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## Review

# Beyond $U_{crit}$ : matching swimming performance tests to the physiological ecology of the animal, including a new fish ‘drag strip’<sup>☆</sup>

J.A. Nelson<sup>a,\*</sup>, P.S. Gotwalt<sup>a</sup>, S.P. Reidy<sup>b</sup>, D.M. Webber<sup>b</sup><sup>a</sup>Department of Biological Sciences, Towson University, Towson, MD 21252, USA<sup>b</sup>Department of Biology, Dalhousie University, Halifax, NS, Canada B3H 4J1

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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 benthic-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.

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**Keywords:** Fish; Exercise; Sprint; Burst swimming; Laser diode; Critical swimming

## 1. Introduction

Locomotor performance of feral animals is of considerable interest from management, physiological, environmental, ecological and evolutionary perspectives. For some animals, success in predator–prey interactions and dominance hierarchy

encounters depend upon locomotor capacity (Webb, 1986; Garland et al., 1990). Similarly, the first response of motile animals to environmental perturbation is usually behavioral; successful movement to more suitable environments and therefore survival may depend upon locomotor capacity (e.g. Breitburg, 1992). Thus, locomotor performance is a potential fitness parameter and scientists have expended considerable effort over the past half-century trying to measure the relative ability of animals to move in several temporal contexts (see Beamish, 1978; Bennett and Huey, 1990; Garland and Carter, 1994; Garland and

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\*Corresponding author. Tel.: +1-410-704-3945; fax: +1-410-704-2405.

E-mail address: jnelson@towson.edu (J.A. Nelson).

67 Losos, 1994; Hammer, 1995; Kolok, 1999 for  
68 reviews).

69 The study of locomotor capacity of fishes, in  
70 particular, has a relatively long history (see  
71 reviews by: Beamish, 1978; Randall and Brauner,  
72 1991; Hammer, 1995; Domenici and Blake, 1997;  
73 Kolok, 1999; Plaut, in press); most of this work  
74 has focused on the mechanism of propulsion by  
75 fish and the use of exercise performance as a  
76 gauge of fish health, stress level or ability to deal  
77 with environmental change. Very little effort has  
78 gone into investigating differences in locomotor  
79 capacity among individual fish and whether these  
80 differences have ecological or evolutionary rele-  
81 vance (Kolok, 1999; Plaut, in press). The majority  
82 of fish locomotion studies have employed a graded  
83 water velocity increment test first developed by  
84 Brett (1964), which was designed to evaluate the  
85 relative ability of salmonid fishes to ascend lotic  
86 waters to natal streams. A smaller number of  
87 studies have employed fixed-velocity tests, chasing  
88 regimes, filming of fish swimming behavior or  
89 other techniques (Beamish, 1978). The years fol-  
90 lowing Brett's (1964) first description of the  $U_{crit}$   
91 test saw the widespread and indiscriminant adop-  
92 tion of his procedure to a multitude of problems  
93 concerning swimming capacity in a variety of fish  
94 species (Hammer, 1995). Beamish (1978) exten-  
95 sively reviewed the state of fish locomotion  
96 research at this point in time, including an already  
97 large number of  $U_{crit}$  studies. Drawing largely upon  
98 his own work with centrarchids (Farlinger and  
99 Beamish, 1977), Beamish (1978) proposed guide-  
100 lines for the magnitude and duration of velocity  
101 increments for subsequent  $U_{crit}$  studies. Brett him-  
102 self (1967) had earlier proposed his own guide-  
103 lines for  $U_{crit}$  studies. The guidelines proposed by  
104 Brett (1967) and Beamish (1978) have largely  
105 been adhered to by investigators in the 1980s and  
106 1990s. One purpose of this presentation is to  
107 propose that graded velocity tests can have utility  
108 outside the parameters suggested by Brett (1967)  
109 and Beamish (1978). We developed a graded water  
110 velocity increment test for blacknose dace (*Rhini-*  
111 *chthys atratulus*) with only 5-min time intervals  
112 that was repeatable over a period of 1 month and  
113 has revealed very interesting information about  
114 this species.

115 Taking into account the diversity of fishes and  
116 swimming styles, we propose the following criteria  
117 for gauging or establishing the utility of swimming  
118 tests: (1) the intra-individual variance of perform-

119 ance in the test over extended time periods  
120 (months to years) should be significantly smaller  
121 than inter-individual variance in performance  
122 among conspecifics (i.e. the test should be repeat-  
123 able through time); (2) The locomotor perform-  
124 ance required of the fish in the test should be  
125 within the range of performances experienced by  
126 the fish within the course of a lifetime and thus  
127 have possible relevance towards determining Dar-  
128 winian fitness of fish in the field; (3) the results  
129 from the performance test should theoretically  
130 supply information relevant to the in situ biology  
131 of the animal, be it behavioral or physiological  
132 information. For the vast majority of published  
133 incremental velocity ( $U_{crit}$ ) studies, it is either  
134 unknown or not reported whether the test con-  
135 formed to these criteria (see Hammer, 1995,  
136 Kolok, 1999; and Plaut, in press, for reviews). We  
137 also believe that new swimming tests, which are  
138 increasingly being developed by fish biologists  
139 (e.g. Jain et al., 1998; Cech et al., 1998; McDonald  
140 et al., 1997), should conform to these criteria to  
141 be of maximal utility.

142 A second purpose of this presentation is to  
143 introduce two new methods for measuring short-  
144 term exercise performance of fishes and to discuss  
145 briefly our attempts at determining whether they  
146 conform to the above-stated criteria. Studies of  
147 fish swimming performance have multifarious  
148 goals. However, if the goal of a study is to  
149 understand performance physiology or to use loco-  
150 motor capacity as a potential fitness parameter, an  
151 isolated incremental velocity test will probably  
152 prove insufficient in most cases. As employed by  
153 most investigators, a critical swimming speed test  
154 causes the fish to use variant swimming modes at  
155 different times during the test. The onset and  
156 duration of these different swimming modes is  
157 quite variable among individuals of a species and  
158 the degree to which an individual uses anaerobic  
159 metabolism to power the swim can also vary  
160 substantially (Nelson, 1990; Hammer, 1995; Kolok  
161 and Farrell, 1994; Nelson et al., 1996). Thus, two  
162 conspecific fish may have identical  $U_{crit}$  values but  
163 may have used quite different physiologies and  
164 may have swum quite differently in arriving at  
165  $U_{crit}$  (e.g. Nelson, 1990; Nelson et al., 1996). In  
166 other words, individual fish of a species show the  
167 variation in exercise physiology we have come to  
168 expect as routine from humans (e.g. Bouchard et  
169 al., 1989). Thus, if the goal of a study is to  
170 characterize the performance physiology of a spe-

171 cies or population, or to assign a performance level  
 172 to an individual fish, additional performance tests  
 173 will improve the veracity of the study. Thus, there  
 174 is a need for more and diverse swimming tests for  
 175 fish. At this point in time, there are very few  
 176 published alternatives to the incremental velocity  
 177 tests. It is also very poorly known how other types  
 178 of swimming performance relate to  $U_{crit}$  perform-  
 179 ance in the same individual; this question has only  
 180 been addressed in a few studies (Kolok, 1999;  
 181 Reidy et al., 2000).

182 The two new swim tests we report on here are  
 183 attempts to resolve swimming performances of  
 184 fish on the scale of seconds to minutes. Fast-start  
 185 performance is usually considered the measure of  
 186 performance with the most predictive value for  
 187 predator–prey interactions (Domenici and Blake,  
 188 1997; Webb, 1986) and thus ecological/evolution-  
 189 ary relevance, yet has been studied relatively little  
 190 in these contexts. Most studies on fast-starts and  
 191 sprint locomotion were designed to discern mech-  
 192 anisms of propulsion by fish and employed hydro-  
 193 dynamic kinematics (Gero, 1952; Gray, 1953),  
 194 high-speed filming, or high-speed filming coupled  
 195 with digital image analysis to calculate swimming  
 196 speed or acceleration (Domenici and Blake, 1997;  
 197 Gamperl et al., 1991; Harper and Blake, 1990;  
 198 Taylor and McPhail, 1985; Wardle, 1975; Webb,  
 199 1975, 1978, 1983). Recent technological advances  
 200 have also allowed the use of piezoelectric accel-  
 201 erometers (Domenici and Blake, 1997; Harper and  
 202 Blake, 1989, 1990) to accurately measure fish  
 203 acceleration. Unfortunately, since we wanted to  
 204 obtain repetitive measurements of performance on  
 205 a large number of animals under conditions ‘field-  
 206 relevant’ for Atlantic cod, none of the traditional  
 207 techniques were optimal. Piezoelectric techniques  
 208 require extensive animal handling. Therefore, to  
 209 measure large numbers of animals with adequate  
 210 recovery times is difficult. Likewise, although  
 211 large numbers of fish can be filmed relatively  
 212 quickly, analysis of films or videotapes to extract  
 213 data can take inordinate amounts of time. High-  
 214 speed filming also requires that the fish perform  
 215 under fairly bright lights, a condition ecologically  
 216 inappropriate for many fishes, including cod.

217 Huey et al. (1981) developed a computer driven,  
 218 multi-beam photocell timing technique based upon  
 219 an earlier dual photocell method introduced by  
 220 Bennett (1980). Huey et al.’s (1981) method  
 221 allowed acceleration and sprint velocity to be  
 222 repeatedly and accurately measured in large num-

223 bers of terrestrial animals relatively quickly (e.g.  
 224 Hertz et al., 1983; Huey and Dunham, 1987;  
 225 Bennett and Huey, 1990). The development of this  
 226 computerized ‘drag strip’ contributed to the flour-  
 227 ishing of knowledge concerning the physiological  
 228 ecology and evolutionary biology of locomotion  
 229 of small terrestrial vertebrates in the 1980s. We  
 230 developed a system, similar to that described by  
 231 Huey et al. (1981), but designed to measure sprint  
 232 performance of aquatic organisms. This new meth-  
 233 od allows the investigator to obtain acceleration  
 234 and swimming speed data from ‘bursts’ of loco-  
 235 motion on a large number of fishes relatively  
 236 quickly. We report on the use of this method for  
 237 measuring sprinting performance of Atlantic cod  
 238 (*Gadus morhua*) over a 2-m distance. In addition,  
 239 we report on the development of a constant accel-  
 240 eration test (CAT) for Atlantic cod utilizing a  
 241 traditional swim tunnel/respirometer.

## 2. Methods and materials 242

### 2.1. New sprint performance method 243

#### 2.1.1. Chamber construction 244

245 The fast start chamber was constructed from 1/  
 246 4" and 3/8" opaque polyvinyl chloride ‘flat stock’  
 247 (Fig. 1). The dimensions of the actual raceway  
 248 were 2.2 m length×0.3 m width×0.3 m height  
 249 which separated a holding chamber and a receiving  
 250 chamber each of equal dimension. We designed  
 251 this chamber for use on 50 cm adult Atlantic cod;  
 252 these dimensions should be scaled appropriately  
 253 for fishes of different size. To allow passage of  
 254 laser light, transparent windows were cut from  
 255 Lexan® Plexiglas and secured to the raceway  
 256 section of the chamber (Fig. 1).

257 Light-emitting laser diodes of 3 mW power  
 258 output, 600–720 nm wavelength and 3 mm beam  
 259 width were placed at 0, 0.3, 0.9, 1.5 and 2.1 m  
 260 positions along the runway (Fig. 1). A 3-mm glass  
 261 rod was attached to the front of the laser lens.  
 262 This rod refracted the beam to project a vertical  
 263 plane or ‘curtain of light’ across the raceway. The  
 264 width, height and intensity of the beam could be  
 265 modified by changing the diameter of the glass  
 266 rod and the distance between the laser and the  
 267 glass rod.

268 A group of six photodarlington detectors of  
 269 detection wavelength 580–720 nm were obtained  
 270 from a local electronics retailer and positioned  
 271 vertically 2.5 cm apart directly across from each

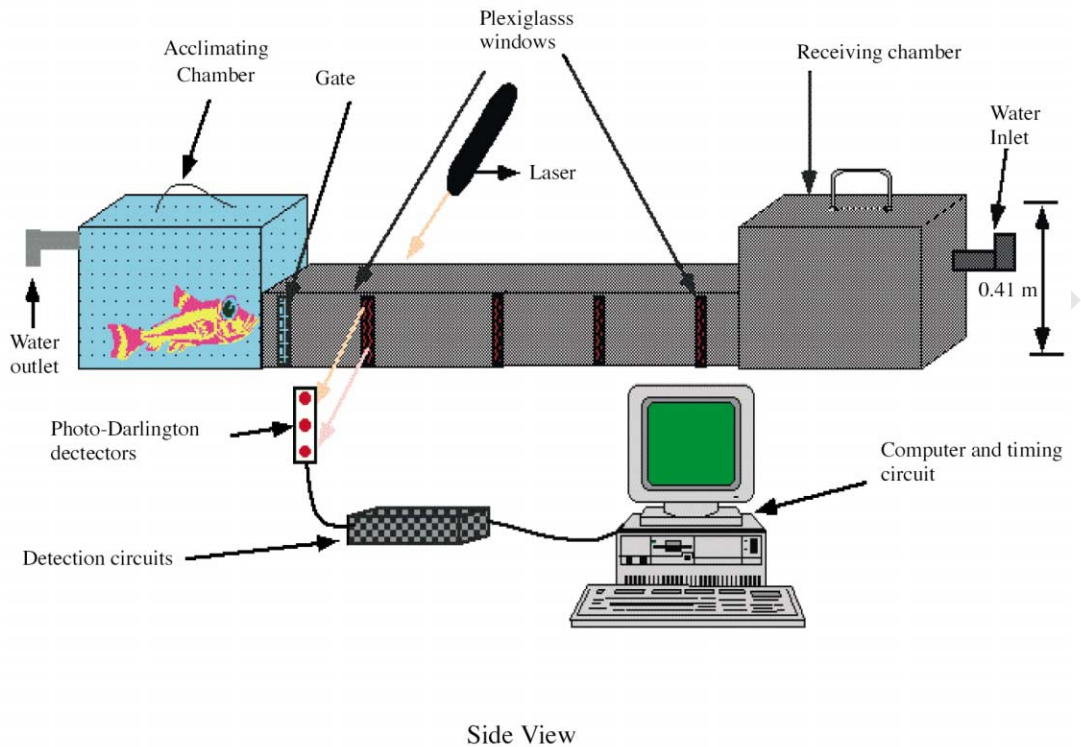


Fig. 1. Diagram of the fast-start chamber used to measure sprint performance in Atlantic cod (*Gadus morhua*): (a) top view (b) side view. All dimensions are in meters.

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 gate goes low and forces the output of the NAND gate to go high (>0.3 V) (Fig. 2). Similar detectors, including 'on board'

NAND gate circuitry, are now available as integrated circuits from Honeywell® Corporation. The computer and digital timer board (MCS6522 Peripheral Interface Adapter, Interactive Microwave Inc. P.O. 771, State College, PA 16801, USA) continuously scan the outputs from NAND gates associated with each bank of detectors. Data from the original incarnation of this sprint chamber were collected by an interrupt driven timer software routine in assembler code on an Apple II computer, operating at 1.023 MHz (code will be supplied free of charge upon request). The software-timing cycle was capable of distinguishing events  $10^{-5}$  s apart and would initiate upon breaking of the first light beam by a fish (Fig. 3). The response time of the detector circuitry was determined to be  $10^{-6}$  s. Data from the described system can now be conveniently collected with commercial analog/digital systems such as Labview® or Powerlab®.

### 2.1.3. Test protocol

Twenty four hours prior to the initiation of a trial, a fish was lightly anaesthetized with MS-222

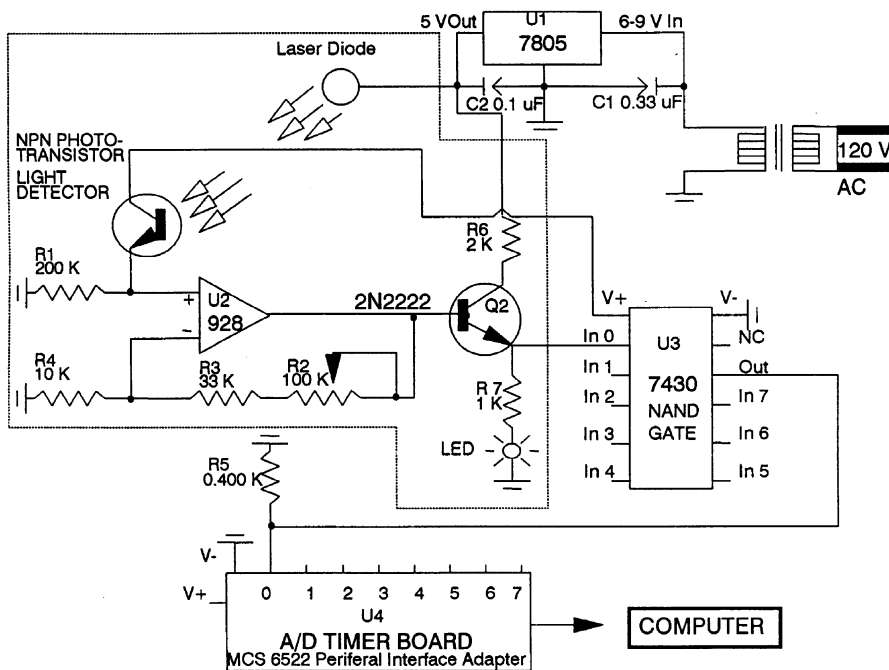


Fig. 2. Diagram of the electronic circuit used to indicate disruption of a laser beam. Note the section of the circuit replicated for each laser beam. Amperage for each circuit (excluding laser) ranged between 10 and 60 mA.

(50 mg/l Sigma®) and placed in the holding section of the chamber (Fig. 1). The fish was kept in this area by a gate that was used to separate the holding chamber from the raceway. Trials for Atlantic cod were conducted in 5 °C, 31‰ water at low, ambient red light so that the fish were in virtual darkness. The following morning, the gate was raised and the fish startled by grasping its caudal peduncle. Electrical, optical and auditory stimuli were also tried as ways to initiate a sprint by Atlantic cod, but tactile stimulation elicited the most intense and reproducible response. Following tactile stimulation, the fish burst down the raceway into the receiving chamber (Fig. 1) where devices for gently decelerating the fish could be located and/or another gate could be closed allowing the fish to rest in this chamber before subsequent treatments. Sprint swimming velocity and acceleration profiles were calculated by the computer software from the time elapsed between breakage of the first laser beam, breakage of subsequent laser beams and the distance between the laser banks.

Operation of the chamber was initially tested with a group of 7 wild Atlantic cod. The procedure was then used on a separate group of 23 Atlantic

cod twice each, with 3 months elapsing between repetitive trials (Reidy et al., 2000); data from both groups of fish are presented here.

## 2.2. Constant acceleration test

This procedure has been previously described in Reidy et al. (2000) as the ' $U_{burst}$ ' test. Briefly, adult Atlantic cod were placed in a 96 l swim-tunnel/respirometer 24 h prior to the procedure. The following day, the water velocity was increased at a rate of  $0.1667 \text{ cm s}^{-2}$  ( $10 \text{ cm s}^{-1} \text{ min}^{-1}$ ) until the fish was exhausted. The water velocity at which the fish exhausted was used as the measure of burst swimming performance ( $U_{burst}$ ). The definition of exhaustion was when a 12 V electric field did not keep the fish off of the downstream retaining wall. The method was initially developed on a group of 8 Atlantic cod that were each tested twice 1 month apart and then 17 of the same 23 cod that were used for the sprint procedure (see above) were also tested with this protocol. Final  $U_{burst}$  velocities were corrected mathematically for the solid blocking effect according to Nelson et al. (1994).

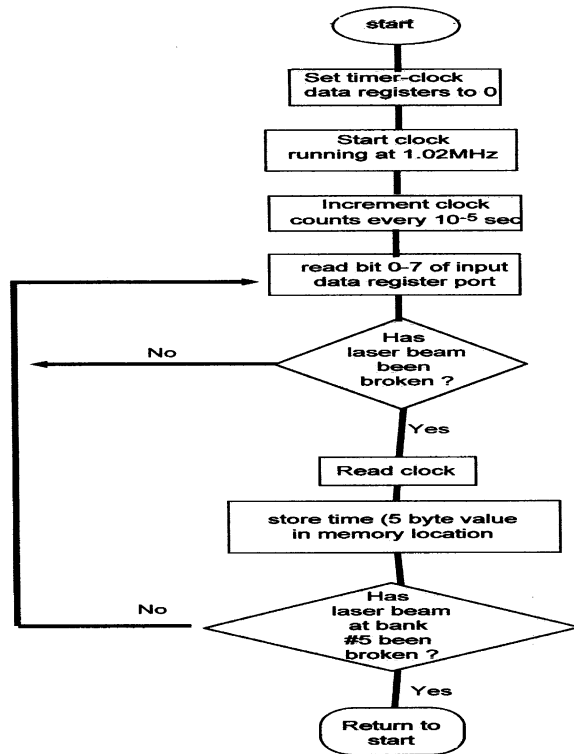


Fig. 3. Flow diagram of software protocol used to detect hardware laser beam breakage and timing between banks. Software was written in BASIC and Assembly Code and is available upon request.

### 2.3. $U_{crit}$ procedure modified for a small, lotic cyprinid

Blacknose dace (*Rhinichthys atratulus*) from three watersheds and five separate locations within Maryland, USA were collected with a Smith-Root Inc<sup>®</sup>. Model 15-D backpack electroshocker. Approximately 20 fish from each site (40–60 mm total length, TL) were returned to the laboratory and restricted to an area of their holding tanks where the current speed was between 1 and 3 cm/s. Animals were fed daily with live adult brine shrimp (*Artemia* sp.), but were fasted 24 h prior to a swimming trial. Fish to be swum, were anaesthetized with MS-222, water concentration of 50 mg/l, until they reached phase I of anaesthesia (loss of equilibrium; Iwama et al., 1989). Anaesthetized fish were transferred to a laminar-flow swim flume (Nelson, 1989) and acclimated to a 5 cm/s current at 24(±1 °C) for 1 h. Fish were then exposed to increasing velocity increments of 5 cm/s at 5 min intervals until exhausted. Exhaust-

tion was defined as the point at which a fish no longer responded to gentle prodding with a rubber eraser. Critical swimming velocity,  $U_{crit}$ , was calculated according to Brett (1964). The formula used was:

$$5U_{crit} = U_i + (T_i/T_{ii} \times U_{ii})$$

where  $U_{crit}$  = critical swimming speed (cm/s),  $U_i$  = highest velocity maintained for a full 5 min interval,  $T_i$  = time of fatigue at last current velocity (min),  $T_{ii}$  = interval length (5 min), and  $U_{ii}$  = velocity increment (5 cm/s). A subset of these fish were re-swum approximately 1 month from the date of initial swimming.

Current speeds of the holding tanks and swim flume were measured with a freshly calibrated Marsh-McBirney Inc.<sup>®</sup> Model 2000 flow meter. In each case, a three-dimensional grid was established (108 stations in the 180×55×35 cm holding tanks, 27 stations in the 32×10×10 cm swimming section of the swim flume) and current readings made at each station. To establish the calibration for the swim flume, current readings were repeated for each station at 5 V increments of the variable transformer supplying power to the motor.

### 2.4. General

All performance tests were conducted without investigator knowledge of that particular individual's performance in any previous test.

## 3. Results and discussion

### 3.1. New sprint performance method

The results from our trials with Atlantic cod show that the chamber described here can effectively measure sprinting performance in an aquatic medium and should be of use to investigators interested in the ecological and evolutionary ramifications of aquatic performance. We support this contention with evidence that the method is significantly repeatable over a period of several months and a finding that the intra-individual variance of swimming speed in repetitive trials is smaller than inter-individual variance.

#### 3.1.1. Swimming speed

Swimming speed increased in a linear fashion when plotted as a function of elapsed time. Thus, the relationship of time versus swimming speed

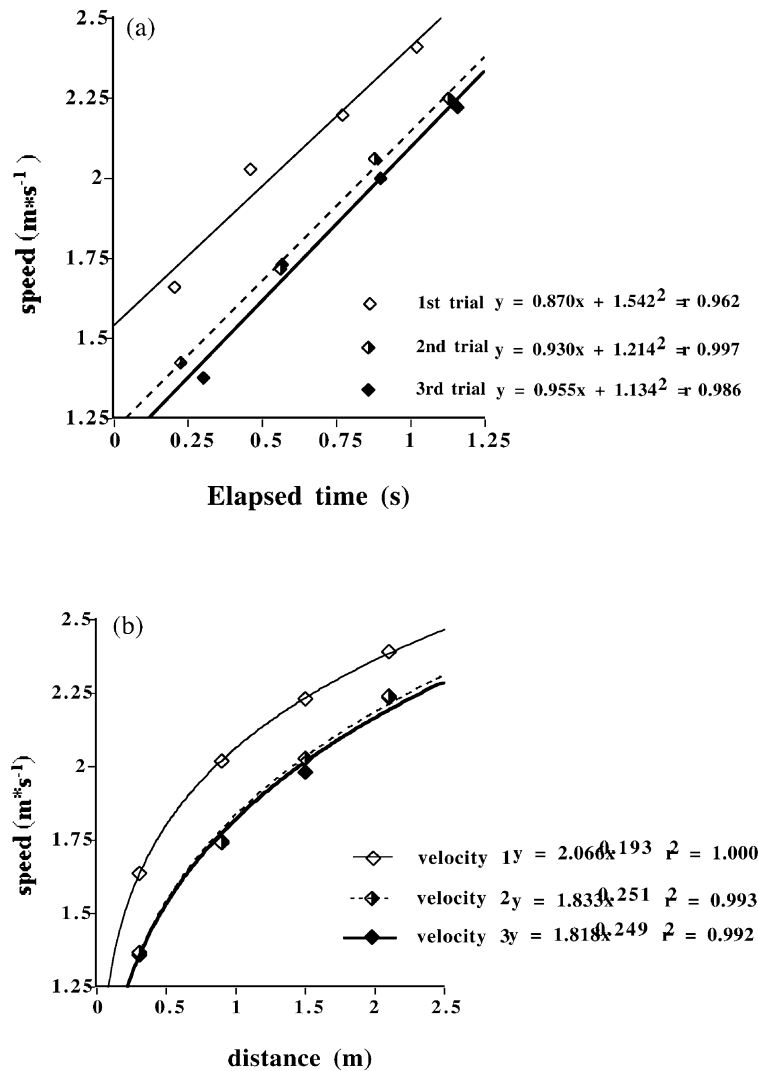


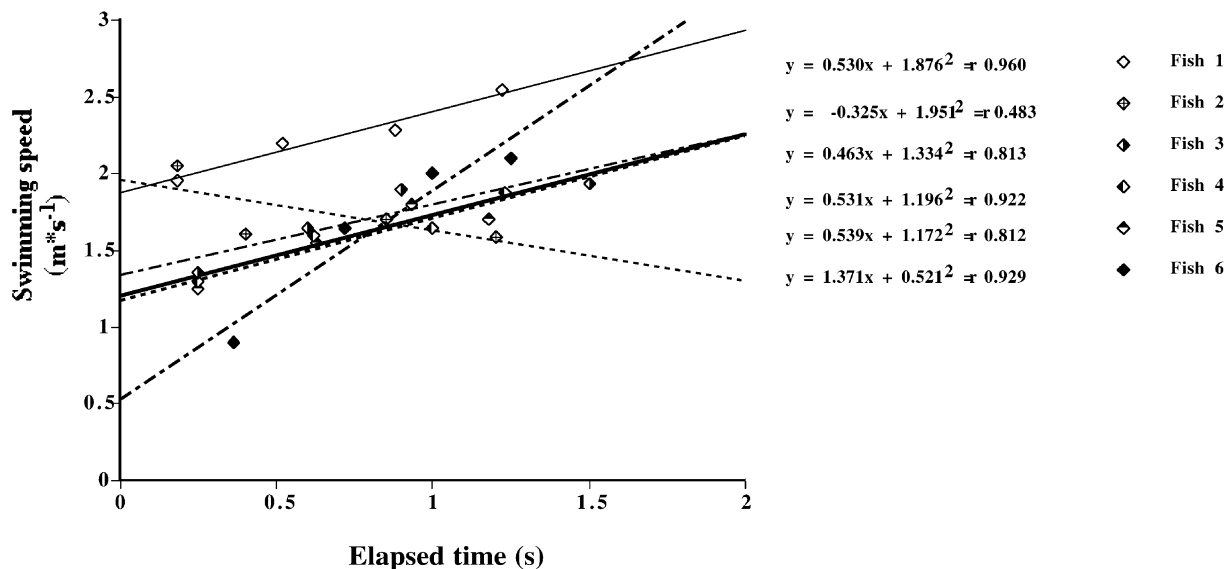
Fig. 4. Swimming speed of an individual Atlantic cod as it burst through the 2.2 m runway after tactile stimulation. Figures show three consecutive trials of the same animal run in a single day. (a) Swimming speed as a function of elapsed time; the equation and correlation coefficient of the least squares 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.

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 three runs were virtually indistinguishable after the fish passed the second detector array (first data

point). This result can be seen numerically by comparing the slopes of the regression lines and the power function exponent (Fig. 4).

Comparison of the velocity profiles for six additional cod (Fig. 5) demonstrates substantial inter-individual variance in sprint performance measured with our apparatus. This graph (Fig. 5) presents the best of three performance trials, run in a single day for each of the six fish. Four of the six fish had similar 'best swims' after the first detector array. In contrast, Fish #2 accelerated better than any other fish through the first two

33  
34

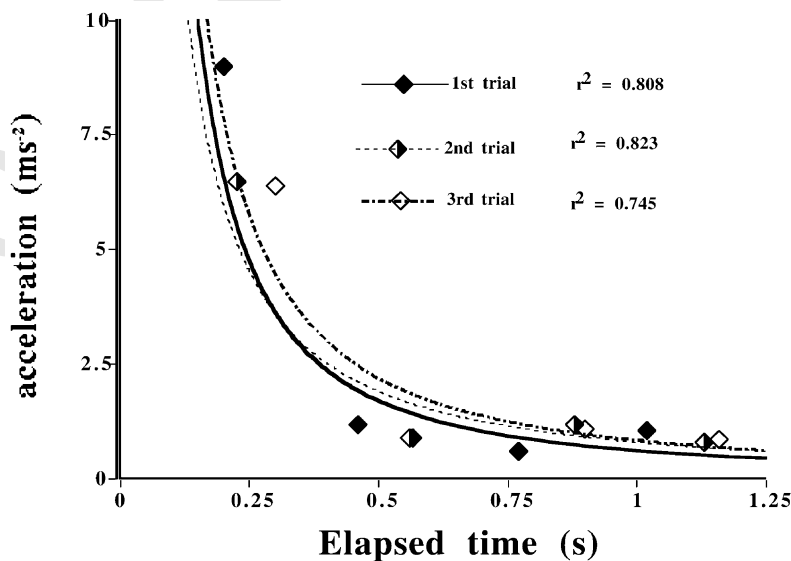


35 Fig. 5. Swimming speed of 6 additional Atlantic cod as they burst through the 2.2 m runway after tactile stimulation. The line for each  
36 fish represents the best of three trials, all performed in a single day, for each individual. Swimming speed is plotted as a function of  
37 elapsed time; the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

458  
459 detector arrays but then basically decelerated  
460 through the remainder of the chamber while Fish  
461 #6 had the slowest start of any fish, but had the  
462 greatest rate of acceleration (approximately  $2 \text{ m s}^{-2}$ )  
463 throughout the remainder of the chamber (Fig. 5).

464 The fish depicted in Fig. 4 was intermediate in  
465 performance between ‘fish 6’ and the three similar-  
466 performing fish (1, 4 and 5). These results can  
467 also be seen numerically by examining the equa-  
468 tions; the slope of the line is the acceleration  
469 through the last three detector arrays and the y-

41  
42



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

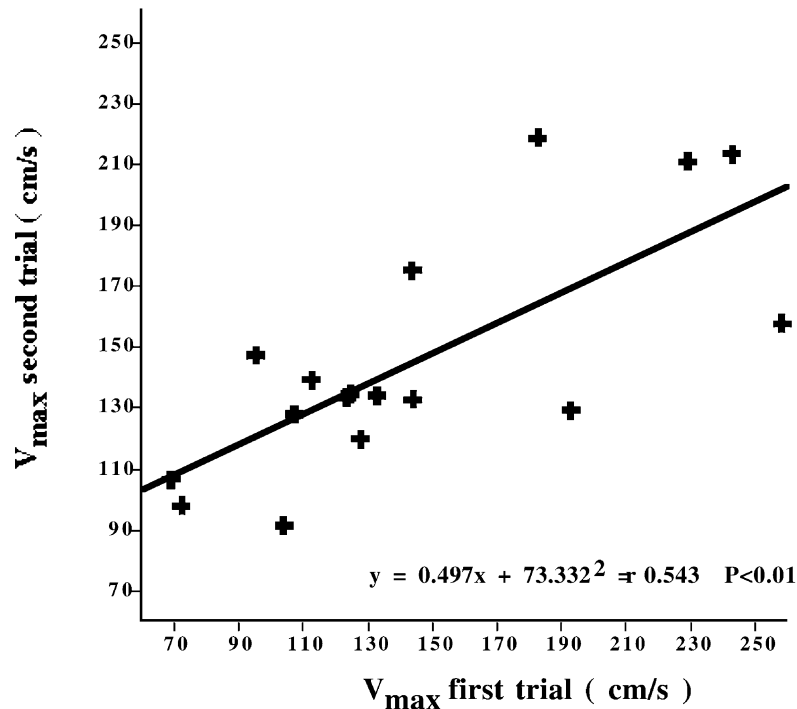


Fig. 7. Maximum swimming speed recorded in two separate sprint trials performed approximately 3 months apart, for each of 17 Atlantic cod. The equation of the least squares linear regression (solid line) and the square of the Spearman rank correlation coefficient are included.

intercept can be considered a rough measure of the animal's starting ability (velocity at 0 time).

### 3.1.2. Acceleration

Fig. 6 plots the acceleration data corresponding to the three trials depicted in Fig. 4. Again, this was the same animal swum three times in a single day.

These data show that the maximal rate of acceleration for this cod undoubtedly occurred before our first detector array (0.3 m) and, that although the fish continued to positively accelerate throughout the swim chamber, the magnitude declined to a steady level after 0.3 m (Fig. 6). These data are in accord with accelerometer data collected on rainbow trout (*Salmo gairdneri*) and northern pike (*Esox lucius*) by Harper and Blake (1990). These authors found maximum acceleration for all types of fast-starts to occur within the first 0.15 s of swim initiation. To get a realistic number for maximal acceleration by Atlantic cod of this size, one would need to have the second photodetector array positioned much closer than 0.3 m from the starting position. For this reason, acceleration data is not analyzed further, although the inter-individual

heterogeneity in acceleration data also exceeded intra-individual acceleration variance (not shown).

### 3.1.3. Long-term repeatability

The sprint performance technique described above was included in an ongoing study on the locomotor performance of Atlantic cod (Reidy et al., 2000). As one of many measurements in Reidy et al. (2000), 17 Atlantic cod had their sprint performance tested twice, with the trials falling approximately 3 months apart. Here we reiterate the maximal swimming velocity reached by the 17 cod for each of the two trials because it illustrates an important point (Fig. 7).

Fig. 7 shows that this method is significantly repeatable ( $P < 0.01$  Spearman-rank order  $r_s = 0.756$ ) over a period of 3 months in a population of wild fish held in the laboratory. By correcting for differences in body size, this relationship became even more robust (not shown). The slope of the regression line relating second trials to first trials is only 0.5; this was largely dictated by the four best performing fish having fairly large reductions 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 fishes. Extracting acceleration and swimming speed data from films can also take hours per fish; the apparatus described above produces swimming speed and acceleration data that can be stored in a computer file, saved to a spreadsheet, or printed immediately. Films also have a number of technical problems described thoroughly by Harper and Blake (1989) and reviewed by Domenici and Blake (1997).

Accelerometers, when properly deployed, are the optimum way to obtain an accurate measurement of a fish's ability to fast-start (Harper and Blake, 1990), however, their use is precluded for small fishes. The extensive animal handling and surgery required for accelerometer implantation also renders their use impractical for evolutionary or ecological studies requiring large sample sizes. The use of accelerometers also requires labor-intensive calibrations, and to obtain the ultimate degree of accuracy these instruments are capable of, one must also film the fish to correct for tangential accelerations (Harper and Blake, 1990).

#### 3.1.5. Method disadvantages

The major disadvantage of the chamber described here is that the performance measurements are relative. Errors induced by wall effects (Webb, 1993) and non-linear swimming paths of the fish compromise the ability of this chamber to measure absolute values of swimming performance. Furthermore, fish with more pointed snouts

will break the portion of the beam impinging upon a detector with greater variance than those with blunter snouts. Thus, deviations of measured speeds and accelerations from actual values will be specific to each species and size class of animal. For example, the 0.3 m horizontal distance between the first two detector banks in our prototype was insufficient to resolve the maximum acceleration capability of Atlantic cod with confidence. This type of error can be limited by reducing the vertical and horizontal distance between photodetectors and more narrowly defining the starting position of the fish (Fig. 1). It is also possible with more complex circuitry to monitor each phototransistor in a bank and thereby quantify and correct for any error due to a vertical swimming component but this will incur further costs and analysis complexity. Likewise, lateral deviations from linearity can be corrected for by also filming the trials. We believe that for studies requiring only relative measures of short-duration swimming performance between individuals, a laser detection 'sprint chamber' like the prototype described here will prove optimal.

#### 3.2. Constant acceleration test

Although interesting information was obtained from this test (Reidy et al., 2000), for the preliminary group of eight fish we used, the test did not conform to the criterion of repeatability over time (Fig. 8).

The relationship between performance in a second trial and initial performance was insignificant ( $F=1.6$ ;  $P=0.26$ ), this was largely due to two of the fish having large (~20%) improvements in performance in the second trial. This was apparent by removing these two fish from the data set, which produced a significant least squares regression between the first and second trial ( $F=11.34$   $P=0.028$ ) despite the sample size of only six fish (Fig. 8). Although the CAT cannot be considered repeatable at the moment, we feel that the question needs to be investigated further before rejecting the method as useful. Even considering the two fish with large improvements in performance between repetitive trials, inter-individual variance in performance exceeded maximal intra-individual variance in performance for this test (Fig. 8). The ecological relevance of this test is discussed in Reidy et al. (2000).

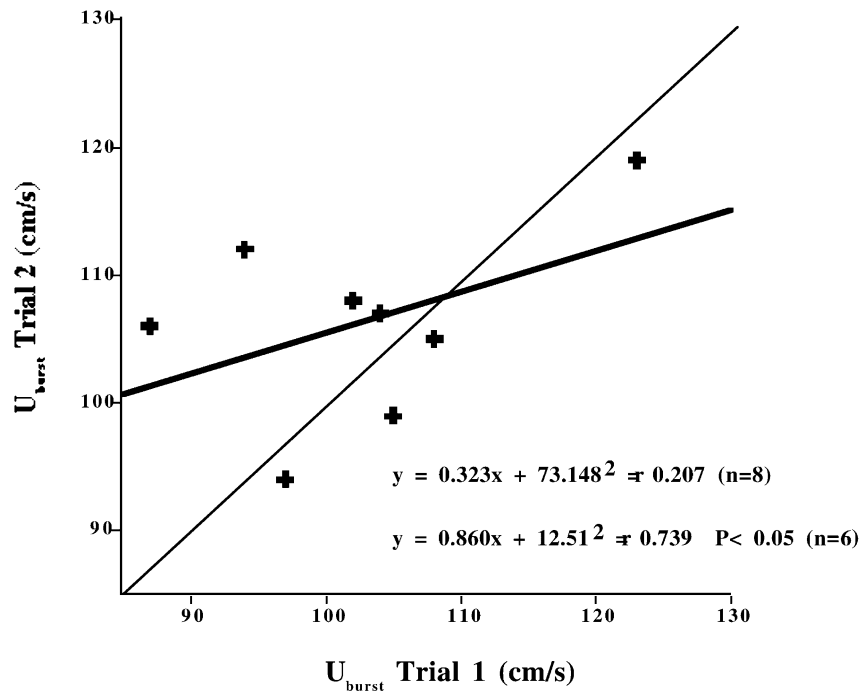


Fig. 8. Swimming speed at fatigue for the 8 Atlantic cod used to initially develop the constant acceleration protocol ( $U_{burst}$  of Reidy et al., 2000) recorded in each of two separate trials performed approximately 1 month apart. The equation of the least squares linear regression (dark line) for 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 was not attributable to the size of the fish. The size of the dace in this study was intentionally limited, but among the dace used, there was absolutely no relationship between length and swimming performance. Even the regression of the logarithm of TL plotted against the logarithm of critical swimming speed was insignificant (Spearman rank order  $r=0.22$ ;  $P=0.19$ ;  $n=40$ ).

### 3.4. General

Although the  $U_{crit}$  method developed by Brett (1964) has produced a wealth of information on

both the performance and metabolism of swimming fish, we think that the time has come for the development of new swimming tests which are more targeted at individual species and swimming modes. The new sprint performance method described here may prove useful to investigators interested in the ecological and evolutionary implications of variance in aquatic locomotor performance. Most of the work in this arena has employed reptilian models (see Bennett and Huey, 1990; Garland and Carter, 1994; Garland and Losos, 1994 for reviews). The few fish studies that have expressed interest in variance of performance have primarily used critical swimming speed as the measure of locomotor capacity (reviewed by Kolok, 1999 and Plaut, in press). Because a final  $U_{crit}$  value is a complex product of multiple swimming modes and changing metabolic support, we predict diminishing utility for this test in studies designed to discern biological causality or draw ecological or evolutionary inference (Nelson et al., 1994, 1996). Indeed, a factor analysis of fin areas and aspect ratios of the cod used in the Reidy et al. (2000) study turned up significant relationships

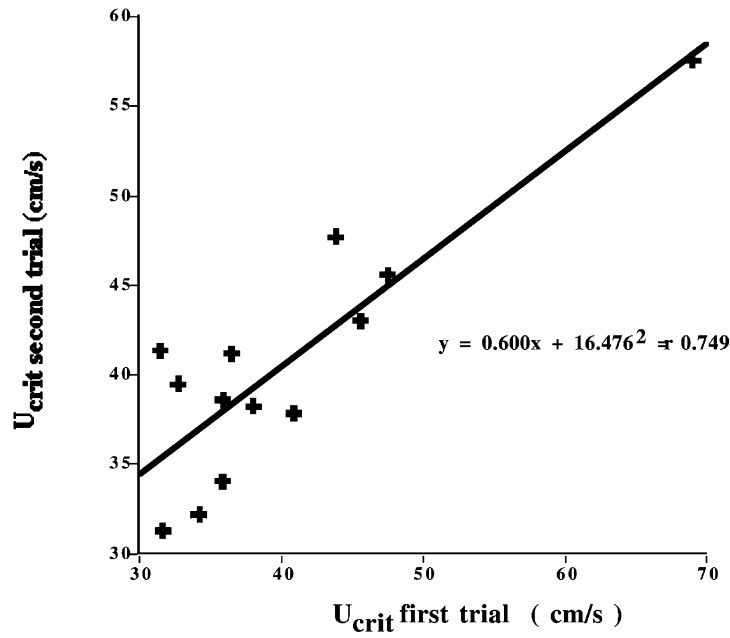


Fig. 9. Critical swimming speed  $\bar{U}_{crit}$  recorded in each of two separate trials run approximately 1 month apart, for each of 14 blacknose dace. The equation of the least squares linear regression (solid line) and the square of the correlation coefficient are included.

with both the new sprint performance method and the constant acceleration method but none with the  $U_{crit}$  procedure. The  $U_{crit}$  procedure also suffers from not mimicking the natural swimming of many fish species; this test was designed to simulate conditions for salmonids ascending lotic freshwaters of decreasing order and should not be indiscriminately applied to all fishes and questions. What is needed for the future are swimming tests designed for individual species and questions that conform to the criteria elaborated here.

Fast start and sprint performances of fish are biologically relevant to factors that can directly relate to success for many species (Webb, 1985). Presumably, the dearth of studies on ecological/evolutionary relevance of fast starts and sprints in fishes comes, in part, from the lack of convenient methods for studying these performances in large numbers of fish. The chamber described here allows investigation of sprint swimming performance under any light levels without a huge investment of investigator time and money. We used this prototype sprint chamber to show that inter-individual variance in performance was greater than intra-individual variance of repetitive trials. The maximum sprint velocity of 17 Atlantic cod measured with this method was significantly repeatable over a period of 3 months (Reidy et al., 2000).

This suggests that the method can be used to explore mechanisms of differences in sprint performance and their ecological/evolutionary relevance. This method has been subsequently used to follow sprint performance of individual cod through cycles of starvation and feeding (Martinez et al., in press). Interestingly, the relative ranking of sprint performances of cod was maintained throughout a feeding/starvation regime whereas those of various muscle metabolic capacities were not. With this degree of interesting information coming from a prototype chamber utilizing a species not generally known for its swimming prowess, we are confident that this method will be of general use for studies of other aquatic animals.

Although the CAT ( $U_{burst}$ ) has not been rigorously shown to be repeatable, it has already helped to increase our understanding of cod biology. The significant, negative relationship with  $U_{crit}$  (Reidy et al., 2000) hints that there are physiological or morphological tradeoffs between the types of swimming used in these two tests. In addition, factor analysis of cod fin areas produced a factor, loaded heavily for pelvic fin areas, that correlated strongly and significantly with the CAT ( $U_{burst}$ ) test ( $r=0.84$ ;  $F=23.6$ ;  $P<0.001$ ). Since cod use a 'flap and glide' swimming style throughout most of the CAT test, this result is logical. Cod depress

718 their pelvic fins during the ‘glide’ phase of this  
719 swimming style to limit backward movement; fish  
720 with relatively large pelvic fins are apparently able  
721 to do this better, leading to a better final perform-  
722 ance value in this test.

723 The  $U_{crit}$  procedure has been modified in prac-  
724 tically every manner possible (Beamish, 1978;  
725 Hammer, 1995); rarely have these modifications  
726 been subject to the most fundamental measure of  
727 scientific veracity, that of reproducibility. Fortu-  
728 nately, when the reproducibility of  $U_{crit}$  procedures  
729 has been tested, they usually are (Randall et al.,  
730 1987; reviewed in Kolok, 1999). Here we add a  
731  $\frac{5}{3}U_{crit}$  procedure with blacknose dace to the list of  
732 significantly repeatable incremental velocity tests.  
733 In addition to the significant repeatability of this  
734 method, there was substantial inter-individual var-  
735 iation, not attributable to size, which will make  
736 this test useful for ecological and evolutionary  
737 studies on dace. The large differences in locomotor  
738 performance among populations of blacknose dace  
739 was strongly correlated with differences in current  
740 flow at the site of their capture and will be the  
741 subject of a separate communication. Thus,  
742 although the  $\frac{5}{3}U_{crit}$  we used was outside the guide-  
743 lines suggested by Brett (1967) and Beamish  
744 (1978), because the test is significantly repeatable,  
745 mimics conditions encountered by dace in their  
746 environment and is yielding important new infor-  
747 mation about this species, we claim that it is a  
748 valid, new test for this species.

#### 749 4. Uncited reference

750 Nelson and Mitchell (1992).

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#### References

- 764
- Beamish, F.W.H., 1978. Swimming capacity. In: Hoar, W.S.,  
765 Randall, D.J. (Eds.), *Fish Physiology*, vol. 7. Academic  
766 Press, New York, pp. 101–187. 767
- Bennett, A.F., 1980. The thermal dependence of lizard behav-  
768 iour. *Anim. Behav.* 28, 752–762. 769
- Bennett, A.F., Huey, R.B., 1990. Studying the evolution of  
770 physiological performance. In: Futyma, D.J., Antonovics, J.  
771 (Eds.), *Oxford Surveys of Evolutionary Biology*, vol. 7.  
772 Oxford Univ. Press, Oxford, pp. 251–283. 773
- Bouchard, C., Tremblay, A., Nadeau, A., et al., 1989. Genetic  
774 effect in resting and exercise metabolic rates. *Metabolism*  
775 38, 364–370. 776
- Breitburg, D.L., 1992. Episodic hypoxia in Chesapeake Bay:  
777 interacting effects of recruitment, behavior, and physical  
778 disturbance. *Ecol. Monogr.* 62, 525–546. 779
- Brett, J.R., 1964. The respiratory metabolism and swimming  
780 performance of young sockeye salmon. *J. Fish Res. Bd.*  
781 Canada 21, 1183–1226. 782
- Brett, J.R., 1967. Swimming performance of sockeye salmon  
783 (*Oncorhynchus nerka*) in relation to fatigue time and tem-  
784 perature. *J. Fish Res. Bd. Canada* 24, 1731–1741. 785
- Cech, J., Swanson, C., Young, P.S., 1998. Swimming behavior  
786 of splittail in multi-vector flow regimes: applications for  
787 fish screens. In: Mackinley, D., Howard, K., Cech Jr., J.  
788 (Eds.), *Fish Performance Studies*. American Fisheries Soci-  
789 ety, Bethesda, pp. 111–114. 790
- Domenici, P., Blake, R.W., 1997. The kinematics and perform-  
791 ance of fish fast-start swimming. *J. Exp. Biol.* 200,  
792 1165–1178. 793
- Draper, N., Smith, H., 1981. *Applied Regression Analysis*.  
794 second ed. Wiley, New York, NY. 795
- Gamperl, A.K., Schnurr, D.L., Stevens, E.D., 1991. Effect of  
796 a sprint-training protocol on acceleration performance in  
797 rainbow trout (*Salmo gairdneri*). *Can. J. Zool.* 69, 578–582.  
798
- Garland, T.J., Carter, P.A., 1994. Evolutionary physiology.  
799 *Annu. Rev. Physiol.* 56, 579–621. 800
- Garland, T.J., Losos, J.B., 1994. Ecological morphology of  
801 locomotor performance in squamate reptiles. In: Wainwright,  
802 P.C., Reilly, S.M. (Eds.), *Ecological Morphology: Integra-  
803 tive Organismal Biology*. University of Chicago Press,  
804 Chicago, pp. 240–302. 805
- Garland, T.J., Hankins, R.E., Huey, R.B., 1990. Locomotor  
806 capacity and social dominance in male lizards. *Funct. Ecol.*  
807 4, 243–250. 808
- Gero, D.R., 1952. The hydrodynamic aspects of fish propul-  
809 sion. *American Museum Novit.* 1601, 1–32. 810
- Gray, J., 1953. The locomotion of fishes. In: Marshall, S.M.,  
811 Orr, P. (Eds.), *Essays in Marine Biology*. Elmhirst Memorial  
812 Lectures. Oliver and Boyd, Edinburgh, pp. 1–16. 813
- Hammer, C., 1995. Fatigue and exercise tests with fish. *Comp.*  
814 *Biochem. Physiol.* 112A, 1–20. 815
- Harper, D.G., Blake, R.W., 1989. On the error involved in  
816 high-speed film when used to evaluate maximum accelera-  
817 tions of fish. *Can. J. Zool.* 67, 1929–1936. 818
- Harper, D.G., Blake, R.W., 1990. Fast-start performance of  
819 rainbow trout *Salmo gairdneri* and northern pike *Esox*  
820 *lucius*. *J. Exp. Biol.* 150, 321–342. 821

- Hertz, P.E., Huey, R.B., Nevo, E., 1983. Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. *Evolution* 37, 1075–1084.
- Huey, R.B., Dunham, A.E., 1987. Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami*. *Evolution* 41, 1116–1120.
- Huey, R.B., Schneider, W., Erie, G.L., Stevenson, R.D., 1981. A field-portable racetrack for measuring acceleration and velocity of small cursorial animals. *Experientia* 37, 1356–1357.
- Iwama, G.K., McGeer, J.C., Pawluk, M.P., 1989. The effects of five fish anaesthetics on acid–base balance, hematocrit, blood gases, cortisol and adrenaline in rainbow trout. *Can. J. Zool.* 67, 2065–2073.
- Jain, K.E., Birtwell, I.K., Farrell, A.P., 1998. Repeat swimming performance of mature sockeye salmon following a brief recovery period: a proposed measure of fish health and water quality. *Can. J. Zool.* 76, 1488–1496.
- Kolok, A.S., Farrell, A.P., 1994. Individual variation in the swimming performance and cardiac performance of northern squawfish, *Ptychocheilus oregonensis*. *Physiol. Zool.* 67, 706–722.
- Kolok, A.S., 1999. Inter-individual variation in the prolonged locomotor performance of ectothermic vertebrates: a comparison of fish and herpetofaunal methodologies and a brief review of the recent fish literature. *Can. J. Fish Aquat. Sci.* 56, 700–710.
- Martinez, M., Guderley, H., Nelson, J.A., Webber D., Dutil, J.D. Once a fast cod, always a fast cod: maintenance of performance hierarchies despite changing food availability in cod (*Gadus morhua*). *Physiol. Biochem. Zool.*, in press.
- McDonald, D.G., McFarlane, W.J., Milligan, C.L., 1997. Anaerobic capacity and swim performance of juvenile salmonids. *Can. J. Fish Aquat. Sci.* 55, 1198–1207.
- Nelson, J.A., 1989. Critical swimming speeds of yellow perch *Perca flavescens*: comparison of populations from a naturally acidic lake and a circumneutral lake in acid and neutral water. *J. Exp. Biol.* 145, 239–254.
- Nelson, J.A., 1990. Muscle metabolite response to exercise and recovery in yellow perch (*Perca flavescens*): comparison of populations from naturally acidic and neutral waters. *Physiol. Zool.* 63, 886–908.
- Nelson, J.A., Mitchell, G.S., 1992. Blood chemistry response to acid exposure in yellow perch *Perca flavescens*: comparison of populations from naturally acidic and neutral environments. *Physiol. Zool.* 65, 493–514.
- Nelson, J.A., Tang, Y., Boutilier, R.G., 1994. Differences in exercise physiology between two Atlantic cod (*Gadus morhua*) populations from different environments. *Physiol. Zool.* 67, 330–354.
- Nelson, J.A., Tang, Y., Boutilier, R.G., 1996. The effects of salinity change on the exercise performance of two Atlantic cod (*Gadus morhua*) populations inhabiting different environments. *J. Exp. Biol.* 199, 1295–1309.
- Plaut, I. Critical swimming speed: its ecological relevance. *Comp. Biochem. Physiol. (B)*, in press.
- Randall, D.J., Brauner, C., 1991. Effects of environmental factors on exercise in fish. *J. Exp. Biol.* 160, 113–126.
- Randall, D.J., Mense, D., Boutilier, R.G., 1987. The effects of burst swimming on aerobic swimming in chinook salmon (*Oncorhynchus tshawytscha*). *Mar. Behav. Physiol.* 13, 77–88.
- Reidy, S.P., Kerr, S.R., Nelson, J.A., 2000. Aerobic and anaerobic swimming performance of individual Atlantic cod. *J. Exp. Biol.* 203, 347–357.
- Taylor, E.B., McPhail, J.D., 1985. Burst swimming and size related predation of newly emerged coho salmon *Oncorhynchus kisutch*. *Trans. Am. Fish. Soc.* 114, 456–551.
- Wardle, C.S., 1975. Limit of fish swimming speed. *Nature (London)* 255, 725–727.
- Webb, P.W., 1975. Acceleration performance of rainbow trout *Salmo gairdneri* and green sunfish *Lepomis cyanellus*. *J. Exp. Biol.* 63, 451–465.
- Webb, P.W., 1978. Fast-start performance and body form in seven species of teleost fish. *J. Exp. Biol.* 74, 115–226.
- Webb, P.W., 1983. Speed, acceleration, and maneuverability of two teleost fishes. *J. Exp. Biol.* 102, 122–211.
- Webb, P.W., 1986. Locomotion and predator–prey relationships. In: Feder, M.E., Lauder, G.V. (Eds.), *Predator–Prey Relationships*. University of Chicago Press, Chicago, pp. 24–41.
- Webb, P.W., 1993. The effect of solid and porous channel walls on steady swimming of steelhead trout *Oncorhynchus mykiss*. *J. Exp. Biol.* 178, 97–108.