. The water velocity in the swim

tunnel was then steadily increased at a rate of 0.1667 cm s^{-2} ($10 \text{ cm s}^{-1} \text{ min}^{-1}$). The water was accelerated at this rate until the fish was exhausted. The water velocity at which the fish exhausted was used as the measure of swimming performance (U_{burst}). Fish became exhausted during this test in less than 5 % of the time it took to exhaust the fish during the U_{crit} test. Reidy et al. (1995) discuss further the differences between the U_{burst} and the U_{crit} protocol. Of the 25 cod, 17 had their swimming performance measured with this protocol.

Because a fish's body has a solid blocking effect and narrows the cross section of water flow, thereby increasing the water velocity around the fish, both the critical swimming speeds (U_{crit}) and maximum velocities reached during the acceleration test (U_{burst}) were mathematically corrected to account for this (Nelson et al., 1994). Briefly, the length, mass and maximal cross-sectional area of each fish were used to calculate shape factors using equations from Pope and Harper (1966) and the velocities were corrected according to Webb (1975).

Sprint swimming performance

The sprint velocity of the 25 fish was measured in a chamber modelled after that described by Huey et al. (1981) for terrestrial animals. Our aquatic version (Fig. 1) consisted of a runway ($2.2 \text{ m} \times 0.3 \text{ m} \times 0.3 \text{ m}$; length \times width \times height) connecting a holding chamber and a receiving chamber (both $1.1 \text{ m} \times 0.3 \text{ m} \times 0.4 \text{ m}$). The entire apparatus had filtered sea water flowing slowly through it (2 cm s^{-2}) to maintain constant O_2 tension, temperature (5°C) and waste levels. Five laser diodes, with beams projected as vertical planes of laser light through clear Plexiglas windows on one side of the runway, were lined up with five vertical banks of photodetectors on the other side of the runway. The photodetectors were connected to light-detection and computer timing circuitry which sensed when the connection between the laser beams and the photodetectors was broken (i.e. when a fish swam through the beam).

Twenty-four hours prior to initiation of a sprint trial, a fish was placed in the holding section of the chamber. A lowered gate separated the holding section of the chamber from the runway. The following morning, the gate was raised and the fish was startled by touching its caudal peduncle. This caused the fish to accelerate down the runway into the receiving chamber. The swimming section was traversed in under 2 s. Velocity and acceleration profiles were calculated from the time elapsed between successive photocell bank activations and the distance between the banks. After approximately 15 min, the fish was returned to the holding chamber and allowed to rest for 3 h. This whole procedure was subsequently repeated twice more for a total of three different trials on the same fish in a period of 1 day. Three months later, this protocol was repeated on all but two of the cod ($N=23$). As with the U_{crit} protocol, this was to test for repeatability of individual performance over an extended period. For this study, the maximum velocity recorded for a fish in any trial was used as a measure of its sprint performance.

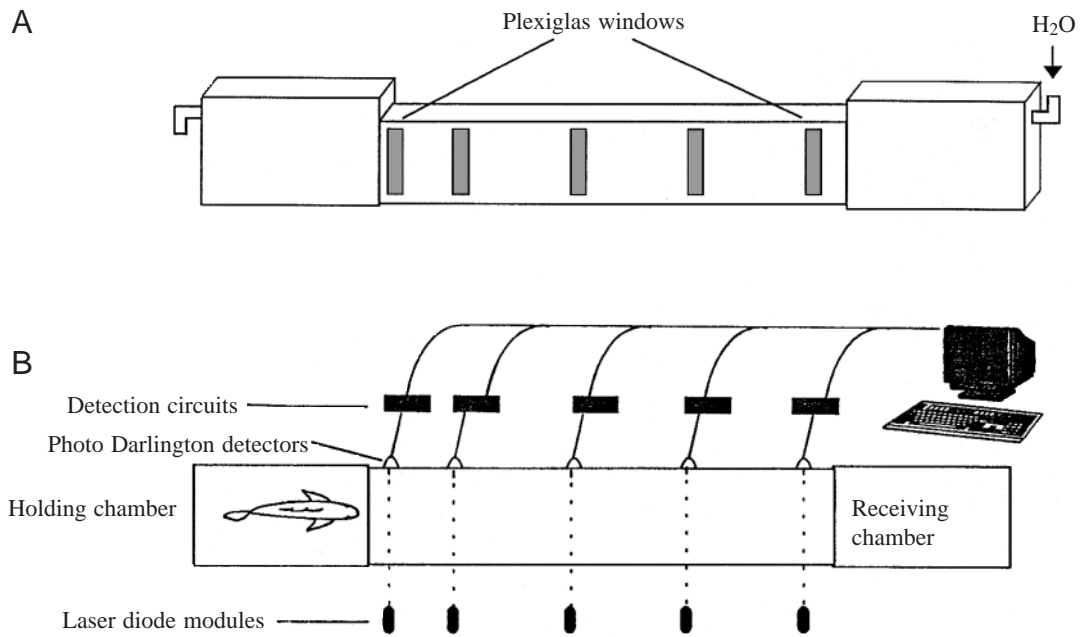


Fig. 1. Schematic diagram of the chamber used to measure the sprint performance of Atlantic cod. (A) Side view; (B) top view.

Morphology and fin surface areas

The mass (g) and fork length FL (cm) of each fish were measured prior to each of the three performance tests as well as at the end of the experiment when the animals were killed with an overdose of the anaesthetic MS-222. From these measurements, a condition factor (K_f ; $100M/FL^3$) was calculated for each fish. Mean K_f , fork length and mass of the cod throughout the experiments are presented in Table 1;

however, for correlations between morphology and swimming performance, we used the individual measurements made at the time of each trial.

After the fish had been killed, all their fins were stretched out and outlined on paper. An Apple graphics tablet/stereometric image-processing program (AGT-SIP) was used to determine the surface area of each fin (cm^2). The surface areas of the three dorsal fins were summed to comprise one group, as were the

Table 1. Descriptive statistics of corrected swimming performance, fin surface area, morphology, age and aerobic scope for activity of Atlantic cod used in this study

	Mean	S.E.M.	Minimum	Maximum	CV (%)	N
Performance (cm s^{-1})						
U_{crit}	58.4	1.66	43.49	71.19	14.2	25
U_{burst}	103.3	2.28	90.93	122.84	9.9	25
Sprint	145.1	10.26	91.03	258.29	35.4	17
Fin surface area (cm^2)						
Tail	59.06	2.13	42.59	75.76	16.5	25
Dorsal	67.03	2.47	45.52	83.53	16.9	25
Anal	39.80	1.80	20.94	56.04	20.7	25
Pelvic/pectoral	69.53	2.57	42.45	87.29	17.0	25
Morphology						
K_f	0.922	0.025	0.676	1.14	13.1	25
Fork length (cm)	52.56	1.21	43.0	65.33	11.3	25
Mass (kg)	1.42	0.112	0.672	2.66	39.3	25
Age (years)	6	0.321	4	9	22.0	17
Measured aerobic scope for activity ($\mu\text{mol O}_2 \text{ kg}^{-1} \text{ min}^{-1}$)	44.4	3.31	19.99	77.93	32.5	19

U_{burst} , burst swimming speed; U_{crit} , critical swimming speed; K_f , condition factor [$=100M/FL^3$, where M is body mass (g) and FL is fork length (cm)]; CV, coefficient of variation; N , number of fish.

Swimming performance was corrected for fish size and parasite load.

areas of the two anal fins and of the pelvic and pectoral fins. Thus, the fin surface areas were treated as four groups: dorsal, anal, pelvic/pectoral and tail. In addition, the cod otoliths were removed and sectioned, and their yearly rings were counted under a microscope to age 17 of the fish.

Statistical analyses

Correlations between two variables may be incorrect or artificially inflated if they are, in turn, both correlated with a third variable (Slinker and Glantz, 1985; Bennett, 1987). Because the fin surface areas were correlated with body size (see Table 2), the confounding effects of body size were removed as follows: the residuals from the allometric regressions of size *versus* the variable in question were added to the mean of the uncorrected data. Adding the residuals to the mean of the uncorrected data converts the data back into the correct units (e.g. cm²) while still eliminating all effects of size.

In addition, because both critical swimming speeds and the rates of oxygen consumption reached by the cod at high speeds during the U_{crit} protocol are reduced by the parasite burden of *Learnocera branchialis* (Copepoda) (S. P. Reidy, J. A. Nelson and S. R. Kerr, in preparation) and eight of the cod were naturally infected with *L. branchialis*, aerobic swimming performance and those rates of oxygen consumption affected by parasite burden were regressed on parasite load of *L. branchialis* (coded as 1 if absent and 2 if present). Again, the residuals were saved and added to the original means to correct for the effects of the parasite load.

Subsequently, all statistical analyses of these variables that were correlated to either size or parasite burden were performed using these corrected data. In addition, all these data presented in both the tables or figures are the corrected data.

Inter-individual correlations among the variables were then examined using both Pearson product-moment correlations (r_p) and Spearman rank-order correlations (r_s). These two tests produced very similar results in our analysis, so only Pearson product-moment correlation coefficients are presented in the tables. Tests examining the repeatability of individual measurements (trial 1 *versus* trial 2 separated by a 3 month period) employed a one-tailed design, while all other correlations were performed using a two-tailed design.

Results

Variability

Maximum sprint velocity was the most variable of the three measures of swimming performance (CV=35.4%), while acceleration (U_{burst}) performance was the least variable (CV=9.9%; Table 1). The means, ranges and variability of cod swimming performance, fin surface areas, aerobic scope for activity, morphology and age are given in Table 1.

Repeatability

Both U_{crit} and sprint swimming performance were found to be significantly repeatable for individual cod (all $P < 0.05$;

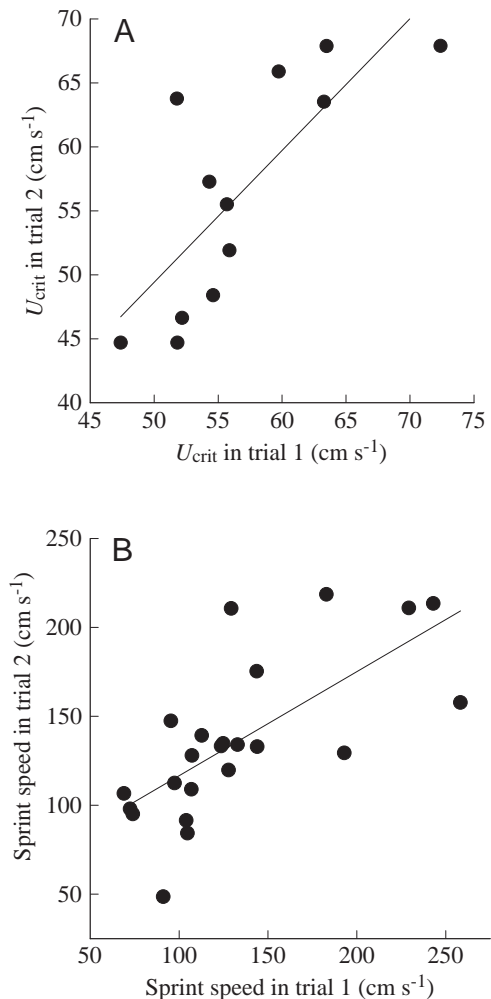


Fig. 2. Repeatability of Atlantic cod swimming performance (corrected for fish size and parasite load) over a 3 month period. (A) Critical swimming speed (U_{crit} ; $y=2.08+1.03x$; $r_p=0.771$, $r_s=0.715$; $P < 0.05$) and (B) maximum sprint speed ($y=58.12+0.585x$; $r_p=0.697$, $r_s=0.756$; $P < 0.05$). r_p , Pearson product-moment correlation; r_s , Spearman rank-order correlation.

Fig. 2). $\dot{M}O_2$ of individual fish during the U_{crit} protocol were also found to be significantly repeatable at swimming speeds of 30, 40 and 50 cm s⁻¹ (all $P < 0.05$; Fig. 3). Of the 10 fish that were used to measure the repeatability of rates of oxygen consumption, only four swam at 60 cm s⁻¹ so a correlation analysis was not performed for that speed. The repeatability correlations between $\dot{M}O_2$ at a swimming speed of 20 cm s⁻¹ and during recovery were also significant using Pearson product-moment correlations (20 cm s⁻¹, $r_p=0.579$, $P < 0.05$; recovery, $r_p=0.841$, $P < 0.05$); however, the data were not normally distributed. This was demonstrated when the non-parametric Spearman rank correlation indicated non-significant relationships (20 cm s⁻¹, $r_s=0.309$, $P > 0.05$; recovery, $r_s=0.679$, $P > 0.05$). Only correlations found to be significant using both Pearson and Spearman tests are presented in Fig. 3.

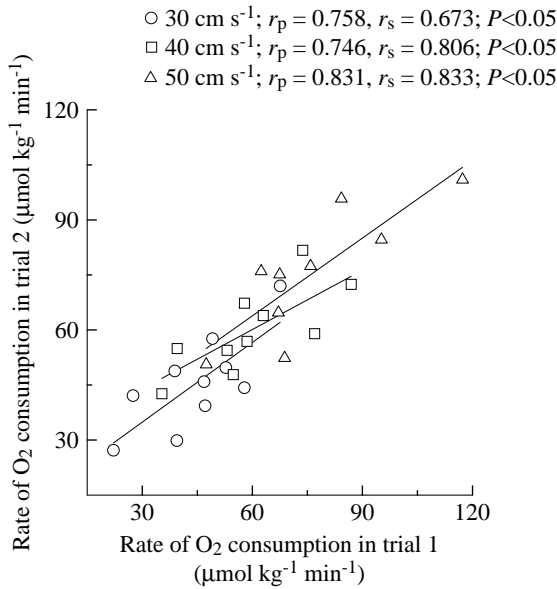


Fig. 3. Repeatability of Atlantic cod rates of oxygen consumption over a 3 month period at different velocities during the critical swimming speed (U_{crit}) protocol. Rates of oxygen consumption at 20 cm s^{-1} and at rest were not significantly repeatable. r_p , Pearson product-moment correlation; r_s , Spearman rank-order correlation.

Morphology

The fin surface areas of the cod were the only variables that were significantly correlated to fork length (Table 2). Almost all the fin surface areas were significantly correlated to one another even following adjustment for differences in the length of the fish (Table 3). The only fins whose areas were not significantly inter-related were the pelvic/pectoral fins and the

Table 2. Inter-individual relationships between Atlantic cod fin surface areas (cm^2 ; SA) and fork length (cm ; FL)

Fin	Equation	r_p
Tail	$SA=2.30FL-63.78$	0.728
Dorsal	$SA=2.12FL-47.39$	0.641
Anal	$SA=1.52FL-41.12$	0.638
Pelvic/pectoral	$SA=1.69FL-20.84$	0.543

All are significant ($P < 0.05$), $N=25$.
 r_p , Pearson product-moment correlation.

Table 3. Pearson product-moment correlations (r_p) of size-corrected surface areas (cm^2) among the different groups of fins

	Tail	Dorsal	Anal
Dorsal	0.625*	–	–
Anal	0.556*	0.511*	–
Pelvic/pectoral	0.507*	0.360	0.579*

* $P < 0.05$.

Table 4. Pearson product-moment correlations (r_p) between Atlantic cod swimming performance (corrected) and morphology, age and metabolic rate

	Aerobic swimming		Anaerobic swimming
	U_{crit}	U_{burst}	Sprint
Total fin surface area (cm^2)	0.143	-0.025	0.021
K_f	-0.248	0.248	-0.014
Age (years)	0.026	-0.116	-0.322
Scope for activity ($\mu\text{mol O}_2\text{ kg}^{-1}\text{ min}^{-1}$)	0.525*	-0.030	0.387

* $P < 0.05$.
 U_{burst} , burst swimming speed; U_{crit} , critical swimming speed; K_f , condition factor (see Table 1).
 Swimming performance was corrected for fish size and parasite load.

dorsal fin ($P > 0.05$). Because of the strong correlations among the fin surface areas, we tested for relationships between swimming performance and total fin surface area rather than each set of fins individually. U_{crit} , U_{burst} and sprint swimming performance were not correlated with total fin surface area or K_f (Table 4).

Metabolic rate

The mean rates of oxygen consumption during the U_{crit} protocol are presented in Fig. 4. Aerobic scope for activity correlated significantly with U_{crit} swimming performance ($r_p=0.525$, $P < 0.05$; $r_s=0.532$, $P < 0.05$; Fig. 5), although not with U_{burst} or sprint performance.

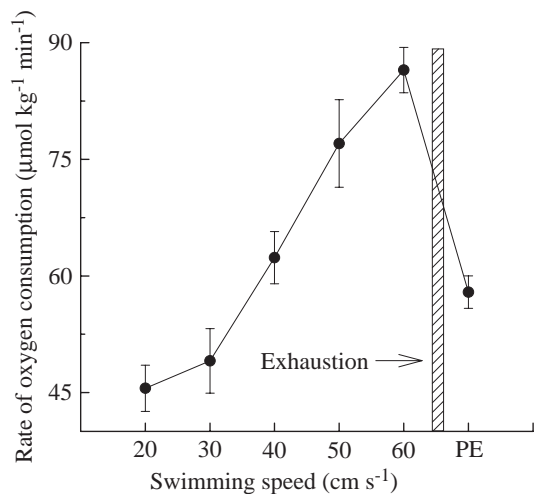


Fig. 4. Corrected oxygen consumption rates (\dot{M}_{O_2} ; means \pm S.E.M.) of Atlantic cod during the critical swimming speed (U_{crit}) protocol and at 10 min post-exhaustion (PE). $N=19$ at all times except 50 cm s^{-1} ($N=16$) and 60 cm s^{-1} ($N=11$) because some fish exhausted sooner than others.

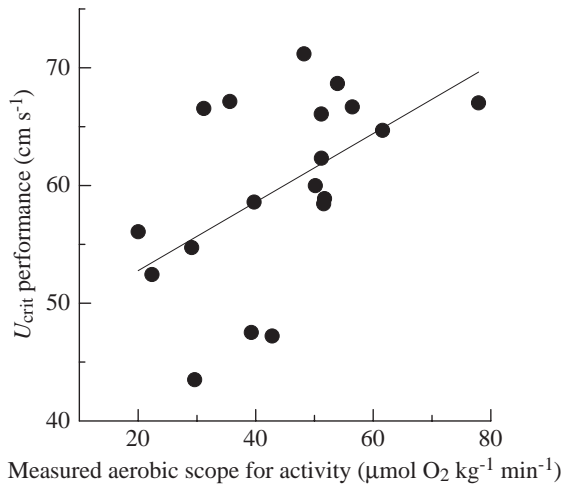


Fig. 5. Relationship between Atlantic cod critical swimming speed (U_{crit}) performance and aerobic scope for activity ($r_p=0.525$, $r_s=0.532$; $P<0.05$). r_p , Pearson product-moment correlation; r_s , Spearman rank-order correlation.

Age and sex

The mean age of the cod was 6 years, and 64 % of them were male. Age was not significantly correlated with any of the performance tests (Table 4); however, female cod had significantly lower U_{burst} results than did male cod (male $107.31 \pm 2.49 \text{ cm s}^{-1}$; female 95.84 ± 4.89 ; $P=0.033$; mean \pm S.E.M.; Fig. 6). There was no effect of gender on either U_{crit} or sprint performance, nor was there an effect of age or gender on any of the measurements of metabolic rate.

Relationships between performance tests

There was a significantly positive correlation between U_{crit} performance and sprint performance ($r_p=0.453$, $P<0.05$; $r_s=0.558$, $P<0.05$; Fig. 7). There was also a significant negative correlation between U_{crit} and U_{burst} performance ($r_p=-0.530$, $P<0.05$; $r_s=-0.574$, $P<0.05$; Fig. 7). U_{burst}

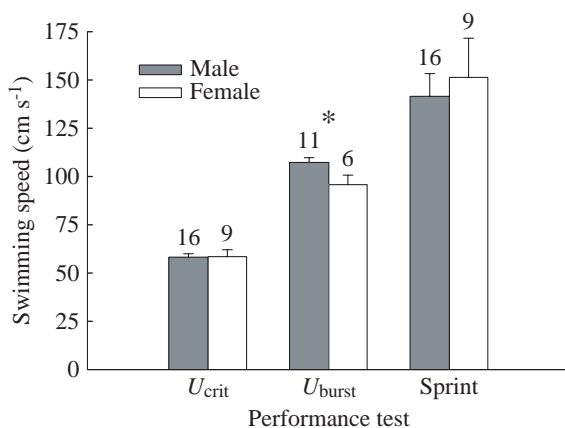


Fig. 6. Differences in swimming performance (corrected for size and parasite load) between male and female Atlantic cod ($*P<0.05$). U_{crit} , critical swimming speed; U_{burst} , burst swimming speed. Values of N are given above each column. Values are means \pm S.E.M.

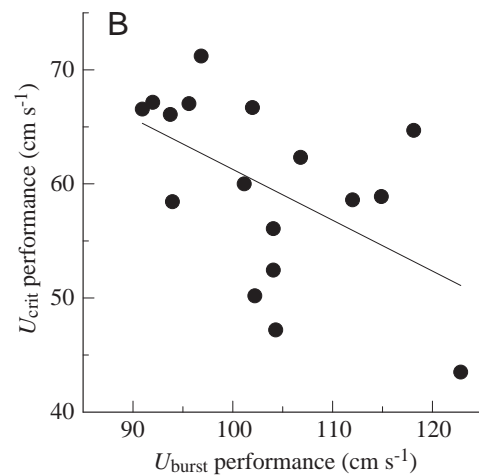
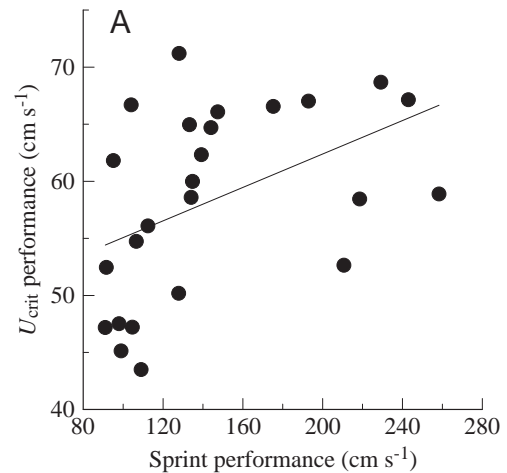


Fig. 7. Relationship between (A) aerobic critical swimming speed (U_{crit}) swimming performance and anaerobic sprint swimming performance ($y=47.76+0.073x$, $r_p=0.453$, $r_s=0.558$; $P<0.05$) and (B) U_{crit} swimming performance and anaerobic acceleration (U_{burst}) performance ($y=105.83-0.446x$, $r_p=-0.530$, $r_s=-0.574$; $P<0.05$). All values have been corrected for any effects of fish size or parasite load. r_p , Pearson product-moment correlation; r_s , Spearman rank-order correlation.

performance and sprint performance were not significantly correlated ($r_p=-0.268$, $P>0.05$).

Discussion

Repeatability of performance and metabolic rate

Both aerobic and anaerobic swimming performance were found to have substantial inter-individual variability and to be significantly repeatable among individual cod. Earlier studies had also found U_{crit} performance to be repeatable in cod (Nelson et al., 1992) and in other fishes such as northern squawfish (*Ptychocheilus oregonensis*; Kolok and Farrell, 1994) and juvenile largemouth bass (*Micropterus salmoides*; Kolok, 1992b). To our knowledge, this is the first report of a repeatable sprint performance by feral fish. Recently, McDonald et al.

(1998) have shown sprint performance to be reproducible in individual hatchery-reared juvenile salmonids. These results parallel the repeatability of sprint performance in tiger salamanders (*Ambystoma californiense*) (Austin and Shaffer, 1992), garter snakes (*Thamnophis sirtalis*) (Garland, 1988) and lizards (*Sceloporus* spp.) (Huey and Dunham, 1987; van Berkum et al., 1989). The significance of these findings is that laboratory studies into the mechanistic bases of variation in swimming performances of cod and possibly other wild fishes can proceed with confidence.

Metabolic rate was also significantly repeatable at high sustainable swimming speeds (Fig. 3). Large inter-individual variation in \dot{M}_{O_2} during swimming protocols is typical of Atlantic cod (Tang et al., 1994) and other fish species (Farmer and Beamish, 1969; Febry and Lutz, 1987) and may, in part, be attributed to stress and/or measurement or equipment error. However, our results show that not only does some of this variation come from intrinsic differences in metabolic rate between animals, but also confirm the commonly held suspicion that much of the variation in resting metabolic rates may be attributed to a variable response to confinement and/or handling of the animals. \dot{M}_{O_2} in the present study was found to be significantly repeatable over a 3 month period among individual cod, but only under our most rigorous of handling criteria (the fish had no visual or physical contact with humans for 2 days prior to swimming or during the procedure) and then only at intermediate to high swimming speeds. Measurements of metabolic rate at low swimming speeds and during recovery from exercise, when the animal had the most flexibility in available movements, were less repeatable. Presumably this variation in 'experiment-induced metabolic rate' would diminish as the number of experimental trials increased. This result implies that, despite the statistical and physiological concerns, estimates of standard metabolic rate made by extrapolation of changes in rates of oxygen consumption with increased work load to zero swimming speed will be more robust for cod than actual measurements of resting metabolic rate made in a static respirometer, especially if regressions from replicate trials at high swimming speeds are averaged. Nonetheless, the significantly repeatable measurements of metabolic rate over a 3 month period demonstrate that inter-individual variation in the rate of oxygen consumption of cod is at least partially due to inherent differences between individuals. Maximum metabolic rate has also been found to be repeatable in exercising garter snakes (Garland and Bennett, 1990) and, interestingly, Walton (1988) found metabolic rate to be significantly repeatable in exercising, but not resting, Fowler's toads (*Bufo woodhousei fowleri*), mirroring our results with Atlantic cod.

Sources of variation in performance and metabolism

Having established that our measurements of performance and metabolic rate are repeatable and, therefore, properties of the animal and not artefacts of our methods, we need to address the approximately twofold variation in all performance measurements made on our study population. These cod were

captured in a single location over a period of less than 1 day and are, therefore, most likely representative of a single population. The animals were treated in an identical manner throughout their laboratory acclimation period; all the animals were feeding well and were in excellent condition (see below). Despite this uniformity of background, these animals exhibited an approximately twofold difference between the best and worst performer for each of the swimming tests (Table 1). Furthermore, the highest metabolic rate at a given swimming speed was also approximately twice the lowest value recorded at that speed (Fig. 3). Considering that fish which did not survive capture or laboratory acclimation because they were either diseased or had a high parasite load would have performed poorly in the swimming tests, this large variance that we measured is probably under-representative of the variance found in nature. Nevertheless, can the measurements we made account for any of this variation?

Differences in morphology were not responsible for the observed variance in performance in this analysis. Total size-corrected fin surface area was not correlated to either aerobic or anaerobic swimming performance. This finding supports that of Webb (1973), who found that U_{crit} in sockeye salmon (*Oncorhynchus nerka*) was unaffected by caudal fin removal, and by Kolok (1992a), who found no morphological correlates of locomotor performance in summer-acclimatized largemouth bass.

Condition factor (K_f) was also not related to the swimming performance of the cod. Fish that were robust did not swim better or worse during the performance protocols than did fish that were thin. Conversely, Kolok (1992a) found a significant positive correlation between K_f and aerobic swimming performance of winter-acclimated largemouth bass. However, no correlation was detected between these two variables for summer-acclimated bass. The condition factor of bass is low during the winter because they go through periods of fasting; thus, it appears that variation in K_f is only correlated to variation in swimming performance when K_f is very low. The Atlantic cod used in this study had relatively high values of K_f , with an average value of approximately 0.9. The condition factor of Atlantic cod in the wild ranges from 0.7 to 0.8 (Krohn et al., 1997); thus, although we did not observe a significant relationship between condition factor and swimming performance, this does not preclude such a relationship had starved cod been included in our analysis.

Although cod use both aerobic and anaerobic metabolism during a U_{crit} protocol (Nelson et al., 1994, 1996), performance during this test has been shown to depend primarily upon the animal's aerobic capacity (Nelson et al., 1996). The present study further supports that hypothesis because the inter-individual relationship between aerobic scope for activity and performance during the U_{crit} protocol was significant (Fig. 5). Other studies have found maximal rates of oxygen consumption to be positively, although weakly, correlated to the inter-individual variation in garter snake stamina (Garland and Bennett, 1990) and the maximum aerobic speeds of toads (Longphre and Gatten, 1994). Walton (1988), however, found

Table 5. Possible limiting factors and relevance to the animal's ecology of the three locomotor tests employed in the present study

Performance test (duration)	Hypothetical limitations	Ecological relevance
Sprint (s)	Morphology; contraction kinetics; excitation–contraction coupling kinetics; degree of motivation	Predator avoidance; prey capture
Burst swimming (min)	Determinants of muscle power output, contractile machinery, glycolytic kinetics, end-product removal kinetics; morphology	Trawl/predator avoidance; manoeuvring through strong current fields
Critical swimming (h)	Oxygen delivery; substrate delivery; morphology	Migration; routine swimming/foraging; spawning in moderate current fields

no relationship between individual variation in toad metabolic rate and locomotor performance.

Relationships between aerobic and anaerobic performance

The performance tests were designed to test different facets of locomotion, each of which has perceived relevance to separate realms of the animal's ecology and each of which is subject to potentially different factors that limit performance (Table 5). The differing nature of these proposed limitations on performance leads to two *a priori* hypotheses concerning how an individual will perform during a given test. The first hypothesis is the 'trade-off hypothesis'. According to this hypothesis, an individual animal that is relatively good at one type of locomotor performance can only achieve this specialization by compromising its ability at others. This hypothesis can be justified mechanistically (e.g. short-distance runners or sprinters have a greater proportion of fast-twitch muscle fibres than do endurance athletes, while endurance runners have a greater proportion of slow-twitch muscle fibres; Komi, 1984) and is illustrated by Olympic-calibre track and field athletes (marathon runners are generally poor sprinters and *vice versa*). Apparently, a trade-off in muscle composition might occur that allows a human athlete to excel at either stamina or speed, but not both.

The alternative hypothesis is the 'good athlete/bad athlete' hypothesis. The heritability and trainability of different performance measures (Bouchard et al., 1988, 1989) can be taken as mechanistic support for this hypothesis. This hypothesis is illustrated by our own human experience in physical education classes where 'natural athletes' can often be found that perform well in any sport. It is necessary to note, however, that support for these hypotheses can depend upon the population from which the subjects are drawn (e.g. the use of elite performers tends to favour the trade-off hypothesis; Garland, 1994).

Interestingly, support for both hypotheses can be gleaned from our study, depending upon which pair of tests is examined. Fish that performed well in the sprint test also performed well during the U_{crit} test (Fig. 7A), supporting the good athlete/bad athlete hypothesis. This is somewhat surprising because, superficially, these tests seem to be the

least alike of the three (Table 5). The sprint test, which is complete in a matter of seconds, is powered by intracellular stores of adenosine triphosphate (ATP) and creatine phosphate and is probably limited by neuromuscular morphology and physiology. Conversely, swimming performance during the U_{crit} protocol is powered aerobically for most of the trial and is probably limited by oxygen delivery and/or metabolite and waste-product flux. However, because locomotor performance is an integrative measure of many physiological and biochemical factors working simultaneously, we cannot be certain that these two swimming modes are independent. A similar relationship between aerobic and anaerobic performance was previously observed by Garland (1988), who found a positive phenotypic and genetic correlation between endurance performance and sprint speed in the garter snake.

Conversely, performance by the cod in the U_{crit} and U_{burst} tests was negatively correlated (Fig. 7B). This negative correlation between aerobic swimming performance and anaerobic acceleration performance suggests that there is an intraspecific trade-off between these two performance types. In natural populations, phenotypic trade-offs in locomotor capacity have previously been observed only between species (theoretically in fish, Webb, 1984; empirically in lizards, Losos and Sinervo, 1989; Sinervo and Losos, 1991; Losos et al., 1993). Even then, these trade-offs were usually a result of interspecific differences in prey or habitat choice. Garland (1988) hypothesised that a trade-off similar to that observed in the present study would occur among garter snakes. However, inter-individual performance of garter snake sprint and endurance performance were positively related. Garland's (1988) method of measuring maximum sprint speeds of snakes was very similar to our sprint performance protocol. It is therefore possible that his hypothesis may have been supported had a performance test more similar to our U_{burst} test been employed. Clearly, more species need to have their sustained sprinting ability (our U_{burst}) tested to determine whether trade-offs between inter-individual performance in this test and in endurance tests are a general phenomenon.

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