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Caudal differential pressure as a predictor of swimming speed of cod (*Gadus morhua*)

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Summary

We report the results of an experiment designed to investigate the feasibility of using differential pressure to estimate the swimming speed and metabolic rate of Atlantic cod (*Gadus morhua*). Seven cod were fitted with a miniature differential pressure sensor mounted on one side of the caudal peduncle immediately anterior to the base of the caudal fin rays. Relationships between differential pressure, tailbeat frequency, tailbeat amplitude, swimming speed and rate of oxygen consumption ($\dot{M}_{O_2}$) were determined as a function of the swimming speed of cod swimming at 5 °C in a recirculating 'Brett-style' respirometer. Tailbeat differential pressure, tailbeat amplitude and tailbeat frequency were highly correlated with swimming speed. The average or integrated pressure ranged from 0 to 150 Pa for speeds up to 0.8 m s^{-1} (1.1 *L* s^{-1}, where *L* is total body length), while the 'pressure difference' (maximum minus minimum pressure) ranged from 0 to 900 Pa. Small changes in swimming speed of less than 0.05 m s^{-1} were readily detected as differences in tailbeat pressure. Burst swimming in the respirometer resulted in huge pressure 'bursts' of up to 5000 Pa 'pressure difference'.

The rate of oxygen consumption increased exponentially and was highly correlated with swimming speed (r^2=0.77). The rate of oxygen consumption was also correlated with tailbeat integrated pressure (r^2=0.68) and with differential pressure (r^2=0.43); regression correlations were always greater for individuals than for combined data from all cod.

The results detailed in this study indicate that an ultrasonic differential pressure transmitter would enable accurate estimates of the swimming speed, rates of oxygen consumption and activity patterns of free-ranging fish in nature.

Key words: cod, *Gadus morhua*, pressure, swimming speed, tailbeat frequency, bioenergetics, oxygen consumption, fish.

Introduction

To date, heart rate (f_H) appears to be the best available predictor of whole-animal energetics in free-ranging fish (Priede and Young, 1977), although recent laboratory experiments have shown that cardiac output ($\dot{Q}$) is a better predictor than is heart rate in the cod *Gadus morhua* (Webber et al., 1998). Measuring f_H or $\dot{Q}$ alone, however, is not sufficient to provide detailed measurements of the activity and behaviour that accompany the various metabolic states. While detailed patterns of $\dot{Q}$ over time should indicate whether the fish is swimming, resting, feeding, digesting or in courtship behaviour, a much clearer indication of the behaviour of a fish can be achieved if we can estimate swimming speed as well as metabolic energetics.

Conventional techniques use radio and ultrasonic transmitters to measure the swimming speed of free-ranging fish by straight-line measurements between poorly defined positions. Today, sophisticated radio-buoy systems can give accurate positions in three-dimensional space (longitude, latitude and depth) and in time for animals equipped with simple ultrasonic transmitters or transmitters encoded with physical or physiological information (O'Dor et al., 1998; Sauer et al., 1997). Such systems, however, are costly and are limited to slow-moving animals, and positioning accuracy is highly dependent on sea swell, wave action, tidal movements, currents and wind.

A different approach is to attach a transmitter with a trailing rotating paddle wheel to a fish (Block et al., 1992). A magnet attached to one of the rotating paddle wheels opens and closes a magnetic switch. The number of switch closures over time indicates the water velocity. This technique is limited to fish of at least 1 m in length swimming at velocities above 0.3–0.5 m s^{-1} because the paddle wheel stalls at lower velocities. In addition, the paddle wheel adds to the drag of the fish, and it can stall if clogged with particulate matter and invertebrate settlement.

A number of authors have shown that a strong relationship

exists between tailbeat frequency and swimming speed for a number of different species (Bainbridge, 1958; Bainbridge, 1960; Hunter and Zweifel, 1971; Wardle et al., 1989; Scharold et al., 1989). However, the amplitude of the tail beat varies considerably below 2–5 tailbeats s^{-1} (Webb, 1971), which is the frequency animals will most often use in nature, so the use of tailbeat frequency alone may not accurately predict the actual swimming speed. Currently, the most widely used technique is the radio transmission of the electromyogram (EMG) signal of contracting red, white and mosaic muscles of the fish caudal peduncle. This technique involves implanting electrodes into the lateral musculature and transmitting radio pulses whose period is a measure of the time it takes for the EMG voltage to sum to a preset threshold (Økland et al., 1997). The intensity of exercise and the corresponding EMG signals are correlated with swimming speed (Briggs and Post, 1997; Økland et al., 1997; Kaseloo et al., 1992; Weatherley et al., 1982), however, the relationship between the timing of EMGs and force generation by muscle is not entirely clear (Videler, 1993), and one obvious disadvantage of the EMG technique is that the implanted electrodes only measure the activity of those muscles in the vicinity of the electrodes.

A more direct approach to measuring swimming speed is to measure directly the power generated by the lateral musculature. Steady-state swimming in fish is essentially the result of power produced by waves of myotomal muscle contractions passing alternately down each side of the body from head to tail. Power is converted to thrust along the body, caudal peduncle or tail depending on the species and swimming mode (Wardle et al., 1995). Power increases approximately with the cube of swimming speed (Webb, 1978). Dubois et al. (Dubois et al., 1974) and Dubois and Ogilvy (Dubois and Ogilvy, 1978) described a technique to measure pressure distribution on the surface of the caudal peduncle of swimming bluefish (*Pomatomus saltatrix*). They observed a relationship between caudal power, pressure and swimming speed using non-differential or gauge pressure sensors mounted on each side of the caudal fin. The forward and lateral power exerted by the tail were calculated from the measured differential pressure exerted by the tail, body velocity, tail displacement and the angle of the tail relative to the swimming axis (Dubois et al., 1974). These sensors measured both depth pressure and tail pressure, and the authors managed to demonstrate a positive relationship between tail pressure, power and swimming speed. This technique should measure the resultant power from all tail muscle types. It is therefore reasonable to suggest that pressure should be highly correlated with swimming speed and activity energetics.

In the last 20 years, there have been significant advances in the design and miniaturization of gauge, absolute and differential pressure sensors. Their low mass (less than 1 g in water), their high sensitivity to small pressure changes and their low electrical power consumption (less than 1 mA at 3–6 V direct current) make these sensors ideally suited to telemetry applications.

In their review, Wardle et al. (Wardle et al., 1995) indicated that the conversion of muscle power to thrust can result primarily from bending body, for example in the eel, or primarily from the tail, for example in the mackerel. We chose to use cod as as an experimental model whose swimming kinematics should lie somewhere between these extremes.

The objective of this study was to develop an alternative method of measuring the swimming speed of fish using differential pressure sensors. An increase in tailbeat frequency and/or in tailbeat amplitude with swimming speed should result in an increase in the pressure exerted against the water by the caudal fin and caudal peduncle. In this study, we measured the pressure exerted against the water, throughout the tailbeat cycle, at a specific point on the tail.

Materials and methods

Swimming speed, tailbeat frequency and tailbeat pressure

Forced swimming trials were conducted in August and September 1998 using seven Atlantic cod (*Gadus morhua*) (mass 1.58–3.7 kg) originating from the Scotian Shelf (Eastern Passage, Nova Scotia, Canada). The cod were maintained in seawater holding tanks at 5 °C and were swum in the respirometer at the same temperature. For experimentation, animals were anaesthetized in sea water containing 0.05 mg l^{-1} tricaine methanol sulphonate (MS-222, Sigma Chemical Co.) and transferred to the operating table, where the gills were irrigated with a lighter dose of anaesthetic (0.025 mg l^{-1}). The pressure sensor was modified by severing each pressure port at the base of the sensor body. An 18 gauge syringe needle was inserted into the positive pressure port and glued in place with slow-setting (24 h) epoxy glue. Two 21 gauge holes were drilled through the body of the pressure sensor such that the suture could be used to attach the sensor to the body wall.

The sensor and the method of attachment are shown in Fig. 1. The sensor was mounted on one side of the caudal peduncle at the position of the second last vertebral centrum approximately 2 cm anterior to the base of the caudal fin rays and approximately 1 cm dorsal to the vertebra. The positive port with the syringe needle was inserted through the body of the caudal peduncle between adjacent neural spines to exit the other side such that the sensor measured the pressure difference across the caudal peduncle. The sensor was attached firmly to the side of the caudal peduncle using suture thread to minimize pressure fluctuations as a result of differences in momentum of the sensor and tail. A four-conductor wire (36 gauge) leading from the sensor was attached to the surface of the body inserted by 2–3 0.5 cm diameter suture loops along the length of the caudal peduncle. The wires exited the swimming chamber from the base of the dorsal fin of the fish. Surgery was completed in 5 min or less, and minimal blood loss occurred in only one specimen.

The same 6.9 kPa differential pressure sensor was used for all fish. The sensor was powered by a ±12 V regulated circuit. The sensor output (–10 to 10 mV) was amplified 500 times with an Analog Devices (model AD624C) high-precision instrumentation operational amplifier. The output from the

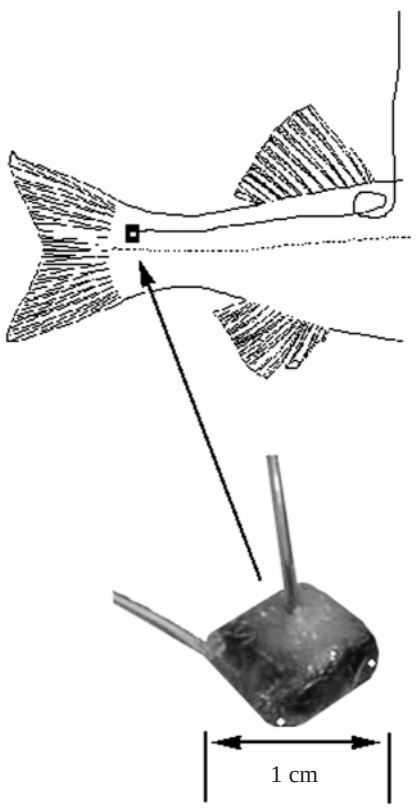

Fig. 1. Diagram of a fish tail illustrating the placement of a differential pressure sensor (1 cm×1 cm×1.25 cm) to measure swimming speed through the measurement of tailbeat differential pressure. The sensor was mounted on one side of the caudal peduncle at the position of the second last vertebral centrum, approximately 2 cm anterior to the base of the caudal fin rays and approximately 1 cm dorsal to the vertebra.

AD624C was input to a single-ended successive approximation analog-to-digital converter circuit (Bsoft Software Inc., Columbus, Ohio, USA). The signal was sampled at 6350 Hz, and every 100 samples were averaged to give a digital value stored on disk at 63.5 Hz. The pressure data were displayed on a CRT computer monitor in real time. The resolution of the system was 1.85 Pa (or 0.0189 cm freshwater) per digital value at 4 °C. The sensor was calibrated against a column of water each day for 4 weeks, and the calibration never changed. Throughout each day, the zero-pressure voltage value from the output of the AD624C drifted up or down by a maximum of 0.05 V or 37 Pa. The voltage drift was not of significance to the results because differential pressure rather than absolute pressure was the variable of interest.

Fish were swum in an 89 l 'Brett-style' swimming respirometer (Brett, 1964). Water currents were generated by a centrifugal pump capable of producing velocities of up to 2 m s^{-1}. A brief description of the working system is as follows: within the toroidal-shaped acrylic pipe, individual fish confined within the straight section (0.2 m in diameter, 1.2 m in length) were forced to swim against the current. Plastic honeycomb grids and stainless-steel wire mesh in front and behind the fish contained the animal and provided a 'directed' micro-turbulent flow of water through the swimming section. A differential pressure sensor of 7.2 kPa full-scale (functioning as a 'Pitot tube') (Bean, 1971) was used to measure water speed through the cross section of the swimming chamber. The output of the pressure sensor was converted to water speed (U, m s^{-1}) using a modified Bernoulli equation:

$$1.1U = [2p^{-1}(P_t - P_s)/1.534]^{0.5}, \quad (1)$$

where p is water density (1026 N s^2 m^{-4} at 10 °C, 30 ‰), P_t is dynamic and static pressure (Pa) and P_s is static pressure (Pa). A significant boundary layer was detectable only at low speeds and only in the rear half of the swimming chamber. Water speed was also measured by injecting dye or milk into the respirometer, upstream from the swimming chamber, and then recording its movement on 8 mm tape (shutter speed 200 Hz). Water speeds calculated using the filming technique and from the pressure sensor were highly correlated (r^2=0.98) and were related to water pump revolutions per minute. A computerized control system enabled the temperature temperature to be controlled to within an accuracy of ±0.05 °C. To maintain the experimental temperature, the water temperature was measured in the respirometer using a temperature transducer connected to an integrating data-acquisition module (model 6B; Analog Devices Ltd, Cambridge, MA, USA). Chilling was provided by a non-toxic propylene glycol/freshwater mixture (0 °C) circulated through a helical titanium coil inside the respirometer. Chilled (2 °C) and heated (20 °C) seawater lines gave flexibility in setting the desired temperatures.

The fish were allowed to recover in the respirometer for a minimum of 24 h before swimming trials were initiated. They were swum at various velocities for periods of 45–60 min. In addition, short-term variations in speed were imposed. Specific swimming protocols were not followed since our objective was to measure pressure on relaxed fish. Water velocity was slowly increased or decreased by 0.01 m s^{-1} to the new velocity to give the animals time to adjust to the velocity change. Fish were filmed from above the swimming chamber using an 8 mm camcorder set at a shutter speed of 200 Hz. The camera was positioned approximately 40 cm above the animal, and the x, y and z axes of the field of view were calibrated to minimize the parallax effect. Tail beats were chosen for analysis only when the cod maintained position and depth in the swimming chamber. The y axis represents the longitudinal axis of the trunk of the fish aligned with the direction of water flow. The x axis, perpendicular to the direction of water flow, represents the lateral component of the tail movements. The x and y coordinates of the tail position were measured from frame-by-frame (30 Hz) playback of the 8 mm film. The position of the tail in each video frame was measured at the differential pressure sensor and at the most posterior tip of the caudal fin rays. Tailbeat amplitude was measured as the lateral distance of tail movement. Voltage, representing the revolutions of the water pump (in revs min^{-1}), was digitized and stored on computer hard disk. Water velocity and pressure measurements were synchronized with the video to 0.1 s. Occasionally, the

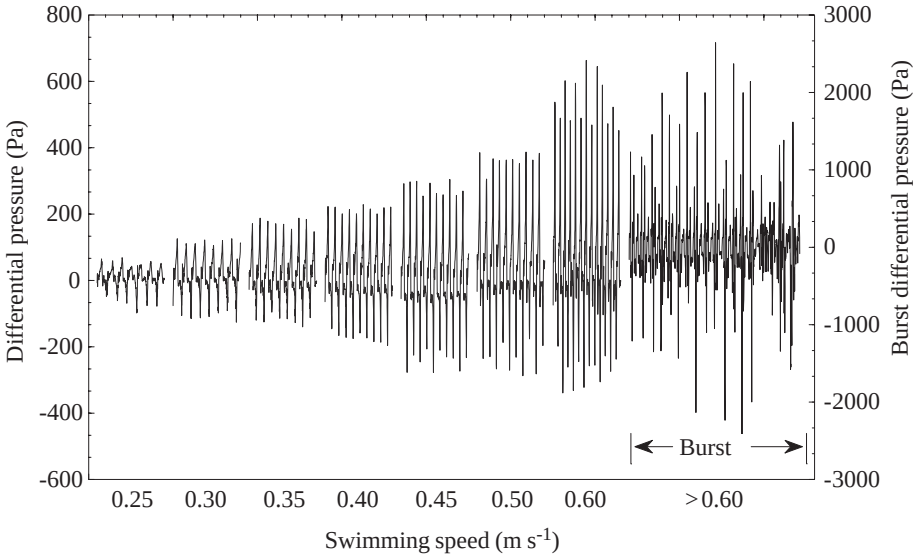

Fig. 2. Tailbeat differential pressure *versus* swimming speed and time for a typical cod (*Gadus morhua*) swimming in a 'Brett-style' respirometer at 5 °C. At each swimming speed, a continuous 9 s segment of pressure data sampled at 63 Hz is shown. Note the increase in positive and negative pressure (amplitude) and in the frequency of the tailbeat pressure signal as swimming speed increases. The section of the recording labelled 'Burst' represents a cod repeatedly burst swimming in the swimming chamber at high speeds prior to exhaustion.

animals would not swim, and it was found that the best technique to encourage a constant swimming response was to quickly increase the water velocity to approximately 0.6–0.8 m s^{-1} and then decrease the velocity to 0.1 m s^{-1}. This forced the cod gently to slide back and then forward in the swimming chamber while initiating tail beats and a swimming response. The fish were never subjected to electric shocks.

Respirometry

Respirometry was conducted on individual fish using the 'Brett-style' respirometer described in the previous section. The respirometer was fed from a 250 l tank in which warm and cold water were mixed to a temperature approximately 0.2–0.3 °C higher than the experimental temperature and aerated to saturation. The mixed water was gravity-fed through a 50 l column to assist degassing. Upon entering the respirometer, the air-saturated water was cooled to the experimental temperature, producing water with an oxygen level slightly less than saturation. This helped to prevent the formation of air bubbles in the respirometer and on the membranes of the oxygen probes contained in the external water circuit (see below).

Oxygen depletion was measured in an external water circuit using an Endeco/YSI (model 1125) pulsed oxygen analyzer and electrode (YSI, Yellow Springs Instruments, Ohio, USA). Decreases or increases in oxygen partial pressure (P_{O_2}) were minimal in the absence of test fish, and the oxygen consumption of each fish was corrected accordingly. The water circuit provided constant flow over the oxygen probes, and a series of two-way valves facilitated periodic recalibration of the oxygen measurement system during the experiments. Voltage inputs from the oxygen meters, temperature sensor and water speed meter were measured in digital format and transformed into real units.

Data analysis

The oxygen consumed by the animal was measured as a decrease in oxygen concentration over time using the linear relationship between P_{O_2} (oxygen gas partial pressure) and the current-to-voltage output of the oxygen sensor and meter. Oxygen consumption was adjusted to a standard body mass of 1 kg using a mass exponent of 0.8 determined by Saunders (Saunders, 1963) for cod at similar temperatures:

$$1.2\dot{M}_{O_2,1kg} = (1/M_b)^{0.8}\dot{M}_{O_2}, \quad (2)$$

where M_b is body mass and $\dot{M}_{O_2}$ is the rate of oxygen consumption (μmol min^{-1} kg^{-1}).

Beat-to-beat tailbeat time intervals were measured using an FFT (Fast-Fourier Transform) analytical software program (ADCFOUR.EXE) written by the D.M.W. The ADCFOUR.EXE computer program analyzed consecutive data windows of 1024 data points. Given that the data sampling frequency was 63.5 s^{-1}, raw pressure data were presented as 16.1 s averages. Tailbeat frequency was calculated by averaging all 16.1 s averages during a swimming trial. Tailbeat pressure was calculated in two ways. The lowest and highest values for pressure were recorded for every 254 measurements (4 s). A 4 s interval was used because it exceeded the period between pressure peaks for the lowest tailbeat frequency observed. The average of all minimum and maximum pressure values for a swimming trial was calculated, and the minimum pressure value was subtracted from the maximum pressure value to give a value termed the 'pressure difference' (*PD*). A digital filter algorithm was used to estimate the baseline of the positive- and negative-going electrical signal from the pressure sensor. The total area of raw pressure data above and below the baseline was calculated and averaged and is termed 'integrated pressure' (*IP*).

Results

The fish were able to maintain an upright position after 1 h of recovery from surgery in sea water. All animals were able to maintain their position in the swimming chamber and swam

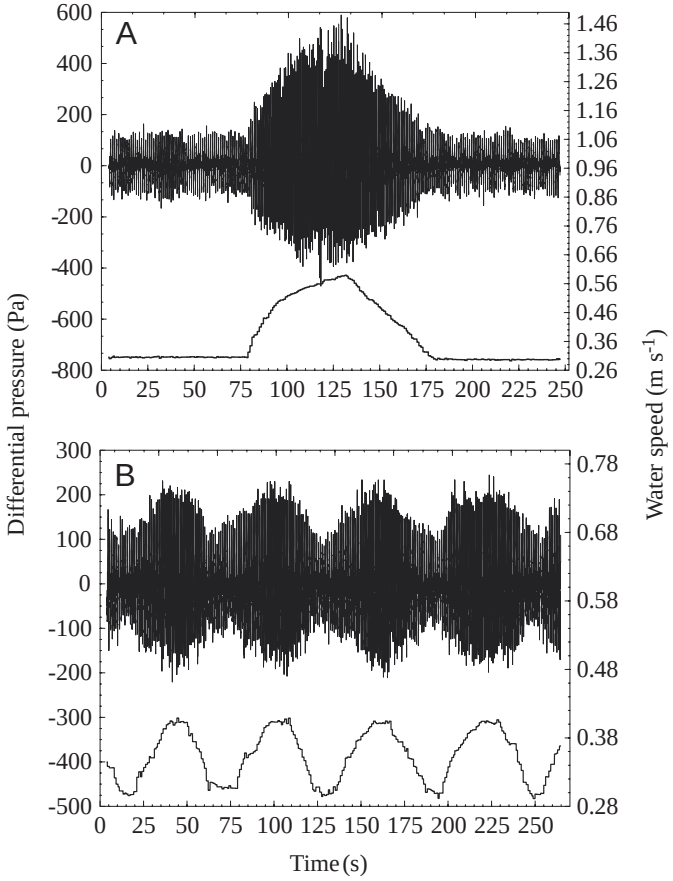

Fig. 3. Tailbeat differential pressure and water speed *versus* time for a typical cod (*Gadus morhua*) swimming in a 'Brett-style' respirometer at 5 °C. (A) A single increase in the water velocity of 0.3 m s^{-1}. (B) Repeated smaller increase in water velocity of 0.1 m s^{-1}. The pressure data were sampled at 63 Hz. The lower traces in A and B represent the water speed setting of recirculating sea water. The upper traces are the tailbeat pressure data. Note the increase in both tailbeat pressure amplitude and tailbeat frequency with increases in water velocity.

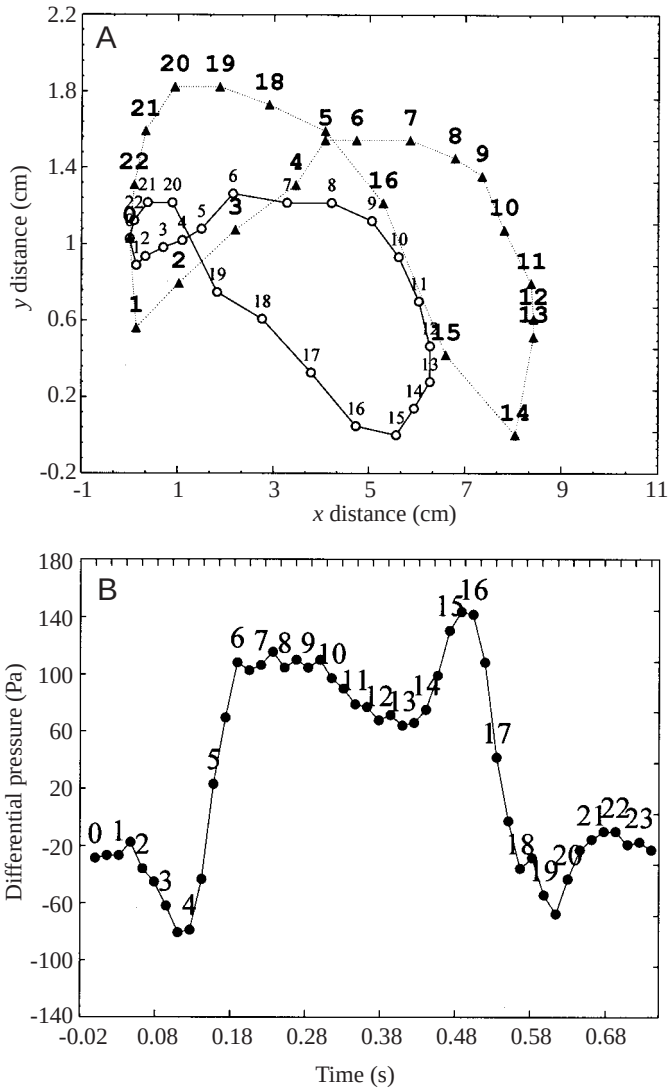

Fig. 4. (A) The classic figure-of-eight path (Pettigrew, 1873) followed by the tail through one pressure cycle or tail beat of a cod (*Gadus morhua*) swimming 0.3 m s^{-1} in a 'Brett-style' respirometer at 5 °C. The larger figure of eight (dotted line, ▲) is the path of the tip of the caudal fin, and the smaller figure of eight (solid line, ○) is the path of the tail at the position where the pressure sensor was sutured to the caudal peduncle. The *x* and *y* coordinates of the tail position were measured from frame-by-frame (30 Hz) playback of 8 mm film. A video frame number is indicated for each *x*,*y* data point. (B) Tailbeat differential pressure with corresponding video frame numbers *versus* time of the tailbeat cycle shown in A.

steadily. At very low velocities, animals occasionally outpaced the current flow, which resulted in unsteady swimming. At higher speeds, water velocity was lowered if animals began to show burst-and-coast swimming (sporadic rapid accelerations), and in no instances did the animals swim to exhaustion. We refer to this sustainable level of activity at higher speeds as 'maximum activity'.

Fig. 2 and Fig. 3 illustrate the raw pressure signals from two cod at various velocities. Tailbeat pressure was very consistent for each velocity. The amplitude and frequency of the pressure signal varied significantly only when the fish did not maintain position (i.e. if it lost or gained position in the swimming chamber) (Fig. 2). This is especially evident when the cod reached maximum sustainable velocities. For example, in Fig. 2, the amplitude of the tailbeat pressure was more variable at 0.6 m s^{-1} and while the cod was burst swimming compared with lower velocities. The amplitude of the pressure cycles was most uniform at intermediate speeds between 0.3 and 0.5 m s^{-1}, and the animals appeared to swim most steadily at those speeds. Fig. 2 and Fig. 3 clearly illustrate the large variation in pressure with small changes in swimming velocity. This is especially evident in Fig. 3B for 0.1 m s^{-1} increments and decrements in velocity. In this experiment, water velocity was increased or decreased in steps of 0.05 m s^{-1}; however, pressure amplitude changes were clearly visible when velocity was changed by as little as 0.01–0.02 m s^{-1}. Burst swimming resulted in pressure increases of an order of magnitude higher than maximum sustained swimming velocities (Fig. 2).

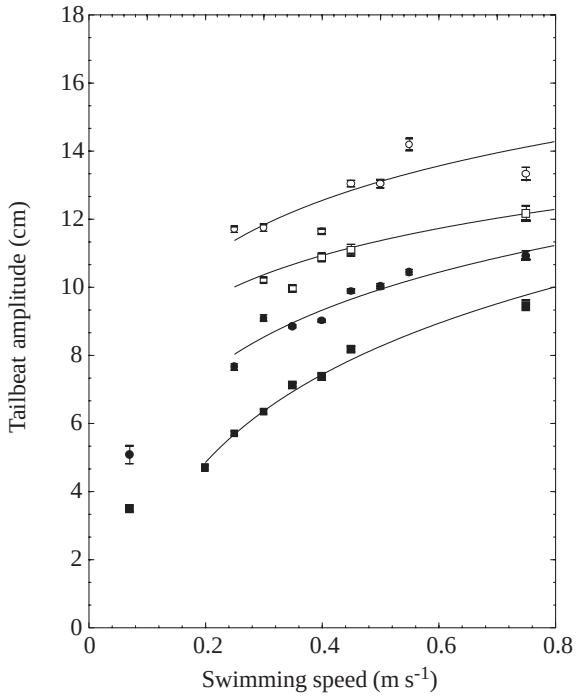

Fig. 5. Relationship between average tailbeat amplitude and swimming speed for two cod (cod_1 and cod_2) (*Gadus morhua*) swimming in a 'Brett-style' respirometer at 5 °C. Amplitude was measured at the tip of the caudal fin (C_{amp}) and at the position of the pressure sensor (S_{amp}). Filled squares, cod_1 (0.58 m), $S_{amp}=10.84+8.56\log_{10}U$, $r^2=0.95$, $N=201$, $P<0.0001$; open squares, cod_1 (0.58 m), $C_{amp}=12.73+4.51\log_{10}U$, $r^2=0.58$, $N=158$, $P<0.0001$; filled circles, cod_2 (0.68 m), $S_{amp}=11.84+6.32\log_{10}U$, $r^2=0.86$, $N=235$, $P<0.0001$; open circles, cod_2 (0.68 m), $C_{amp}=14.84+5.75\log_{10}U$, $r^2=0.68$, $N=189$, $P<0.0001$; where U is swimming speed in m s^{-1}. Values are means ± S.E.M.

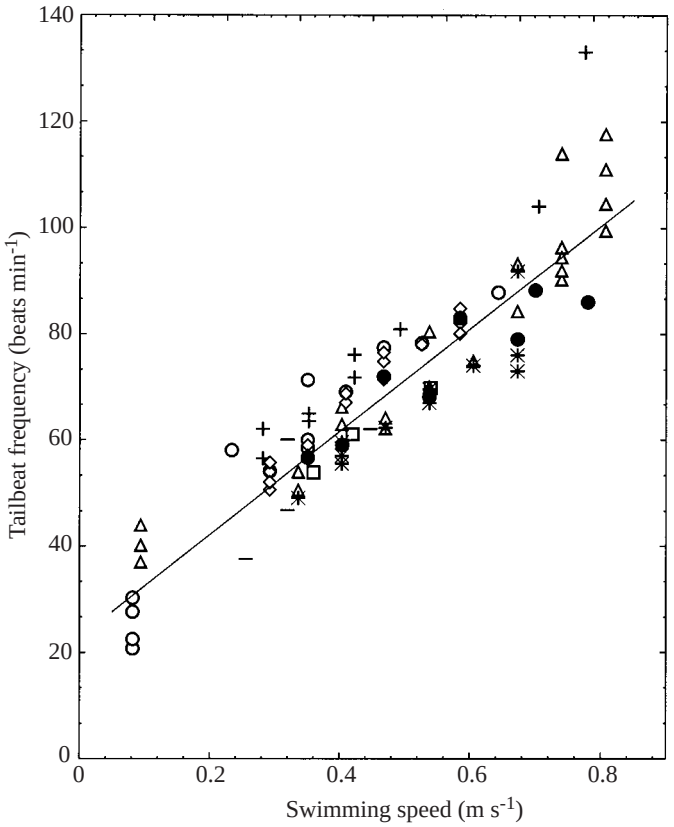

Fig. 6. Tailbeat frequency *versus* swimming speed for seven cod (*Gadus morhua*) fitted with pressure sensors and two cod without instrumentation (filled circles) swimming in a 'Brett-style' respirometer at 5 °C. $f_{TB}=22.73+97.08U$, $r^2=0.85$, $P<0.0001$, $N=144$; where f_{TB} is tailbeat frequency in beats min^{-1} and U is swimming speed in m s^{-1}.

The timing of the pressure signal with the tailbeat position for a cod swimming at 0.3 m s^{-1} is illustrated in Fig. 4. The classic figure-of-eight path described by Pettigrew (Pettigrew, 1873), that is followed by the tail through one pressure cycle or tail beat of a cod, is shown in Fig. 4A. In this case, tailbeat amplitude was approximately 8.5 cm at the tip of the caudal fin. When the tail is at its maximum velocity moving across the linear axis of forward motion, the pressure peaks to a maximum positive value or a maximum negative value (Fig. 4B). The tail slows down and stops instantaneously when it reaches its maximum amplitude. At this time, the differential pressure approaches 0 Pa. The tail then accelerates through the centre axis, and the pressure rises again in the opposite direction. The tail then swings to the other side of the body and the pressure returns to 0 Pa. At higher constant swimming velocities, the tailbeat and pressure cycle were shorter; the amplitude of the tail beat increased and the period of the tail beat decreased. The tail therefore moved much faster and with more force through the water, and the peak positive and negative pressures increased. Logarithmic regressions of average tailbeat amplitudes against swimming speeds for two of the best-swimming cod are illustrated in Fig. 5. These data illustrate the amplitude of the tail beat at the position of the pressure sensor and at the tip of the caudal fin. An analysis of variance for the two cod indicated that amplitude increased significantly with swimming speed; however, amplitude appears to level off at higher speeds.

Fig. 6 illustrates the linear relationship between tailbeat frequency and swimming velocity. Swimming speeds ranged between 0.1 and 0.8 m s^{-1}. There was no apparent difference in tailbeat frequency between instrumented and control cod. Two of the six cod were swum at high speeds. Above 0.9 L s^{-1}, where L is total body length, tailbeat frequency appeared to increase with little change in velocity for these two cod.

The relationships between 'pressure difference' and 'integrated pressure' and swimming velocity are illustrated in Fig. 7. 'Pressure difference' increased by almost an order of magnitude throughout the range of swimming velocities, and 'integrated pressure' increased by three- to tenfold. Both pressure variables were highly correlated with swimming velocity. The relationships between pressure and swimming velocity were fitted best with exponential models.

The rate of oxygen consumption ($\dot{M}_{O_2}$) as a function of swimming speed and pressure, is shown in Fig. 8 and Fig. 9.

The correlation coefficient for $\dot{M}_{O_2}$ *versus* speed for each individual was always higher when fitted to logarithmic than to linear coordinates (Fig. 8), and the pooled data also gave a slightly higher correlation for a logarithmic model compared with a linear model. The predicted standard metabolic rate at $0\,m\,s^{-1}$ was $22.3\,\mu mol\,O_2\,min^{-1}\,kg^{-1}$, and that for maximum aerobic metabolic rate was $70.8\,\mu mol\,O_2\,min^{-1}\,kg^{-1}$. These values correspond to 0 and approximately $1\,L\,s^{-1}$, and they can be used to calculate absolute metabolic scope for activity, i.e. the difference between maximum and standard $\dot{M}_{O_2}$ ($48\,\mu mol\,O_2\,min^{-1}\,kg^{-1}$ at 5 °C). There was also a good correlation between $\dot{M}_{O_2}$ and *IP* and *DP* (Fig. 9A,B). At zero pressure, the predicted values for $\dot{M}_{O_2}$ were $23.4\,\mu mol\,O_2\,min^{-1}\,kg^{-1}$ for *IP* and $34.7\,\mu mol\,O_2\,min^{-1}\,kg^{-1}$ for *DP*.

Discussion

The results of this study indicate that tailbeat pressure offers an alternative method of measuring the swimming velocity of fish in nature. At the very least, tailbeat frequency can be calculated, and tailbeat frequency is related to swimming velocity with a high regression analysis correlation (Fig. 6). The measurement of pressure includes both the frequency of the tail beat and its amplitude. Pressure is therefore likely to be a better predictor of swimming speed than frequency, especially for low speeds at which swimming incorporates amplitude modulation as well as frequency modulation.

In a number of studies in teleosts, a positive linear relationship has been observed between tailbeat frequency and swimming speed (Bainbridge, 1958; Hunter and Zweifel, 1971; Webb, 1971; Wardle et al., 1989; Scharold et al., 1989). These authors have applied equations that relate tailbeat frequency, as a function of body length, to relative swimming speed. Videler (Videler, 1993), however, has shown that the prediction of swimming velocity on the basis of tailbeat frequency is not straightforward. Even when relative swimming velocity is plotted against tailbeat frequency, separate slopes for fish of different length are evident, such that using a generalized equation would overestimate relative swimming velocity for a large fish and underestimate relative swimming velocity for a small fish. Bainbridge (Bainbridge, 1958) disregarded frequencies of less than 5 Hz, and Hunter and Zweifel (Hunter and Zweifel, 1971) excluded low velocities from their data set. Videler (Videler, 1993) suggested that amplitude modulation may be partly responsible for providing thrust at low velocities. Certainly, the video analysis of amplitude for the two fish examined in detail in the present study shows that amplitude is indeed important at low swimming speed (Fig. 5). Amplitude modulation is less important at higher speeds. Since fish in nature spend the majority of their time swimming at low

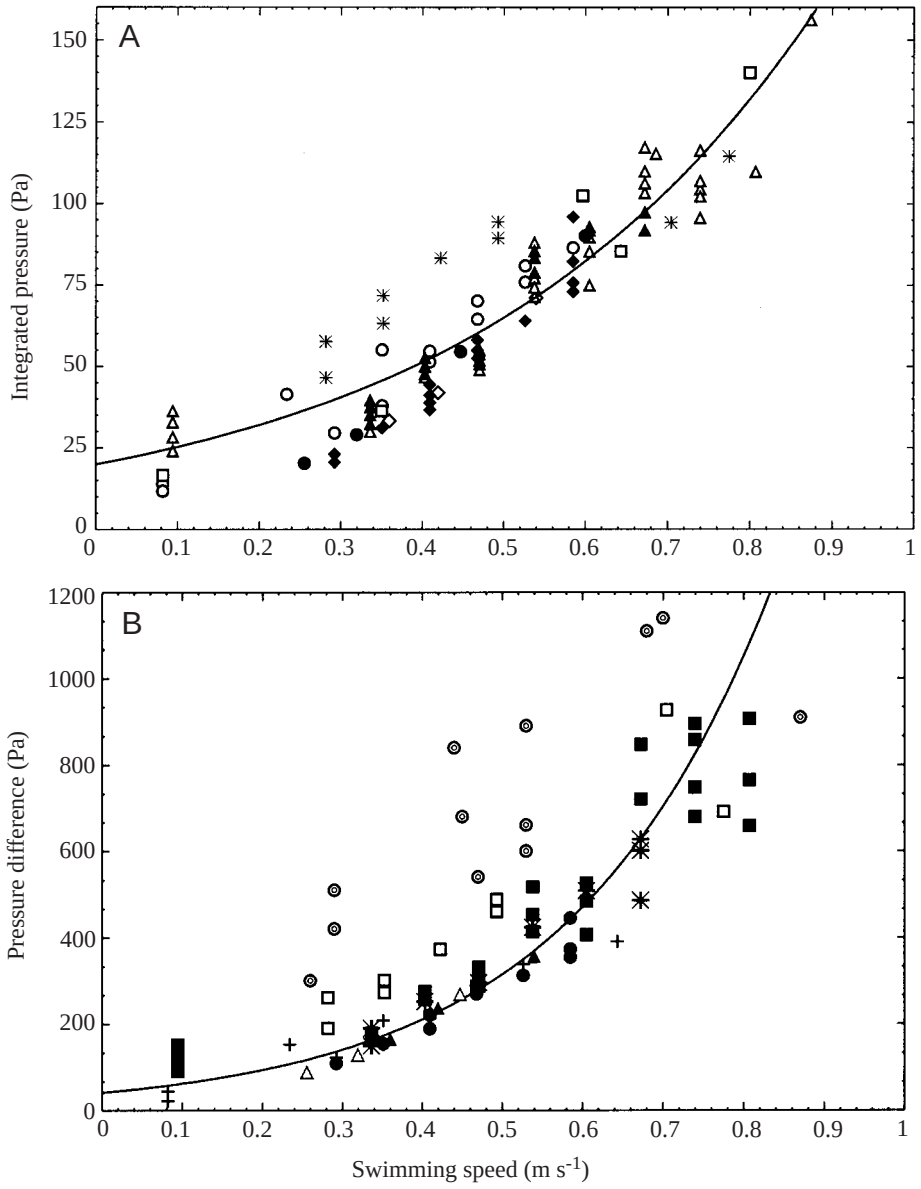

Fig. 7. (A) Integrated tailbeat pressure *versus* swimming speed for seven cod (*Gadus morhua*) swimming in a 'Brett-style' respirometer at 5 °C. $IP=19.934\times10.611^{U}$, $N=84$, $r^2=84.9$, $P<0.0001$; where *IP* is 'integrated pressure' (Pa) and *U* is swimming speed ($m\,s^{-1}$). (B) Maximum minus minimum pressure or 'pressure difference' *versus* swimming speed for seven cod. $PD=44.63\times48.22^{U}$, $r^2=0.87$, $P<0.0001$, $N=147$, where *PD* is 'pressure difference' (Pa). The double circles represent pressure data calculated from Dubois and Ogilvy (Dubois and Ogilvy, 1978) for swimming bluefish (*Pomatomus saltatrix*).

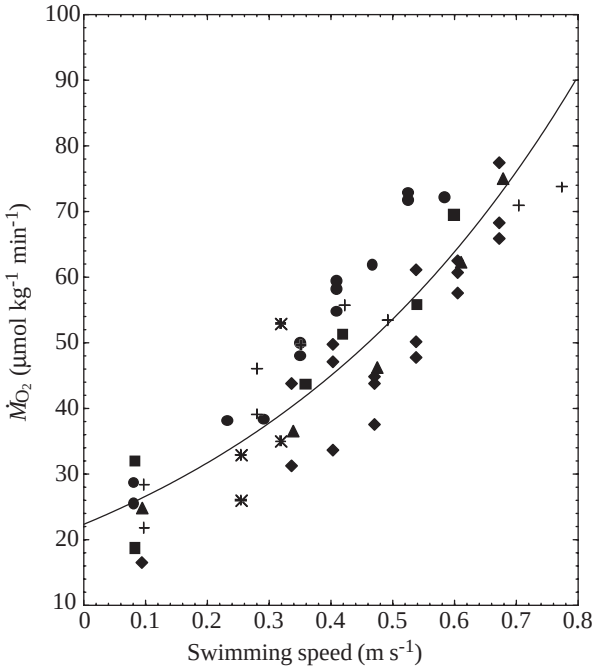

Fig. 8. Rate of oxygen consumption ($\dot{M}_{O_2}$; μmol min^{-1} kg^{-1})*versus* swimming speed (*U*; m s^{-1}); for six cod (*Gadus morhua*) swimming in a 'Brett-style' respirometer at 5 °C. Different symbols represent individual fish. $\dot{M}_{O_2}=22.33\times5.75^{U}$, $r^2=0.77$, $P<0.0001$, $N=60$, where 22.33 is $\dot{M}_{O_2}$ at zero velocity (the standard metabolic rate).

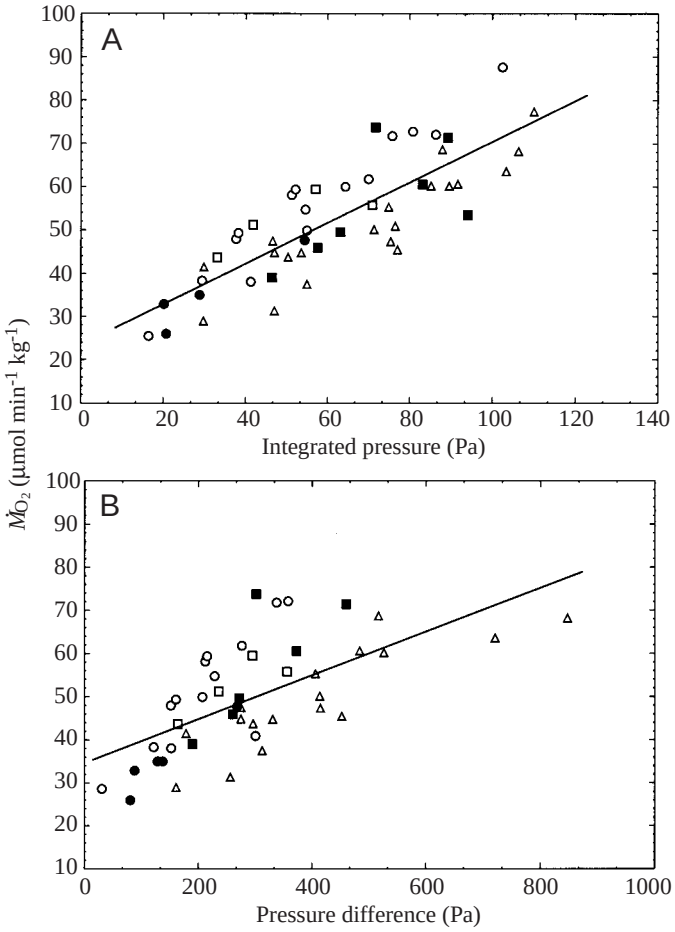

Fig. 9. Rate of oxygen consumption ($\dot{M}_{O_2}$; μmol min^{-1} kg^{-1}) *versus* integrated (*IP*) and difference (*DP*) pressure (Pa) for six cod (*Gadus morhua*) at 5 °C. Different symbols represent individual fish. (A) $\dot{M}_{O_2}=23.4+0.469IP$, $r^2=0.68$, $P<0.0001$, $N=52$, where 23.4 μmol min^{-1} kg^{-1} is $\dot{M}_{O_2}$ at zero 'integrated pressure'. (B) $\dot{M}_{O_2}$ *versus* maximum minus minimum pressure or 'pressure difference' (*PD*). $\dot{M}_{O_2}=34.7+0.051PD$, $r^2=0.43$, $P<0.0001$, $N=48$, where 34.7 μmol min^{-1} kg^{-1} is $\dot{M}_{O_2}$ at zero pressure difference.

speeds, it is reasonable to conclude that pressure, rather than tailbeat frequency, would be the preferred method of measuring swimming speed. Pressure will increase with both increases in frequency and amplitude with speed, whereas measuring frequency alone excludes the contribution of amplitude changes to thrust production.

The total power output of a fish against the water is the total power exerted on the water by the backward-travelling wave. The capability of measuring pressure directly using miniature sensors is ideal. Dubois and Ogilvy (Dubois and Ogilvy, 1978) estimated the power output and propulsive efficiency of the tail of bluefish using non-differential pressure sensors hard-wired to data-acquisition systems. The differential sensors used in the present study could easily be implanted in the musculature with small-diameter rigid ports exiting the body wall. The use of differential sensors allows the experimenter to treat pressure as an alternating signal (back-and-forth tail motion), reducing error due to zero drift of the pressure sensor. In addition, any changes in depth pressure as a result of vertical movement have no effect on the pressure output of the signal, making this sensor ideal for field applications. The sensor used in the present study could be miniaturized further without significantly impeding the power production of the tail or without adding significantly to frictional and pressure drag. These features should permit accurate laboratory estimates of tail power output and enable researchers to examine locomotor efficiencies. The pressure ports could also be used in such a way as to measure the pressure difference between positions on or near the body of the fish.

The measurement of tailbeat pressure is an alternative technique to radio telemetry of electromyograms (EMGs). The advantage of measuring EMGs is the capability of analyzing the function of red, white or mosaic muscle types in relation to the behaviour of the fish in nature. However, the technique depends on the proper placement of electrodes so that the measured electrical signal reflects closely the power output of the tail musculature. The electrodes must not shift over weeks and months (scar tissue impedes the signals), and it must be assumed that the electrochemical nature of the muscle fibres does not change with training and temperature. Temperature affects the recruitment of different muscle types, but there are very few data showing how temperature affects EMG signals in spontaneously active fish in the laboratory and in the field. The pressure technique described here measures pressure as a

function of power output, which does not change with swimming speed over different temperatures (Rome, 1990). Pressure generated for a given speed should be independent of temperature, so a single calibration of pressure *versus* speed for a fish should be sufficient for predicting swimming speed at different temperatures in nature. It is important to note that we have not performed long-term laboratory tests on the pressure sensor to investigate the effects of temperature on the electrical integrity of the sensor and on the tailbeat pressure *versus* speed relationship. Also, we do not know how well the pressure sensor will perform in situations where fast-flowing water is present. Clearly, both the EMG and pressure techniques need more rigorous investigation before they can be universally accepted. Transmitters measuring EMGs and differential pressure could be used on the same fish. This would elucidate the relationship between the use of various muscle fibre types and tail pressure in nature.

The results from this study suggest that both 'difference pressure' and 'integrated pressure' are appropriate measures of swimming speed and $\dot{M}_{O_2}$, and both measurements are also easy to obtain. Radio and ultrasonic transmitters are now equipped with micro-controllers that can execute small software programs that are capable of pre-processing raw data into a more manageable format. These microprocessors have on-board real-time clocks and analog-to-digital converters that can operate at data sampling frequencies of 100 Hz or higher. Many physiological events occur over short time periods, e.g. fractions of seconds, and the raw data cannot be reported in real time on an ultrasonic frequency. This is because ultrasonic transmission through water takes considerable power. For example, a V16 transmitter (Vemco Ltd, Shad Bay, Nova Scotia, Canada) can report data at 3–10 Hz for only 24–48 h when measuring the jet pressures of swimming squid, e.g. (Webber and O'Dor, 1986), but when the data are integrated the transmitter can report integrated and baseline jet pressure for 4 weeks at a data transmission rate of 1 Hz (D. M. Webber, personal observation). 'Pressure difference', 'integral pressure' and tailbeat frequency could easily be reported using radio or ultrasonic transmitters with microprocessors. In the present study, both pressure values were calculated by measuring a pressure baseline over a short period on the basis of the minimum time expected for a complete tailbeat cycle for cod (i.e. 4 s). This time period could easily be programmed into a microprocessor to adjust to slower or faster minimum tailbeat periods. A microprocessor-controlled transmitter designed to measure squid jet pressure that reports baseline and integral pressure is currently being used and could easily be modified to measure fish tailbeat pressure.

Many laboratory studies that report on the energetics of fish and on other behavioural and physiological measurements with regard to constant swimming speed use various techniques to try to minimize spontaneous activity that elevates the energetic cost of swimming. Many oxygen consumption rates are measured over periods of 30 min to several hours, whereas spontaneous activity bursts occur over seconds to hours. Some of the observed variability in $\dot{M}_{O_2}$ and other measurements is almost certainly caused by spontaneous bursts of activity rather than by the experimental treatment *per se*. Tailbeat pressure would be a very useful measure for indicating the relative proportion of spontaneous *versus* constant activity. For instance, on several occasions, we observed that cod were 'too active' at very low speeds (accelerating and decelerating) or they 'burst swam' (anaerobic metabolism) or supported themselves against downstream grids at high speeds. Real-time measurements of pressure allow the experimenter to assess the swimming 'smoothness' of the animal.

In conclusion, this study illustrates that differential pressure measurements of water speed and tailbeat undulation will be very useful for measuring the swimming speeds and activity patterns of fish in nature. If such pressure measurements can be coupled with a heart rate or cardiac output transmitter, it should be possible to define the energetic expenditures of free-ranging fish in nature with much greater precision than has been attained previously.

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