In situ investigation of burst swimming and muscle performance in the deep-sea fish *Antimora rostrata* (Günther, 1878).

David M. Bailey*, Philip M Bagley, Alan Jamieson, Martin A. Collins, Imants G. Priede

Ocean Laboratory, University of Aberdeen, Newburgh, Aberdeenshire, AB41 6AA, UK.

*Corresponding author. Tel.: +44 (0)1224 274413; Fax; +44 (0)1224 274402

E-mail address: d.bailey@abdn.ac.uk (D.M. Bailey)

Abstract

The few existing measurements of deep-sea fish physiology consistently indicate reduced basal metabolism and metabolic power. A possible explanation for this is the reduction in selective pressure for burst activity capacity due to a reduction in the frequency and duration of predator-prey interactions in the sparsely distributed fish community and continuous darkness. Video recordings of stimulated fast-starts in deep-sea fish were obtained by a lander vehicle and analysed to give the swimming velocities, accelerations, and inertial power requirements of fast-start swimming in *Antimora rostrata*. With a mean peak velocity of 0.7 $m.s^{-1}$, and white muscle power output of only 17.0 $W.kg^{-1}$ *A. rostrata* is a slow moving fish, but no slower than shallow-water fishes at the same temperature.

Keywords: Deep Water; Fish Physiology; Hydrostatic Pressure; Marine Technology; Swimming; Temperature; North Atlantic, Porcupine Seabight

1. Introduction

In situ studies of whole fish (Smith, 1978; Bailey et al., in press) and *in vitro* experiments with metabolic enzymes (Childress and Somero, 1979; Childress, 1995) suggest that the metabolic rates of deep-sea fish are lower than those of related shallow-water species at similar temperatures. Possible explanations for these findings have included direct pressure-limitation of metabolic capacity (Somero and Siebenaller, 1979), food limitation (Childress, 1971; Smith and Hessler, 1974; Collins et al., 1999), and a reduction in selective pressure for high metabolic power (Cowles et al., 1991; Childress, 1995). This last, "relaxation", hypothesis proposes that in the absence of light and with low abundance of animals in the deep-sea the frequency and duration of interactions between animals is reduced, resulting in a decreased selective pressure for burst high activity capacities (Bennett, 1991). If selection for performance is relaxed then variables such as whole-animal swimming velocities and accelerations, muscle shortening velocities and power outputs may also be lower than would be expected for shallow-water fish at similar environmental temperatures.

Fish generally exhibit their maximum muscle and whole-body swimming performances during "fast-starts". A fast-start is typically an escape or attack behaviour characterised by a high-energy, unsteady, form of swimming usually beginning from rest or imposed upon steady swimming (Johnston et al., 1995; Domenici and Blake, 1997; Wakeling, 2001). A generalised form of fast-start is initiated by contraction of the white muscle on one side of the body and adoption of a C or S-shaped posture. Rapid contraction of the opposing (contralateral) muscle group then rapidly propels the animal forward.

Measuring fast-start performance provides a non-invasive but quantitative measure of maximum activity capacity and may indicate the relative importance of burst performance to the animal. Although marine studies are lacking, the importance of burst activity capacity in increasing survival has been demonstrated for terrestrial (Jayne and Bennett, 1990) and freshwater (Watkins, 1995) animals. Burst performance may be traded-off against other priorities within a species (Andraso and Barron, 1995; Andraso, 1997; Reidy et al., 2000; Boily and Magnan, 2002; Wilson et al., 2002), allowing species to rapidly adapt to an unpredictable environment (Scheiner, 1993), and between species (Bailey, 2001; Boily and Magnan, 2002) due to niche differentiation.

No burst activity performance measurements currently exist for deep-sea fishes, though comparative investigations of prolonged (Cohen, 1977) and sustained swimming (Collins et al., 1999) exist. The morid fish *Antimora rostrata* (Günther, 1878) is an active scavenger found across the North Atlantic continental shelf at depths of 300-3000 m (Cohen et al., 1990). The high routine activity level of this species is thought to be key to the competition between this fish and other scavengers in this habitat (Collins et al., 1999). As an active fish *A. rostrata* is useful for testing the simple null hypothesis that deep-sea fish may have similar capabilities for muscular work as shallow-water fish. Due to the difficulties involved in recovering deep-sea fish to the surface alive, and the need to obtain animals in good condition, no data exist for burst swimming or muscle performance for any obligate deep-sea species. In the present study all experiments were undertaken *in situ* using a purpose-designed autonomous lander vehicle. These experiments were undertaken as part of a

larger study utilising an autonomous fish respirometer lander, and measurements of fish routine activity by camera and acoustic tracking. These systems are described separately (Priede et al., 1991; Bagley, 1992; Bailey et al., in press).

2. Methods

2.1. Lander operations

The Sprint lander vehicle was deployed from RRS Discovery at 4000 m and 2500 m in the Porcupine Seabight, North Atlantic (Figure 1) during 15th-22nd March 2002. The vehicle consisted of an aluminium tripod frame on which two acoustic releases (RT/AR 661 B2S-DDL, Oceano Instruments, France), control, stimulation, and camera systems were mounted (Figure 2). A 40 kg ballast block was attached by a levered catch to each of the legs, making the lander negatively buoyant on deployment. Ballast was dropped by acoustic command at the end of the experiment, after which the vehicle was returned to the surface by a buoyant mooring (Trimsyn TS2-6000, CRP, UK). A large flag, radio beacon (Novatec, Canada), and strobe (Novatec, Canada) attached to a buoy (Trimsyn TS2-6000, CRP, UK) at the end of the mooring aided recovery.

2.2. Experimental protocol

A typical experiment lasted 2 h after lander touch-down. Fish were attracted to the lander by 3 kg of mackerel (*Scomber scombrus*). Under the control of the onboard computer electrical stimulation was used to trigger fast-start behaviours in view of a digital video camera.

At a pre-set time filming and stimulation began (allowing time for the lander to reach the seafloor and for scavenging fish to accumulate), after which stimulations were made at regular intervals over the following 2h. The lander was recovered after 5-24h on the bottom depending on other ship operations. All lander systems, except the acoustic releases, were under the control of the onboard controller based around a 68000 microcontroller (Onset Computer Corp., USA) The controller used a text based control program to schedule events relative to controller switch-on time.

2.3. Filming

A purpose-built digital video camera system was contained within an aluminium pressure housing. Video images were recorded to a digital video recorder (GV-D300E, Sony, Japan) at a frame rate of 25 Hz by a digital video camera (TK-C1380, JVC, Japan) with a wide-angle, auto-iris lens (HG361AFCS-3, Computar, Japan).

Illumination was provided by two 50W lamps (Deep Multilite, Deep-Sea Power and Light, USA) mounted beneath the lower deck of the lander and slaved to the camera. The lander frame formed the tripod for the camera, which faced directly downwards at a range of 2.8 m from the seabed, giving a field of view of 1.8 x 2.6 m (frame diagonal of approximately 5.6 fish lengths for *A. rostrata*). The pale colour of the seabed, and the lighting angles allowed sharp silhouettes of the fish to be obtained (Figure 3). Power for the camera system was provided by a 12 v pressure-compensated lead-acid battery (SeaBattery, Deep-Sea Power and Light, USA).

2.4. Electrical stimulation

The electrical stimulator unit was mounted on the lower deck, connected by two paralled 4 core cables to two stainless steel (ASTM 316) electrodes (0.02m diameter, 1.5 m long), mounted 1 m apart and 0.2 m above the seabed. The stimulator consisted of a switched capacitor charge circuit capable of generating voltage pulses of up to 57 V at current of up to 1000 Amps. Power for the stimulator was supplied by a second 12 V battery (SeaBattery, Deep-Sea Power and Light, USA).

Stimulation was given by single, square electrical pulses, delivered across the electrodes when triggered by the onboard computer. Pulse amplitudes of up to 40 v were utilised, at pulsewidths of 1, 2, or 5 ms. Pulse amplitude was varied by adjustment of the fixed, maximum voltage setting within the stimulator unit, and by changing the period for which the capacitors were charged by the battery before the stimulating pulse was delivered. A light-emitting diode (LED) mounted on each electrode allowed the exact moment of stimulation to be determined (±0.04 s).

In initial deployments pulse characteristics were varied independently to determine a reliable stimulation regime, resulting in consistent and vigorous escape responses. At each voltage (10, 20, and 40 V) the pulse widths were cycled through 1, 2, and 5 ms. Following optimisation, stimulation characteristics were fixed for the final experiment at 2500 m depth at 40 V amplitude, 2 ms pulsewidth with an interval of 2 min, beginning 20 min after lander touch-down. Filming took place for 30 s before and after each stimulation, with a 1 min interval in between, during which the camera and lights were turned off.

149 An acoustic Doppler current meter (Aquadopp, Nortec AS, Norway) was mounted on
150 the lower deck and recorded current velocity and direction in three dimensions at 1
151 min intervals throughout the deployment. Mean current velocity in x and y for 5
152 minutes either side of the stimulation was calculated and used to remove the effects of
153 water flow on fish movement.
154
155 2.5. Kinematic analysis
156 Only sequences for which the fish was completely within the field of view of the
157 camera for the initial and contra-lateral contractions of the escape response were
158 analysed. The length and spacing of the stimulator electrodes were measured (±1mm)
159 and used as a scaling reference in the x and y directions.
160
161 Digital video recordings were replayed and fast-start sequences were captured as .avi
162 files (Final Cut Pro 2 software, Apple Macintosh G4 computer). The sequence files
163 were then replayed frame-by-frame on a PC (Genie P3 866, Viglen). In each frame
164 10 equally spaced points along the centreline of the fish, including the snout and the
165 tip of the tail, were selected manually. The co-ordinates of each point were recorded
166 by a program in Visual Basic 4 (Microsoft) and exported as a text file to a program in
167 Mathematica (Wolfram Inc.) for analysis. Much of the kinematic analysis is based on
168 the techniques developed by Wakeling and Johnston (1998) and the detailed methods
169 provided by Wakeling (2000).
170
171 2.6. Anatomical measurements
172 Fish body depth and width, total and white muscle mass were determined from digital
173 photographs of 8 equally spaced latitudinal cross-sections cut from 5 frozen

174 specimens of the same size and sampling location as the animals filmed. The
175 resulting 9 compartments were each weighed (± 1 g) and the mean cross-sectional
176 area of white muscle for each compartment was calculated (assuming zero m^{-2} white
177 muscle at the tip of the snout and tail). The total mass of white muscle was calculated
178 from the sums of the volumes of white muscle in each compartment and an assumed
179 muscle density of 1060 $kg.m^{-3}$ (Mendez and Keys, 1960). This density is likely to be
180 a slight overestimate given the higher water contents of some deep-sea fishes and
181 therefore could result in an underestimate of specific power output.
182
183 2.7. Calculation of fish swimming performance
184 The instantaneous position of the centre of mass of the animal was determined from
185 the above measurements of fish length-wise mass distribution and the digitised
186 positions of the spine co-ordinates in the video recordings. Spine (vertebral column)
187 position was assumed to be approximately beneath the midline of the silhouette of the
188 fish (Wakeling and Johnston, 1998).
189
190 The digitised spine positions divided the fish into 9 lengthwise compartments,
191 matching those from which mass distributions had been obtained. The position of the
192 lengthwise centre of each section was calculated using a quintic spline function fitted
193 through the co-ordinate data. The instantaneous position of the fish centre of mass in
194 the x and y directions was calculated from the sum of the products of the section mass
195 and its co-ordinate, divided by mean section mass (m)
196
197 $$\left(\sum m_n \cdot x_n\right) \cdot \hat{m}^{-1}$$
198

199 Moving cubic regressions were used to calculate smoothed first and second order
200 derivatives of the centre of mass position vs. time data providing velocity and
201 acceleration in the x and y directions. The component of fish movement caused by
202 water flow through the lander was deducted using the current meter data. The x-y
203 velocity and acceleration data were resolved to give total velocity (U) and
204 acceleration (A_{total}). Tangential acceleration (A_{tang}) was determined by differentiation
205 of the total velocity vs. time data. The correct smooth width was determined using the
206 criteria of Wakeling and Johnston (1998).
207
208 The inertial power ($P_{inert,}$ W) required to move the centre of mass was calculated from
209 the product of fish wet mass (m, kg) plus estimated added mass of water (m_a, kg), the
210 fish's movement velocity (U, m.s^{-1}) and tangential acceleration (A_{tang}, m.s^{-2}). A value
211 of 0.2m was used for m_a (Webb, 1982). Muscle mass specific hydrodynamic power
212 output (P_{total} W.kg^{-1}) was calculated from the inertial power requirement, predicted
213 fish white muscle mass (m_w) and an estimated efficiency term (η). A value of 0.31 is
214 used for η (Frith and Blake, 1995).
215
216 $$P_{total} = (m + m_a) \cdot U \cdot A_{\text{tang}} \cdot \eta^{-1} \cdot m_w^{-1}$$
217
218 The measured fish length in the field of view of the camera was used to calculate
219 length-specific velocity ($\hat{U}$, length-s^{-1}) and acceleration ($\hat{A}_{tang}$, lengths.s^{-2}). Peak
220 values were calculated for each variable and are denoted by the subscript "$_{max}$". A_{max}
221 refers to tangential acceleration, P_{max} refers to maximum muscle mass specific
222 hydrodynamic power output.
223

3. Results

3.1. Fast-start behaviour

Fish of 4 species were attracted by the bait and observed by the lander video camera. At 4000 m only *Coryphaenoides armatus* were observed, while at 2500 m *C. armatus* (Hector 1875), *Antimora rostrata*, the eel *Histiobranchus bathybius* (Günther, 1877), and the skate *Bathyraja richardsoni* (Garrick, 1961) were present. Of these species the greatest number of usable escape responses was recorded in *A. rostrata*. The reasons for this were the high sensitivity of this species to the stimulator and that for operational reasons the deployments after optimisation of the stimulation system were at 2500 m. In the study area fish occurred in known depth zones, allowing the species to be experimented upon to be selected according to the depth of water in which the equipment was deployed. The 8 sequences analysed were for *A. rostrata* at 2500 m, mean total body length 0.51±0.02 m (1 S.E.). *A. rostrata* was responsive to the stimulus, typically beginning to bend due to the ipsilateral muscle contraction within 2-3 frames (0.08-0.12 s) of the electrical stimulation. On two occasions fish were observed resuming feeding immediately after performing an escape response, indicating that no lasting harm had been caused by the electrical field. As animals would sometimes return to the bait it is possible that 2 sequences for 47 cm animals and 2 for 56 cm animals were second stimulations of the same animal.

Escape responses in *Antimora rostrata* (Figure 3) were highly variable, but were all "C-starts" followed by one or more propulsive tailbeats. Power output and acceleration were rapid immediately following initiation of the escape response but acceleration did not continue during the second tailbeat (figure 4). Escape responses were typified by short bursts of movement followed by gradual deceleration. The

caudal fin of *A. rostrata* appeared to be extremely flexible and trailed behind the caudal peduncle, often twisting so that it lay parallel to the direction of tail movement. This structure appeared to be too weak to generate hydrodynamic force at high velocities.

Figure 3.

Figure 4.

3.2. Comparative velocity, acceleration and power output

Swimming velocities, accelerations and power outputs were calculated from 8 escape responses (Figures 5 and 6). Swimming velocity calculations resulted in a U_{max} of 0.70±0.1 m.s^{-1} (Figure 5B) and $\hat{U}_{max}$ of 1.41±0.23 body lengths.s^{-1} (Mean ± S.E.) (Figure 6A). Tangential accelerations calculated from the fish velocity gave an A_{max} of 3.79±0.72 m.s^{-2} (Figure 5C) and $\hat{A}_{max}$ of 7.56±1.57 body lengths.s^{-2} (Figure 6B) P_{max} was 17.0±5.9 W.kg white muscle^{-1} (Figure 5A). The mean duration of the first muscle contraction (stage 1) was 0.17±0.01s, with an overall response duration of 0.40±0.01s (stage 1 + stage 2). The whole-body and muscle performances of *Antimora rostrata* are compared to those of other fish species are presented in Figure 5. No performance parameter scaled significantly with fish total length over the limited size range (0.44-0.56 m total length) available in this study.

Figure 5

Figure 6

Analysis of Covariance was used to compare the U_{max}, $\hat{U}_{max}$, A_{tang} and $\hat{A}_{max}$ of *A. rostrata* to data for shallow-water fish provided by Domenici and Blake (1997) and Wakeling and Johnston (1998). These data cover wide taxonomic (18 spp. of 6 orders), temperature (0-25^{o}C), and size (0.05-0.4 m) ranges. There was no significant difference in $\hat{U}_{max}$ or $\hat{A}_{max}$ between *A. rostrata* and the mean values for the pooled shallow-water fish species once temperature and fish length had been taken into account ($F_{1,34}$=1.41, p=0.244, p=$F_{1,34}$=3.25, p=0.08, respectively). U_{max} and A_{max} were significantly higher in shallow-water fishes than in *A. rostrata* ($F_{1,34}$=21.49, p<0.001, p=$F_{1,34}$=12.17, p=0.001, respectively).

3.3. Relative turning ratios

This ratio expresses the manoeuvrability of the animal in terms of the radius of the circular path of the animals centre-of-mass divided by its total length. Mean relative turning ratio was 0.17±0.01 (1 S.E.). Relative turning radius was significantly related to peak length specific tangential acceleration (in lengths.s^{-2}, R^2=0.58, df=6, p=0.27). Scaling relationships and correlation between turning ratio and other performance variables were apparent but not significant due to the low number of data points available.

4. Discussion

4.1. Comparative fast-start performance of *A. rostrata*.

With peak burst swimming speeds averaging only 0.7 m.s^{-1}, and acceleration of less than 8 m.s^{-2} *Antimora rostrata* is one of the slowest fish for which fast-start measurements have been obtained. A variety of possible features of the ecology and environment of the deep-sea systems inhabited by *A. rostrata* could explain this low

298 activity capacity, the most straightforward of which being direct thermodynamic
299 limitation of metabolic processes by pressure and temperature.
300
301 The effects of temperature and pressure on biological systems, and the mechanisms by
302 which fish are able to "tune" their physiology to these features of their environment,
303 are well documented and include modifications to enzymes (Johnston and Walesby,
304 1979; Johnson and Bennett, 1995; Sebert, 2001), membranes (Sebert, 2001), muscle
305 fibres (Johnston et al., 1998), mitochondrial density (Johnston and Altringham, 1985),
306 and intracellular environment (Clarke, 1983; van Dijk et al., 1999; Yancey and
307 Siebenaller, 1999). It has been possible to separate the physiological influences of
308 acute temperature from the effects on swimming of the physical differences in water
309 characteristics at different temperatures (Johnson et al., 1998).
310
311 Cold-water fish do not typically show compensation for low temperatures in terms of
312 their muscle performance (Johnston et al., 1991; Franklin and Johnston, 1997;
313 Wakeling and Johnston, 1998) but may show rates of metabolic recovery similar to
314 those of temperate fish (Hardewig et al., 1998; Van Dijk et al., 1998). While
315 mechanisms for rate limitation by temperature and pressure exist, the enzymes of
316 teleost fish hearts and brains have similar activities at all studied depths (Childress
317 and Somero, 1979), indicating that the effects of these variables can be overcome
318 given sufficient selective pressure to do so.
319
320 In the case of *Antimora rostrata*, whole-animal performances, estimates of muscle
321 power output, and turning ability demonstrate activity capacities similar to shallow-
322 water species at similar temperatures when expressed in length-specific terms (Moon

et al., 1991; Anderson and Johnston, 1992; Domenici and Blake, 1997; Wakeling and Johnston, 1998). This is consistent with published data for maximum prolonged swimming speed of 1.45 body lengths.s^{-1} for an individual 27 cm *A. rostrata* chased by a submersible (Cohen, 1977). This value is similar to many shallow water species and remarkably fast for prolonged swimming at 2^{o}C. The above value is similar to the mean value for peak velocity for fast-starts in the present study. Mean sustained swimming speed for *A. rostrata* at the present study site is 0.39 lengths.s^{-1}, with a maximum one-minute average of 1.13 lengths.s^{-1} (Collins et al., 1999). Acceleration rates from the present study do appear to be reduced compared to shallow-water fish, though this may be a result of the high degree of smoothing necessary at the low frame-rates and magnifications available with the present camera system.

Relative turning ratios are important in predator-prey interactions as they determine in part the ability of the animal to manoeuvre and capture or evade the other animal. *Antimora rostrata* demonstrates turning ratios similar to those of Rainbow trout. Highly manoeuvrable fish with high fineness ratios can turn more sharply, while stiff round-bodied open-ocean fishes such as tunas have turning ratios up to three times those of *A. rostrata* (see Domenici and Blake (1997) for review).

4.2. Scaling

The *Antimora rostrata* individuals filmed here are amongst the largest fish to be used in fast-start studies. In Domenici and Blake's (1997) recent review of fast-start performance in fish, animals of up to 0.4 m were considered. While larger fish such as tuna (Block et al., 1998; Block et al., 2001) and basking sharks (Priede, 1984; Sims, 2000) have been tracked, few measures of burst activity in large aquatic animals

348 exist outside of marine mammals (Domenici, 2001; Rohr et al., 2002). Re-plotting
349 existing fast-start data demonstrates that both specific velocity and acceleration
350 decline with increasing animal length (Figure 6), and that once temperature and fish
351 length are taken into account the length-specific performances of *A.rostrata* do not
352 differ significantly from those of shallow-water fish.
353
354
355 4.3. Limitations of the methods and equipment
356 In the present study the sampling frequency of the camera is low (25 Hz) and the field
357 of view of the camera large. These factors are a limitation of the equipment available
358 for this pilot study and the unpredictable behaviour and position of free-swimming
359 fish. A large field of view was required in order to observe the maximum number of
360 fish and therefore determine their responses to the stimulator. High frame-rates are
361 not as advantageous at low image magnifications due to the increases in measurement
362 error incurred. For fast-starts of the duration observed in this study (see Results) a
363 mean sampling rate of 9.25 frames-per-fast-start was achieved, under two-thirds of the
364 mean sampling rate of the fish kinematic studies reviewed by Domenici and Blake
365 (1997). As a result of the low frame rate it is possible that estimates of acceleration
366 from our films may be only 53% of true values (Harper and Blake, 1989b; Harper and
367 Blake, 1989a). The moving piecewise cubic regression technique used in the present
368 study will reduce this over-smoothing error compared to the linear regression
369 technique in the above studies or the cubic regression used in Walker's (1998) critique
370 of motion analysis methods. In a simulation test we found that the over-smoothing
371 error using the present program on 25 Hz data resulted in acceleration values which
372 were 64% of accelerations calculated from a perfectly smooth displacement trace at

800 Hz. The data obtained from this study will allow the development of a more sophisticated system in which higher frame-rates will be available and increased image resolution will enable greater image magnification during analysis. Electrical stimulation does not give a directional stimulus and therefore may result in a reduction in fish turning rate (Nissanov et al., 1990). Fast-starts stimulated by electrical fields are otherwise kinematically identical to those initiated by tactile or visual stimuli (Webb, 1975).

The net result of the technical limitations of the study is most likely to be underestimation of the velocities and accelerations of the fish. As the major result of this study is to demonstrate that the fish moved more quickly than had been expected of deep-sea animals the technical problems do not give cause to doubt this finding.

4.4. Conclusions

Antimora rostrata does not appear to show the reduction in performance expected of deep-sea fish as a result of continuous darkness (Childress et al., 1990; Childress, 1995) . As the cold-water fish with which *A. rostrata* is most similar are Antarctic animals, and therefore also from a food-limited habitat (Clarke, 1983), it is difficult to conclusively state whether the low muscle performances seen in the present study are a result of low temperature or reduced dietary energy supply (Childress and Somero, 1979; Collins et al., 1999).

In any case the theory that the darkness of the deep-sea should allow reduced activity capacity is worth questioning, at least in demersal systems where animal abundance is relatively high. In complex shallow-water environments such as weed beds and reefs

motile animals may only be visible to each other for short periods. This leads to high levels of burst performance and manoeuvrability in the fishes inhabiting these systems (Domenici and Blake, 1997) as prey capture must occur before the victim can escape into cover. Might the darkness of the deep-sea be analogous to a complex or cloudy shallow-water system? Fish are able to track the wakes of other fish (Pohlmann et al., 2001), observe bioluminescence (Warrant, 2000), and detect the sound of accelerating predators (Sand and Karlsen, 2000). It is possible then that the interactions between predators and prey may be every bit as furious in the deep-sea as in photic systems, with short bursts of activity necessary to attack or escape before disappearing into the darkness.

References

Anderson, M.,Johnston, I.A., 1992. Scaling of power output in fast muscle fibres of the Atlantic cod during cyclical contractions. Journal of Experimental Biology 170, 143-154.

Andraso, G.M., 1997. A comparison of startle response in two morphs of the brook stickleback (*Culaea inconstans*): Further evidence for a trade-off between defensive morphology and swimming ability. Evolutionary Ecology 11, 83-90.

Andraso, G.M.,Barron, J.N., 1995. Evidence for a trade-off between defensive morphology and startle-response performance in the brook stickleback (*Culaea inconstans*). Canadian Journal of Zoology 73, 1147-1153.

Bagley, P., 1992. A code-activated transponder for the individual identification and tracking of deep-sea fish. In *Wildlife Telemetry: Remote monitoring and tracking of animals*, eds I. G. Priede and S. Swift), pp. 111-119. Chichester:

Ellis Horwood.

Bailey, D.M., 2001. The thermal dependence of swimming and muscle physiology in temperate and Antarctic scallops. In *PhD Thesis*, pp. 138. St. Andrews: University of St.Andrews.

Bailey, D.M., Jamieson, A.J., Bagley, P.M., Collins, M.A.,Priede, I.G., in press. Measurement of *in situ* oxygen consumption of deep-sea fish using an autonomous lander vehicle. Deep-Sea Research I.

Bennett, A.F., 1991. The evolution of activity capacity. Journal of Experimental Biology 160, 1-23.

Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., Boustany, A., Teo, S.L., Seitz, A., Walli, A.,Fudge, D., 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. Science 293, 1267-8.

Block, B.A., Dewar, H., Farwell, C.,Prince, E.D., 1998. A new satellite technology for tracking the movements of Atlantic bluefin tuna. Proceedings of the National Academy of Sciences of the United States of America 95, 9384-9389.

Boily, P.,Magnan, P., 2002. Relationship between individual variation in morphological characters and swimming costs in brook charr (*Salvinus fontinalis*) and yellow perch (*Perca flavescens*). Journal of Experimental Biology 205.

Childress, J.J., 1971. Respiratory rate and depth of occurrence of midwater animals. Limnology and Oceanography 16, 104-106.

447 Childress, J.J., 1995. Are there physiological and biochemical adaptations of
448 metabolism in deep-sea animals. Trends in Ecology & Evolution 10, 30-36.
449
450 Childress, J.J., Price, M.H., Favuzzi, J.,Cowles, D., 1990. Chemical-composition of
451 midwater fishes as a function of depth of occurrence off the Hawaiian-islands
452 - food availability as a selective factor. Marine Biology 105, 235-246.
453 Childress, J.J.,Somero, G.N., 1979. Depth-related enzyme activities in muscle, brain
454 and heart of deep-living pelagic marine teleosts. Marine Biology 52, 272-283.
455 Clarke, A., 1983. Life in cold water: the physiological ecology of polar marine
456 ectotherms. In *Oceanography and Marine Biology Annual Review*, (ed. M.
457 Barnes). Aberdeen: Aberdeen University Press.
458 Cohen, D.M., 1977. Swimming performance of the gadoid fish *Antimora rostrata* at
459 2400 m. Deep-Sea Research I 24, 275-277.
460 Cohen, D.M., Inada, T., Iwamoto, T.,Scialabba, N., 1990. FAO Species Catalogue.
461 Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and
462 illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes
463 known to data. In *FAO Fisheries Synopsis No. 125*, vol. 10, pp. 354.
464 Collins, M.A., Priede, I.G.,Bagley, P.N., 1999. *In situ* comparison of activity in two
465 deep-sea scavenging fishes occupying different depth zones. Proceedings of
466 the Royal Society B 266, 2011-2016.
467 Cowles, D.L., Childress, J.J.,Wells, M.E., 1991. Metabolic rates of midwater
468 crustaceans as a function of depth of occurrence off the Hawaiian islands -
469 food availability as a selective factor. Marine Biology 110, 75-83.
470

471 Domenici, P., 2001. The scaling of locomotor performance in predator-prey
472 encounters: from fish to killer whales. Comparative Biochemistry and
473 Physiology A 131, 169-182.
474 Domenici, P.,Blake, R.W., 1997. The kinematics and performance of fast-start
475 swimming. Journal of Experimental Biology 200, 1165-1178.
476
477 Franklin, C.,Johnston, I., 1997. Muscle power output during escape responses in an
478 Antarctic fish. Journal of Experimental Biology 200, 703-12.
479 Frith, H.,Blake, R., 1995. The mechanical power output and hydromechanical
480 efficiency of northern pike (*Esox lucius*) fast-starts. Journal of Experimental
481 Biology 198, 1863-73.
482 Hardewig, I., Van Dijk, P.L.,Pörtner, H.O., 1998. High-energy turnover at low
483 temperatures: recovery from exhaustive exercise in Antarctic and temperate
484 eelpouts. American Journal of Physiology 274, R1789-96.
485 Harper, D.G.,Blake, R.W., 1989a. A critical analysis of the use of high-speed film to
486 determine maximum accelerations of fish. Journal of Experimental Biology
487 142, 465-471.
488 Harper, D.G.,Blake, R.W., 1989b. On the error involved in high-speed film when used
489 to evaluate maximum accelerations in fish. Canadian Journal of Fisheries and
490 Aquatic Science 67, 1929-1936.
491 Jayne, B.C.,Bennett, A.F., 1990. Selection on locomotor performance capacity in a
492 natural population of garter snakes. Evolution 44, 1204-1229.
493 Johnson, T.P.,Bennett, A.F., 1995. The thermal acclimation of burst escape response
494 in fish: an integrated study of molecular and cellular physiology and

495 organismal performance. Journal of Experimental Biology 198, 2165-2175.
496
497 Johnson, T.P., Cullum, A.J.,Bennett, A.F., 1998. Partitioning the effects of
498 temperature and kinematic viscocity on the c-start performance of adult fishes.
499 Journal of Experimental Biology 201, 2045-2051.
500 Johnston, I., Calvo, J.,Guderley, Y.H., 1998. Latitudinal variation in the abundance
501 and oxidative capacities of muscle mitochondria in perciform fishes. Journal
502 of Experimental Biology 201, 1-12.
503
504 Johnston, I.A.,Altringham, J.D., 1985. Evolutionary adaptation of muscle power
505 output to environmental temperature: force-velocity characteristics of skinned
506 fibres isolated from antarctic, temperate and tropical marine fish. Pflugers
507 Archiv, European Journal of Physiology 405, 136-40.
508 Johnston, I.A., Johnson, T.P.,Battram, J.C., 1991. Low temperature limits burst
509 swimming performance in Antarctic fish. In *Biology of Antarctic Fish*, eds G.
510 Di Prisco B. Maresia and B. Tota).
511 Johnston, I.A., Van Leeuwen, J.L., Davies, M.L.F.,Beddow, T., 1995. How fish
512 power predation fast-starts. Journal of Experimental Biology 198, 1851-1861.
513 Johnston, I.A.,Walesby, N.J., 1979. Evolutionary temperature adaptation and the
514 calcium regulation of fish actomyosin ATPases. Journal of Comparative
515 Physiology - B 129, 169-177.
516 Mendez, I.,Keys, A., 1960. Density and composition of mammalian muscle.
517 Metabolism 9, 184-188.
518 Moon, T.W., Altringham, J.D.,Johnston, I.A., 1991. Energetics and power output of
519 isolated fish fast muscle fibres performing oscillatory work. Journal of

520 Experimental Biology 158, 261-73.
521
522 Nissanov, J., Eaton, R.C.,DiDomenico, R., 1990. The motor output of the Mauthner
523 cell, a reticulospinal command neuron. Brain Research 517, 88-98.
524 Pohlmann, K., Grasso, F.W.,T., B., 2001. Tracking wakes: The nocturnal predatory
525 strategy of piscivorous catfish. Proceedings of the National Academy of
526 Science of the United States of America 98, 7371-7374.
527 Priede, I.G., 1984. A basking shark (*Cetorhinus maximus*) tracked by satellite together
528 with simultaneous remote sensing. Fisheries Research 2, 201-216.
529
530 Priede, I.G., Bagley, P.M., Armstrong, J.D., Smith, K.L.,Merrett, N.R., 1991. Direct
531 measurement of active dispersal of food-falls by deep-sea demersal fishes.
532 Nature 351, 647-649.
533 Reidy, S.P., Kerr, S.R.,Nelson, J.A., 2000. Anaerobic and anaerobic swiming
534 performance of individual Atlantic cod. Journal of Experimental Biology 203,
535 347-357.
536 Rohr, J.J., Fish, F.E.,Gilpatrick Jr., J.W., 2002. Maximum swim speeds of captive and
537 free-ranging delphinids: Critical analysis of extraordinary performance.
538 Marine Mammal Science 18, 1-19.
539 Sand, O.,Karlsen, H.E., 2000. Detection of infrasound and linear acceleration in
540 fishes. Philosophical Transactions of the Royal Society of London B 355,
541 1295-1298.
542 Scheiner, S.M., 1993. Genetics and evolution of phenotypic plasticity. Annual Review
543 of Ecology and Systematics 24, 35-68.

544 Sebert, P., 2001. Fish at High Pressure: a hundred year history. Comparative
545 Biochemistry and Physiology Part A 131, 575-585.
546
547 Sims, D.W., 2000. Filter-feeding and cruising swimming speeds of basking sharks
548 compared with optimal models: they filter-feed slower than predicted for their
549 size. Journal of Experimental Marine Biology and Ecology 249, 65-76.
550 Smith, K.L., 1978. Metabolism of the abyssopelagic rattail *Coryphanoides armatus*,
551 measured *in situ*. Nature 274, 362-364.
552 Smith, K.L.,Hessler, R.R., 1974. Respiration of benthopelagic fishes: *In situ*
553 measurements at 1230 metres. Science 184, 72-73.
554 Somero, G.N.,Siebenaller, J.F., 1979. Ineffective lactate dehydrogenases of deep-sea
555 fishes. Nature 282, 100-102.
556
557 van Dijk, P.L., Tesch, C., Hardewig, I.,Pörtner, H.O., 1999. Physiological
558 disturbances at critically high temperatures: a comparison between
559 stenothermal antarctic and eurythermal temperate eelpouts (Zoarcidae).
560 Journal of Experimental Biology 202 Pt 24, 3611-21.
561 Van Dijk, P.L.M., Hardewig, I.,Pörtner, H.O., 1998. Exercise in the cold: high energy
562 turnover in Antarctic fish. In *Fishes of Antarctica. A biological overview*, eds
563 G. di Prisco E. Pisano and A. Clarke), pp. 362. Heidelberg: Springer Verlag.
564 Wakeling, J.M., 2000. Computational methods for the analysis of swimming
565 biomechanics. Experimental Biology Online 5, 2.
566 Wakeling, J.M., 2001. Biomechanics of fast-start swimming in fish. Comparative
567 Biochemistry and Physiology Part A 131, 31-40.

568 Wakeling, J.M.,Johnston, I.A., 1998. Muscle power output limits fast-start
569 performance in fish. Journal of Experimental Biology 201, 1505-1526.
570
571 Walker, J.A., 1998. Estimating velocities and accelerations of animal locomotion: A
572 simulation experiment comparing numerical differentiation algorithms.
573 Journal of Experimental Biology 201, 981-995.
574 Warrant, E., 2000. The eyes of deep-sea fishes and the changing nature of visual
575 scenes with depth. Philosophical Transactions of the Royal Society of London
576 B 355, 1155-1159.
577 Watkins, T.B., 1995. Predator-mediated selection on burst swimming performance in
578 Tadpoles of the Pacific Tree Frog, *Pseudacris regilla*. Physiological Zoology
579 69, 154-167.
580 Webb, P.W., 1975. Acceleration performance of rainbow trout (*Oncorhyncus mykiss*).
581 Journal of Experimental Biology 63, 451-465.
582
583 Webb, P.W., 1982. Fast-start resistance of trout. Journal of Experimental Biology 96,
584 93-106.
585 Wilson, R.S., James, R.S.,Van Damme, R., 2002. Trade-offs between speed and
586 endurance in the frog, *Xenopus laevis*: a multi-level approach. Journal of
587 Experimental Biology 205, 1145-1152.
588 Yancey, P.H.,Siebenaller, J.F., 1999. Trimethylamine oxide stabilizes teleost and
589 mammalian lactate dehydrogenases against inactivation by hydrostatic
590 pressure and trypsinolysis. Journal of Experimental Biology 202, 3597-3603.
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608 Figure 1. The Porcupine Seabight in the North Atlantic, the area in which the Sprint
609 lander vehicle was deployed. The area used for the lander experiments described is
610 enclosed by the dotted line. Deployment stations are indicated by the black points,
611 Station A is at 4000 m while Stations B and C were at 2500 m. Stimulator
612 optimisation was carried out at Stations A and B, with the majority of the fast-start
613 data presented below being collected at Station C.
614
615 Figure 2. The Sprint lander vehicle used to elicit and record escape responses in the
616 deep-sea fish *Antimora rostrata.* The parts of the lander indicated in the figure are:
617 "A" Acoustic Release, "B" Camera System in pressure housing, "C" On-board
618 computer in pressure housing, "D" 12 v battery, "E" Acoustic current meter, "F"
619 Electrical stimulator unit, "G" 50v lamp, "H" Ballast clamp, "I" Electrodes.
620
621 Figure 3. Fast-start behaviour in *Antimora rostrata* at 2500 m in the Porcupine
622 Seabight. A) The entire field of view of the camera is shown. The electrodes ran
623 from left to right at the top and bottom of the frame (indicated by solid black arrows).
624 The bait was suspended in the centre of the frame (dashed arrow). An individual *A.*
625 *rostrata* is shown approaching the bait from the bottom of the frame. B) The fast
626 start is initiated and results in the characteristic C-shape at the end of stage 1
627 (initiation + 0.16 s). C) Contraction of the contra-lateral white muscle results in the
628 propulsive tailbeat (+ 0.4 s).
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Figure 4. Typical whole-body and muscle performance parameters in a 0.56 m *Antimora rostrata* (pictured in figure 3). Velocity (U, $m.s^{-1}$) and tangential acceleration (A_{tang}, $m.s^{-2}$) are plotted on the left-hand y-axis (dashed and solid lines respectively), with muscle mass specific hydrodynamic power output (P_{total}, $W.kg^{-1}$) on the right-hand y-axis (dotted line). This animal accelerates at a rate of 5 $m.s^{-2}$ to a peak velocity of 0.86 $m.s^{-1}$ during the first muscle contraction (stage 1), using a peak muscle power output of 34.7 $W.kg^{-1}$. Stage 1 duration was 0.16 s, stage 2 was more extended at 0.24 s.

Figure 5. Peak whole-body and muscle performances of *Antimora rostrata* (open point) compared to those from laboratory studies by Wakeling and Johnston (1998) of a range of shallow-water fish species across a 25°C temperature range (solid points). The shallow-water species are "a" *Notothenia corriceps*, "b" *N. rossii*, "c" *Myoxocephalus scorpius*, "d" *Serranus cabrilla*, "e" *Scorpaena notata*, and "f" *Paracirrhites forsteri*. While peak muscle mass specific hydrodynamic power outputs (P_{max}, Figure 5A) and velocities (U_{max}, Figure 5B) in *A. rostrata* are low they are similar to data for other cold-water fishes such as the *Notothenia* spp (0 and 1°C). Tangential acceleration (A_{max}, Figure 5C) is reduced compared to other species.

Figure 6. Scaling of length specific velocity ($\hat{U}_{max}$, Figure 6A) and acceleration ($\hat{A}_{max}$, Figure 6B) across a wide range of fish sizes Open points are data for *Antimora rostrata*. Solid points are kinematic data for a range of marine and freshwater fish species from Domenici and Blake (1997) and Wakeling and Johnston (1998) at temperatures of 0-25°C. Both $\hat{U}_{max}$ and $\hat{A}_{max}$ are low in *A. rostrata* but as the largest fish in the present study this is in line with predictions for shallow-water species.

When temperature and fish length were taken into account using ANCOVA the length-specific swimming performance of *A. rostrata* does not differ significantly from those of the shallow-water species (see text for details).

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685 Figure 1
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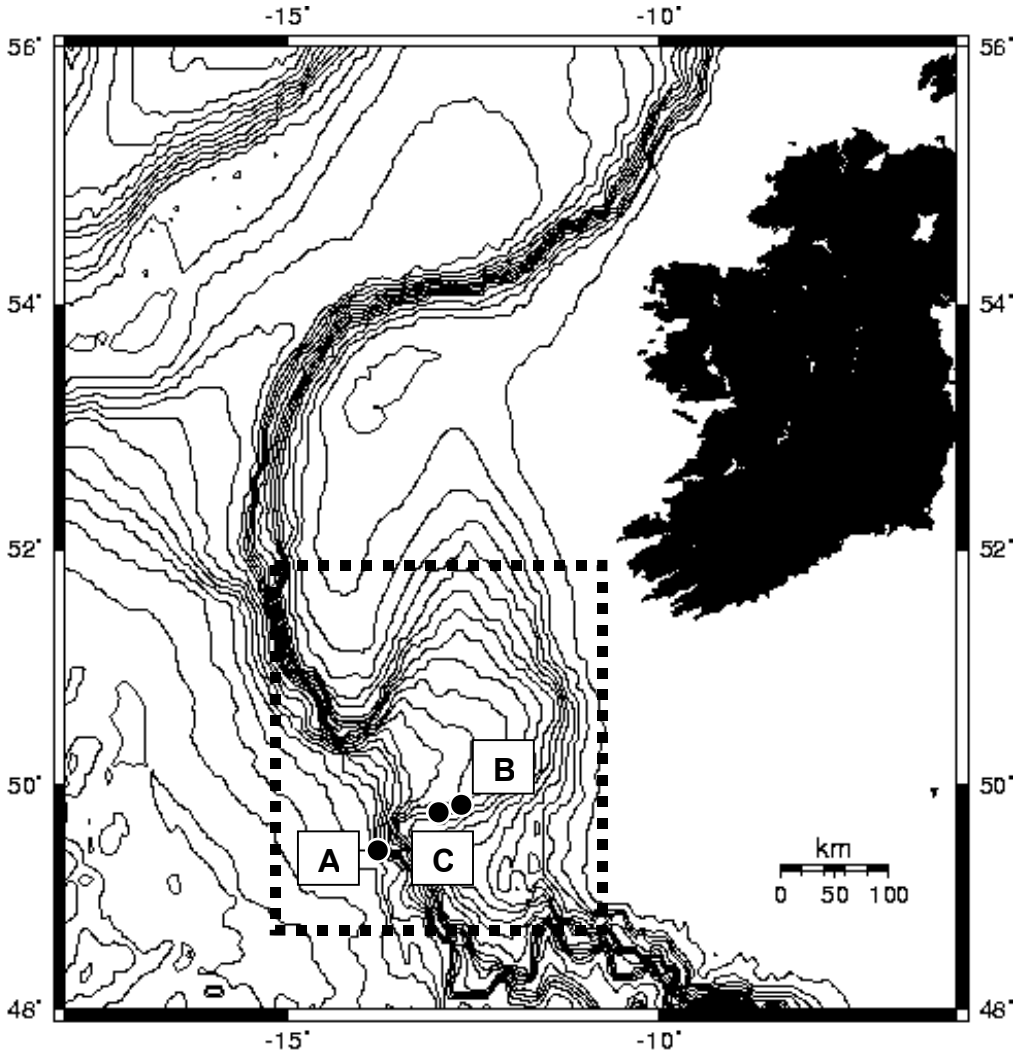

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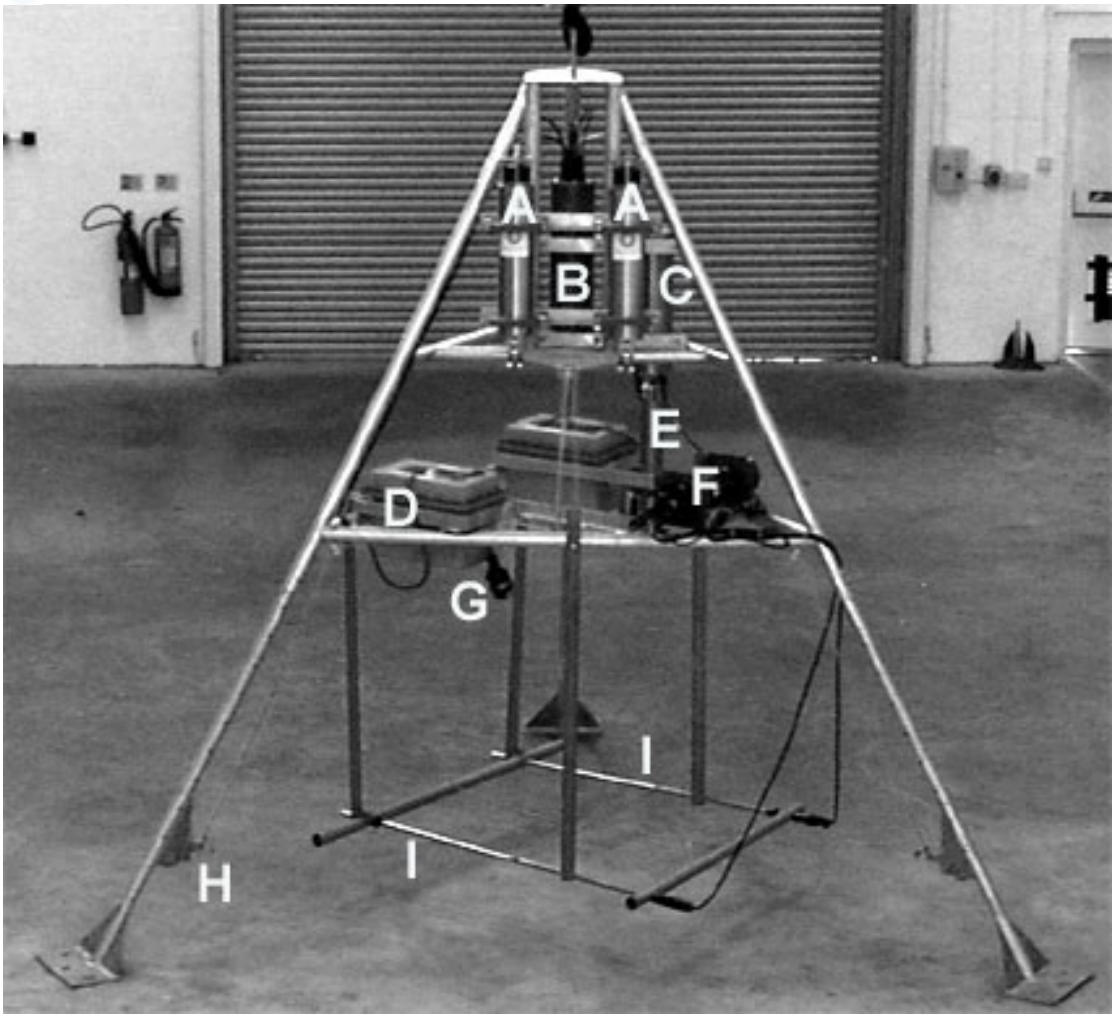
Figure 2



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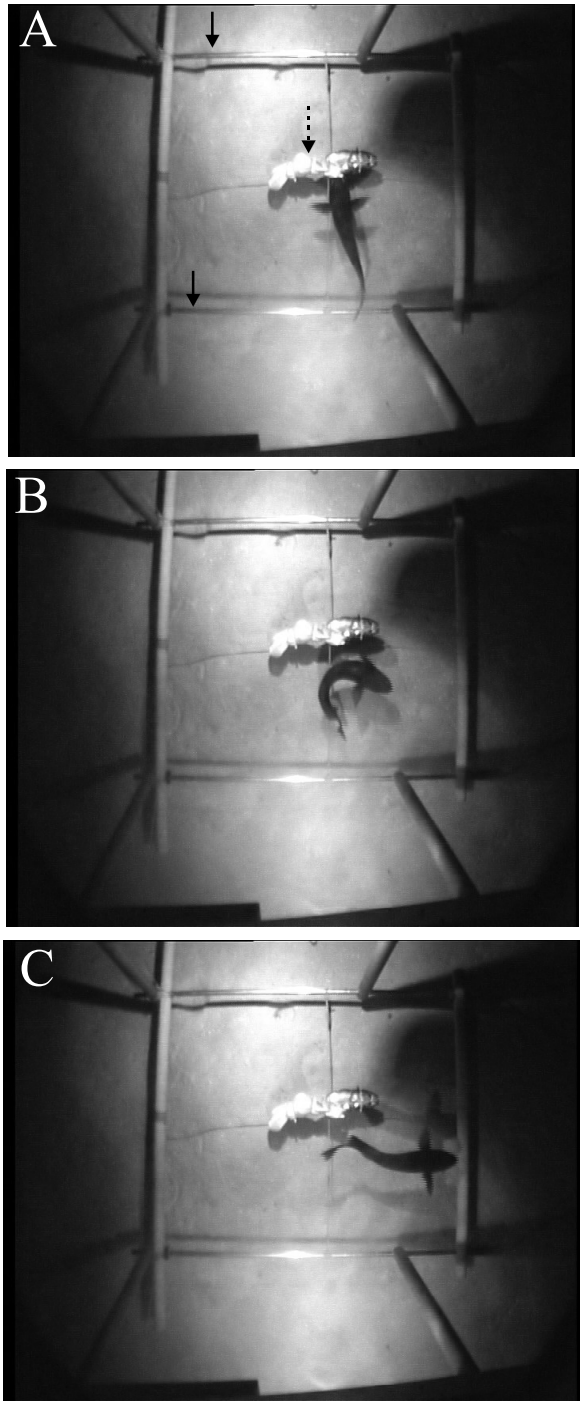


Figure 4

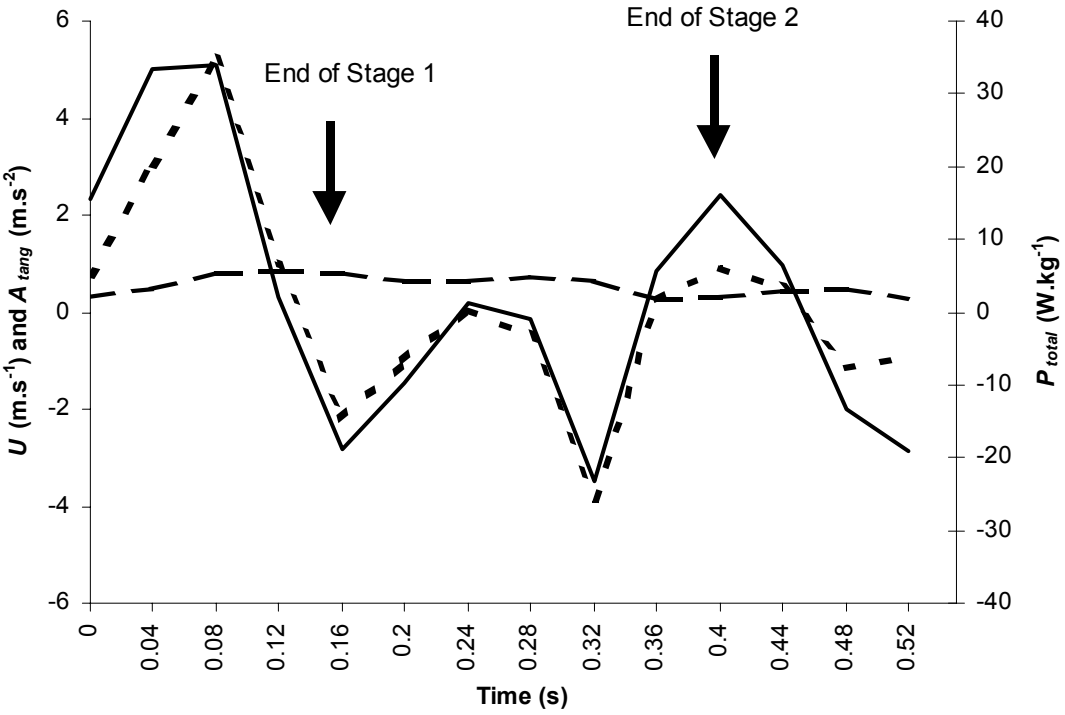

End of Stage 1
End of Stage 2
U (m.s-1) and A tang (m.s-2)
P total (W.kg-1)
Time (s)
6
4
2
0
-2
-4
-6
40
30
20
10
0
-10
-20
-30
-40
0
0.04
0.08
0.12
0.16
0.2
0.24
0.28
0.32
0.36
0.4
0.44
0.48
0.52

Figure 5

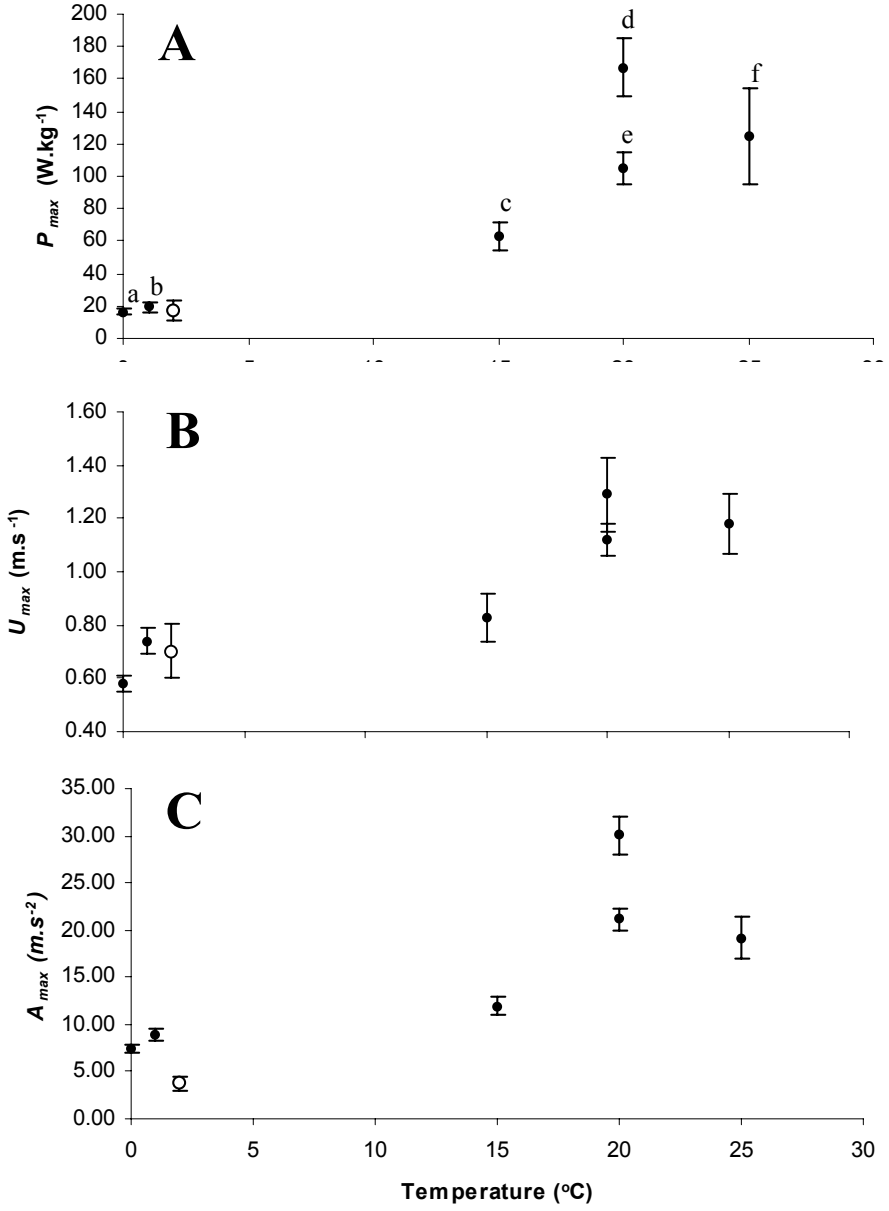
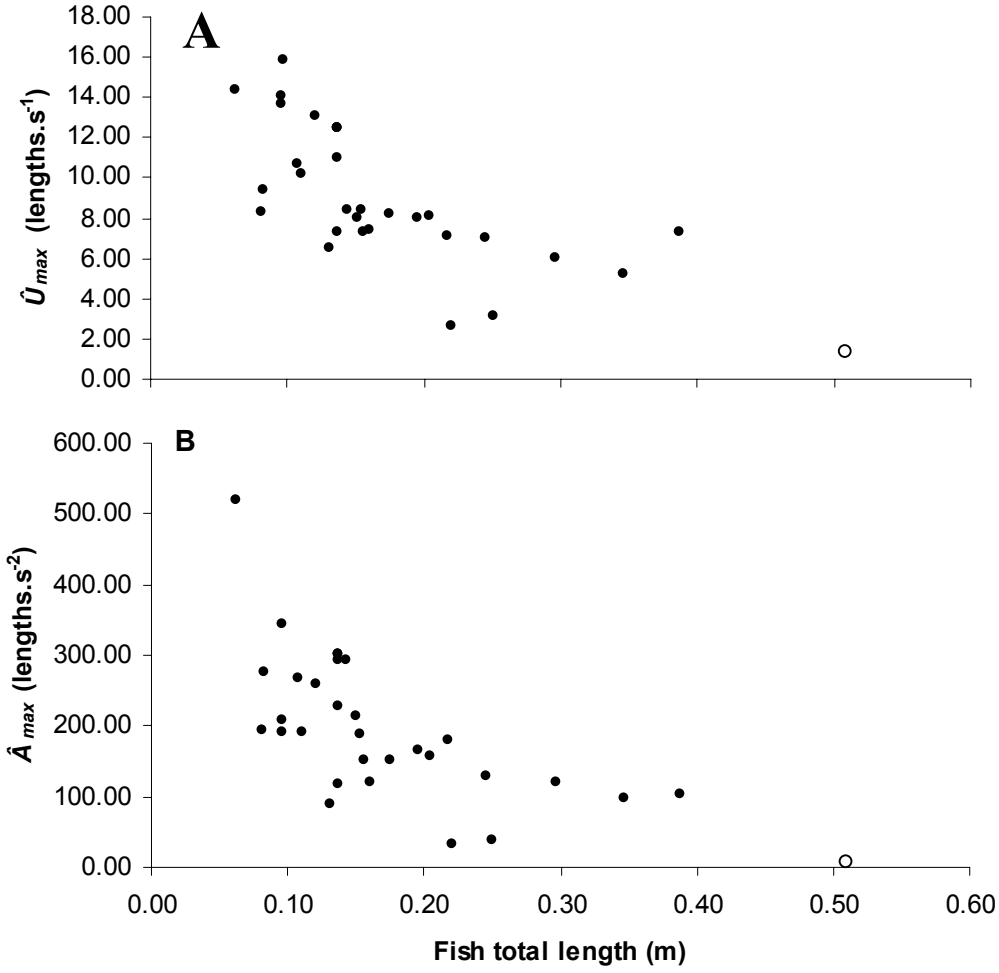


Figure 6


A
B
$\hat{U}_{max}$ (lengths.s^{-1})
$\hat{A}_{max}$ (lengths.s^{-2})
18.00
16.00
14.00
12.00
10.00
8.00
6.00
4.00
2.00
0.00
600.00
500.00
400.00
300.00
200.00
100.00
0.00
0.00
0.10
0.20
0.30
0.40
0.50
0.60
Fish total length (m)