Review

Beyond U_{crit}: matching swimming performance tests to the physiological ecology of the animal, including a new fish 'drag strip' ☆

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Abstract

Locomotor performance of animals is of considerable interest from management, physiological, ecological and evolutionary perspectives. Yet, despite the extensive commercial exploitation of fishes and interest in the health of various fish stocks, the relationships between performance capacity, natural selection, ecology and physiology are poorly known for fishes. One reason may be the technical challenges faced when trying to measure various locomotor capacities in aquatic species, but we will argue that the slow pace of developing new species-appropriate swim tests is also hindering progress. A technique developed for anadromous salmonids (the U_{crit} procedure) has dominated the fish exercise physiology field and, while accounting for major advances in the field, has often been used arbitrarily. Here we propose criteria swimming tests should adhere to and report on several attempts to match swimming tests to the physiological ecology of the animal. Sprint performance measured with a laser diode/photocell timed 'drag strip' is a new method employing new technology and is reported on in some detail. A second new test involves accelerating water past the fish at a constant rate in a traditional swim tunnel/respirometer. These two performance tests were designed to better understand the biology of a bentho-pelagic marine fish, the Atlantic cod (*Gadus morhua*). Finally, we report on a modified incremental velocity test that was developed to better understand the biology of the blacknose dace (*Rhinichthys atratulus*), a Nearctic, lotic cyprinid.
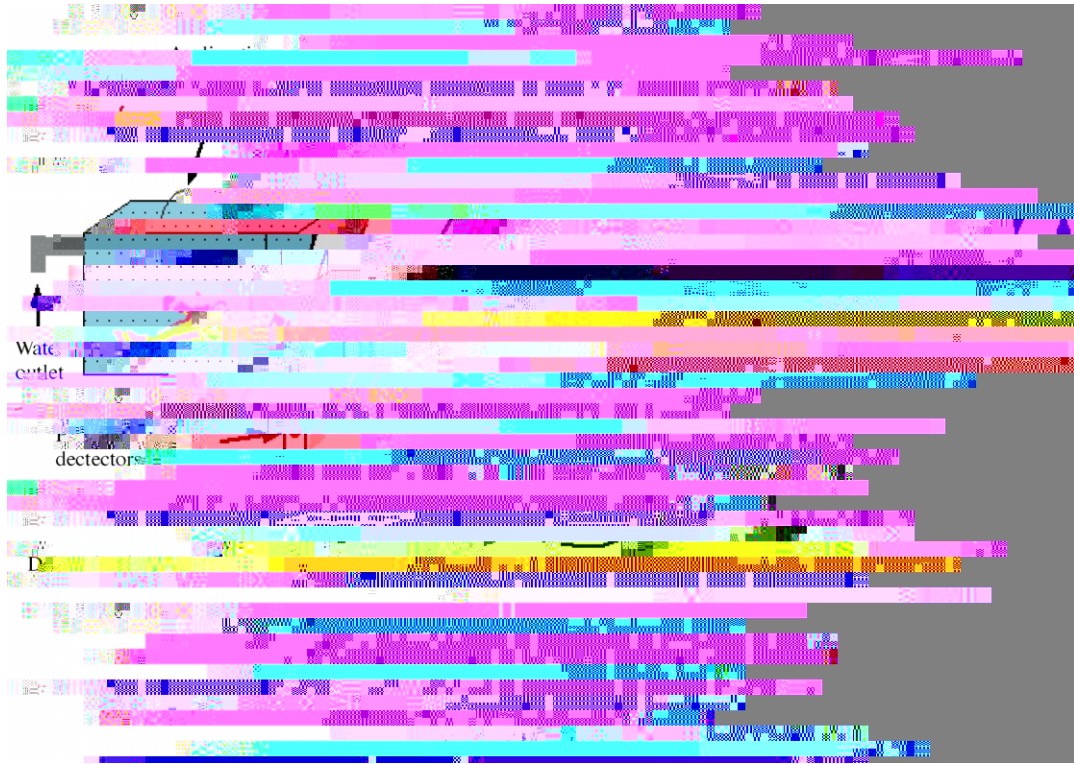©

Fig. 1. Diagram of the fast-start chamber used to measure sprint performance in Atlantic cod (*Gadus morhua*): (a) top view (b) side view. All dimensions are in meters.

plexiglass window (total of 30 detectors). This separation distance assured that a beam would be broken with the first 2 cm of a fish that crossed it (for the size and shape of cod we used). Smaller fish would require a greater density of detectors. These detectors and lasers are produced commercially for various applications and are therefore readily available and inexpensive.

2.1.2. Operational details

The light detection and computer timing circuitry for an individual detector of a bank is shown in Fig. 2 and a flow diagram describing the software protocol is illustrated in Fig. 3. In summary, when activated by light, the photodarlington detector signal is amplified and triggers a 2N2222 transistor which puts out a 5 V TTL signal to 1 of 8 inputs into an 8-input NAND Gate (7430). When all six detectors in a bank are saturated, the NAND gate output is low (<0.3 V). However, if one of the beams is broken, the corresponding input to the NAND gategal the
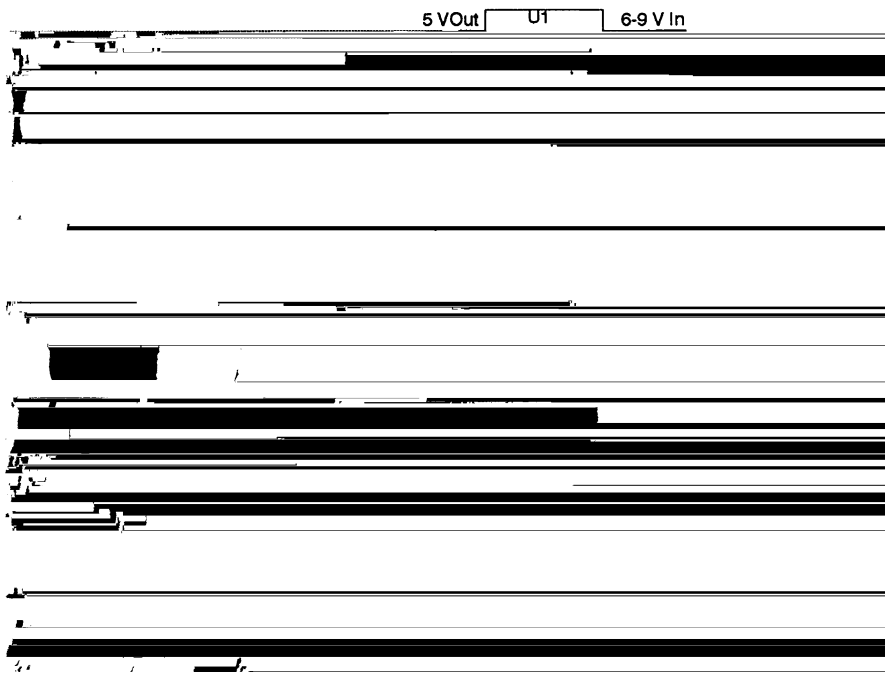
Fig. 2. Diagram of the electronic circuit used to indicate disruption of a laser beam. Note the section of the circuit replicated for each laser beam. Amperage for each circuit (excluding laser) ranged between 10 and 60 mA.
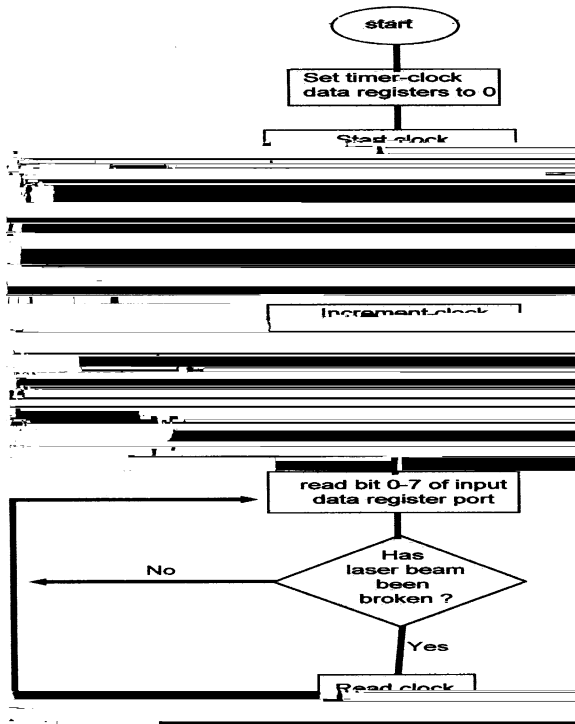
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Fig. 3. Flow diagram of software protocol used to detect hardware laser beam breakage and timing between banks. Software was written in BASIC and Assembly Code and is available upon request.

2.3. U_{crit} procedure modified for a small, lotic cyprinid
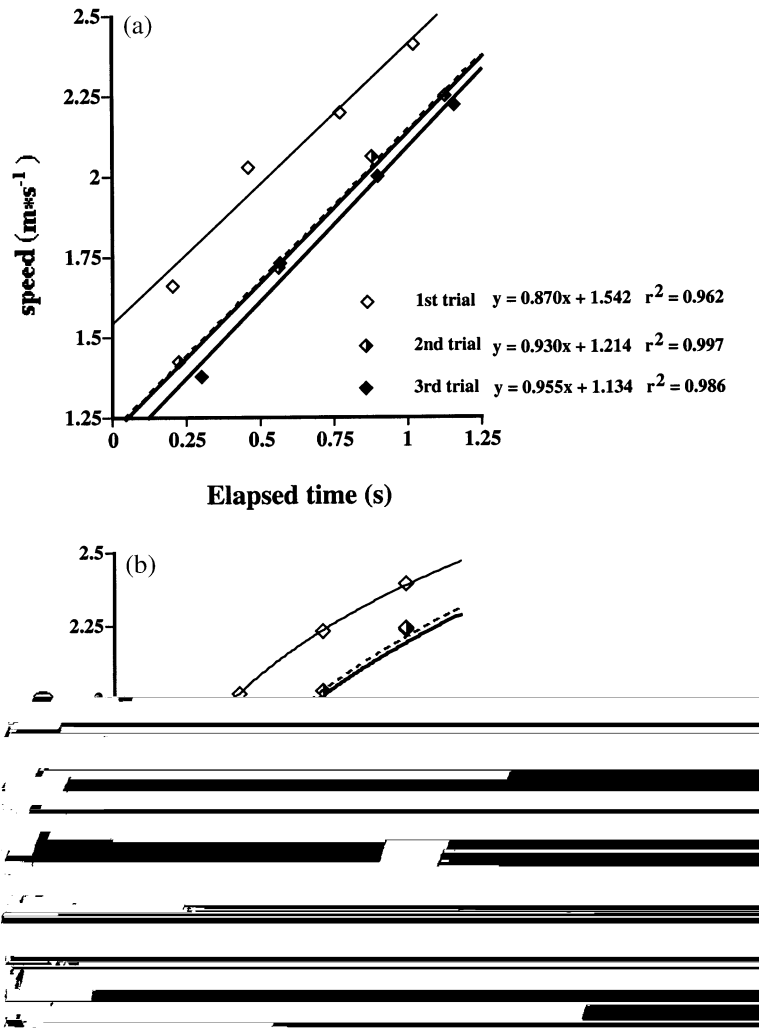
Blacknose dace (

Fig. 4. Swimming speed of an individual Atlantic cod as it burst through the 2.2 m runway after tactile stimulation. Figures show three consecutive trials of the same animal run in a single day. (a) Swimming speed as a function of elapsed time; the equation and correlation coefficient of the least squares linear regression describing each line are included. (b) The same trials depicted in Fig. 4a with swimming speed plotted as a function of distance traversed; the equation and correlation coefficient of the best-fit power function are included.

the relationship of time versus swimming speed was fit with least-squares linear regressions, the lines and equations of which are presented in Fig. 4a for a single animal swum repeatedly, thrice in the same day. When swimming speed is plotted as a function of distance traveled, the relationship was best described by a power function; Fig. 4b shows the same three trials as Fig. 4a, but with speed plotted as a function of distance. Fig. 4 illustrates that much of the variability in repetitive runs occurs with initiation of the fast start; the

$$y = 0.530x + 1.876 \quad r^2 = 0.960$$

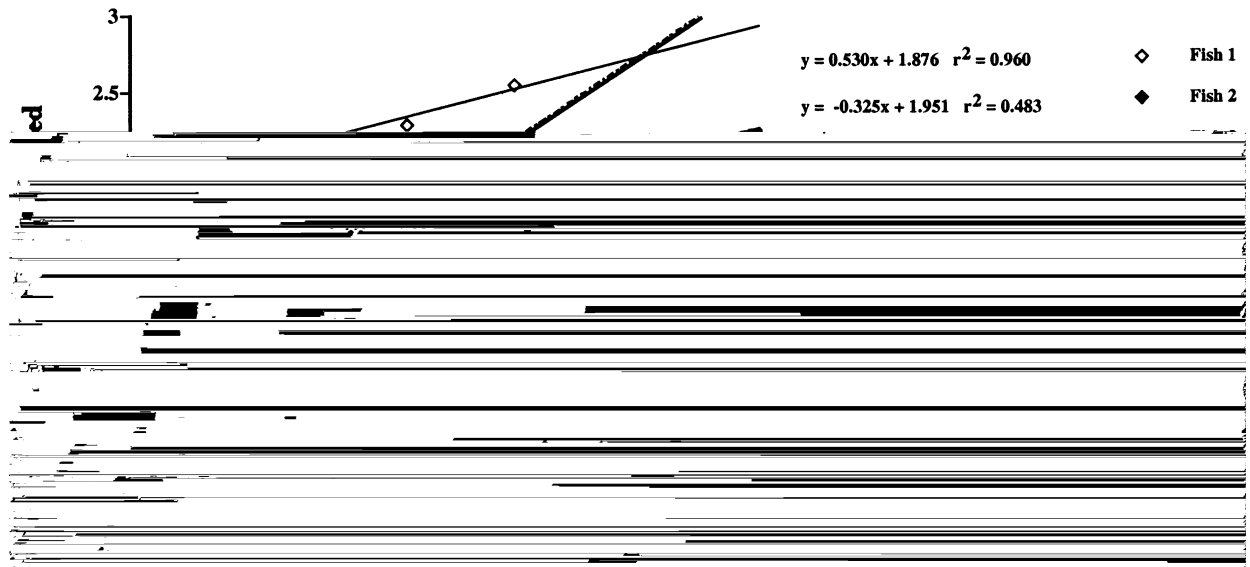$$y = -0.325x + 1.951 \quad r^2 = 0.483$$

◇ Fish 1

◆ Fish 2

Fig. 5. Swimming speed of 6 additional Atlantic cod as they burst through the 2.2 m runway after tactile stimulation. The line for each fish represents the best of three trials, all performed in a single day, for each individual. Swimming speed is plotted as a function of elapsed time; the equation and correlation coefficient of the least squares linear regression describing each line are included.

through the remainder of the chamber while Fish #6 had the slowest start of any fish, but had the greatest rate of acceleration (approximately 2 m s^{-2}) throughout the remainder of the chamber (Fig. 5).

The fish depicted in Fig. 4 was intermediate in performance between 'fish 6' and the three similar-performing fish (1, 4 and 5). These results can also be seen numerically by examining the equations; the slope of the line is the acceleration

◆——— 1st trial $\quad r^2 = 0.808$

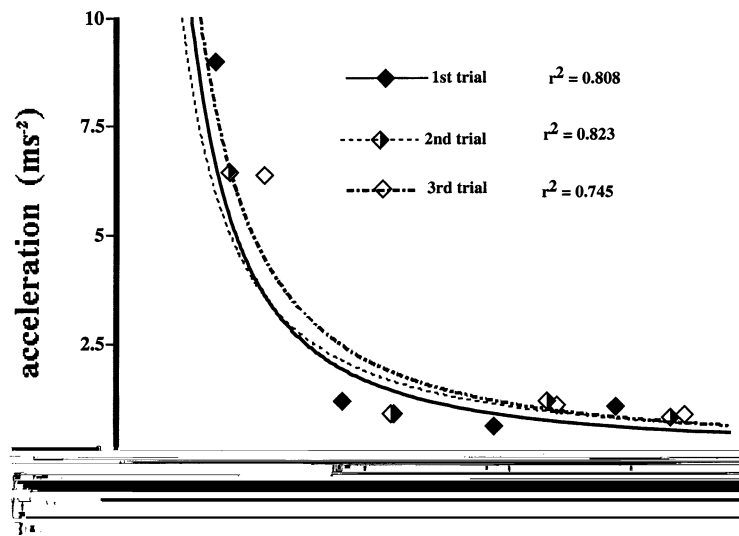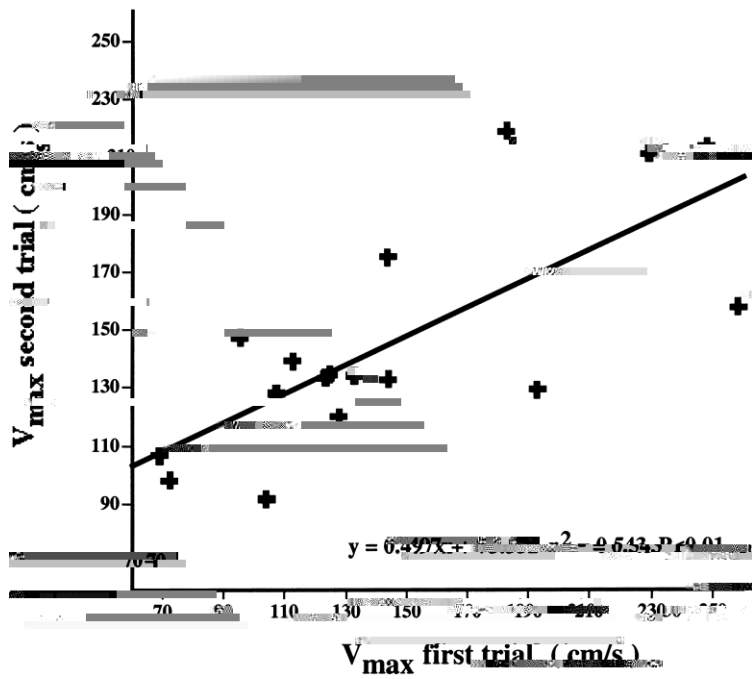◇---- 2nd trial $\quad r^2 = 0.823$

◇—··— 3rd trial $\quad r^2 = 0.745$

Fig. 6. Acceleration of Atlantic cod as they burst through the 2.2 m runway after tactile stimulation. The equation and correlation coefficient of the 'best-fit' power function for each curve are included. Acceleration curves are for the same three consecutive trials depicted in Fig. 4.

$y = 0.497x + \ldots \ r^2 = 0.543, P < 0.01$

tions in performance the second time (Fig. 7). Data points at the extreme of a linear regression have a disproportionate effect on the location of the 'best fit' line (Draper and Smith, 1981). Since nine of the fish had a faster second trial, seven fish had a faster first trial, and one fish had identical trials, we feel safe in concluding that there was no learning effect nor did the fish's health deteriorate over the 3-month period between trials.

3.1.4. Method advantages

The major advantage of this technique is that it allows the investigator to obtain acceleration and swimming speed data on a large number of fish under natural light levels fairly quickly. The rate at which animals can be processed can be increased by making the chamber bi-directional or by reducing acclimation time. Although filming fast-starts of fish is no more time-intensive than our method, high-speed cinematography must occur at light levels that are appropriate only for neustonic fishen''l
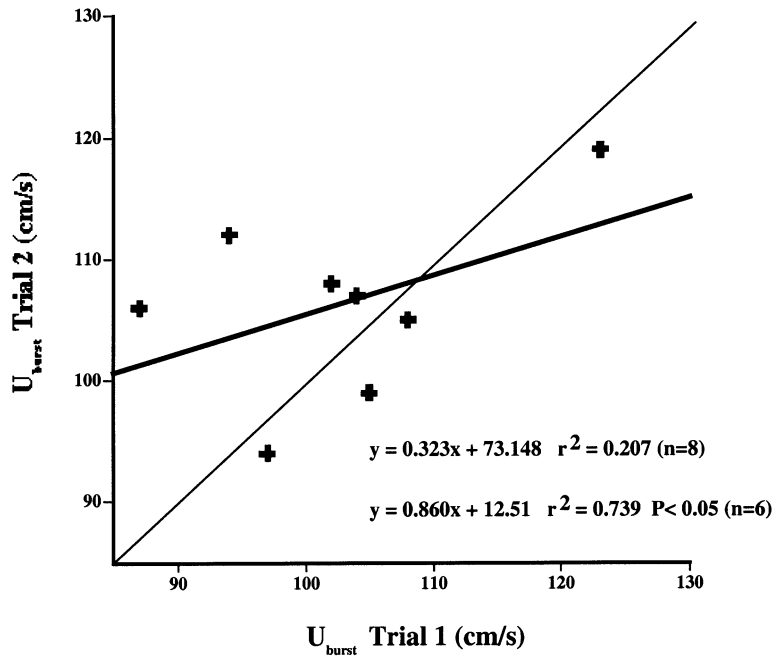
Fig. 8. Swimming speed at fatigue for the 8 Atlantic cod used to initially develop the constant acceleration protocol (U_{burst} of Reidy et al., 2000) recorded in each of two separate trials performed approximately 1 month apart. The equation of the least squares linear regression (dark line) for all eight fish and the same equation with the two worst performing fish removed (both of which had substantial improvement on a second trial) and respective correlation coefficients are included. The lighter line is the line of perfect identity.

3.3. U_{crit} procedure modified for a small, lotic cyprinid

The modified U_{crit} procedure we employed to gauge performance of blacknose dace was very repeatable (Fig. 9). The line relating second performance to first was highly significant by both least squares ($F=62.5$, $P<0.0001$) and non-parametric techniques (Spearman rank order $r=0.771$; $P=0.001$). There was also substantial inter-individual variance in performance among dace that ovie:o7Tja:bot-7]TZ:o7TjlocomotN4N'Ns

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