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1 **High swimming and metabolic activity in the deep-sea eel *Synaphobranchus kaupii* revealed by integrated *in situ***  
2 **and *in vitro* measurements.**

3

4

Running head: Swimming and metabolism of deep-sea eels

1 **ABSTRACT**

2 Several complementary studies were undertaken on a single species of deep-sea fish (the eel *Synaphobranchus kaupii*)  
3 within a small temporal and spatial range. *In situ* experiments on swimming and foraging behaviour, muscle  
4 performance, and metabolic rate were performed in the Porcupine Seabight, North Atlantic alongside measurements of  
5 temperature and current regime. Deep-water trawling was used to collect eels for studies of animal distribution and for  
6 anatomical and biochemical analyses, including white muscle citrate synthase (CS), lactate dehydrogenase (LDH),  
7 malate dehydrogenase (MDH) and pyruvate kinase (PK) activities. *Synaphobranchus kaupii* demonstrated whole animal  
8 swimming speeds similar to those of other active deep-sea fish such as *Antimora rostrata*. Metabolic rates were an order  
9 of magnitude higher ( $31.6 \text{ ml} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$ ) than those recorded in other deep-sea scavenging fish. Activities of CS, LDH,  
10 MDH and PK were higher than expected and all scaled negatively with body mass, indicating a general decrease in  
11 muscle energy supply with fish growth. Despite this apparent constraint, observed *in situ* burst or routine swimming  
12 performances scaled in a similar fashion to other studied species. The higher than expected metabolic rates and activity  
13 levels, and the unusual scaling relationships of both aerobic and anaerobic metabolism enzymes in white muscle,  
14 probably reflect the changes in habitat and feeding ecology experienced during ontogeny in this bathyal species.

15  
16 **Introduction**

17 The fish communities found on the continental slopes and abyssal plains of the world's oceans are abundant, diverse, and  
18 despite many years of careful study, remain relatively poorly understood. The technical difficulties involved in studying  
19 deep-sea fishes, and in particular the sensitivity of many species to being recovered to the surface, means that our  
20 understanding of the physiology of these animals lags many years behind that of shallow-water species.

21  
22 When measured *in situ*, or after decompression, deep-water fish and other mobile animals show reduced rates of oxygen  
23 consumption (Childress and Nygaard 1974; Smith and Hessler 1974; Smith 1978; Childress et al. 1990; Bailey et al.  
24 2002) and lower metabolic enzyme activities than equivalent shallow-water animals (Somero and Siebenaller 1979;  
25 Somero et al. 1983). The low metabolic activity levels of mobile deep-sea animals are associated with their conventional  
26 image as slow-moving or "sit and wait" generalist feeders, for whom extreme metabolic efficiency is of the greatest  
27 importance. Allied to this image is the hypothesis that reduced light levels in deep-water should reduce the frequency

1 and duration of predator-prey interactions, further moving the optimum level of activity capacity away from the high-  
2 performance but metabolically expensive and towards the slow but economical (Childress 1971; Cowles et al. 1991;  
3 Childress 1995).

4  
5 While the above scenario may be true for many deep-sea species, some animals are relatively active and  
6 demonstrate high levels of routine activity (Priede et al. 1991) or locomotory performance (Cohen 1977; Koslow 1997;  
7 Bailey et al. 2003). This, and the wide variations in brain anatomy observed in deep-sea fishes (Wagner 2001), indicates  
8 that even within the constraints of the deep-sea environment a variety of niches can exist which allows for a spectrum of  
9 behavioural strategies and activity capacities, with attendant costs and benefits.

#### 10 11 A need for integrated studies of species with large natural depth ranges

12 To determine the relative influences of depth and associated environmental and ecological variables on fish physiology  
13 and behaviour, it would be extremely useful to have integrated studies of individual species over wide depth ranges,  
14 combining measures of abundance, behaviour, metabolism, activity level, and muscle performance. As performance  
15 adaptations are driven by both the physical environment and interactions with other organisms, it would be useful to have  
16 information on the abundances of conspecifics and the other species (predators, competitors and prey) with which the  
17 animals will interact. Many features of an environment are difficult, if not impossible to quantify. Of these features food  
18 supply is the most important and one of the most problematic to measure. While energy supply in the form of particle  
19 flux to the system can be measured, the effect of differences in net supply on feeding opportunity in particular species of  
20 higher animal is very difficult to estimate. For this reason it is advantageous to minimise the potential effect of spatial  
21 variability in surface production by collecting all data within a limited geographical range.

22  
23 In this study we present new information on the whole-animal and aerobic muscle metabolism of the Kaup's  
24 arrowtooth eel, *Synphobranchus kaupii* Johnson 1862. The known depth range of this eurybathic species is enormous  
25 (235-3200 m) and spans the transition from well-lit surface waters to the darkness of the lower continental slope. The  
26 data presented here are for fish captured or observed in the Porcupine Seabight, Northeast Atlantic. *In situ* video

1 observations of routine and burst swimming speeds and metabolic rate measurements were obtained geographically and  
2 temporally close to each other and to the trawling which obtained animals for *in vitro* analyses.

### 3 **Methods**

#### 4 Study area

5 Lander experiments and trawls took place in the Porcupine Seabight, North East Atlantic Ocean (Figure 1), at depths of  
6 775-2467 m. The majority of the work centred along the 1000 m contour running from the coral reef areas of the  
7 “Belgica mounds province” (51°30’N, 11°45’W), south to the Goban Spur. Experiments took place between 21st  
8 September 2000 and 23rd March 2002 with three cruises in the Autumn (August-October) and two in the Spring (March  
9 and April).

#### 10 Lander operations

11 Observations of fish behaviour and swimming speed were made using downward-looking video cameras mounted above  
12 the seafloor on the ISIT (Battle et al. 2002) and Sprint (Bailey et al. 2003) lander systems as previously described.  
13 Metabolic rate measurements were made *in situ* using the FRESP autonomous respirometer lander (Bailey et al. 2002).  
14 Temperature and current meter recordings were made by acoustic current meters (Sensotec or Nortec Aquadopp,  
15 Norway) mounted on the ISIT and Sprint landers. Temperature was also recorded by the FRESP oxygen electrode. Each  
16 lander was allowed to free-fall to the seabed, and operated autonomously for periods of up to 12 h, during which time  
17 animals were attracted to bait (mackerel, *Scomber scombrus*) mounted in the centre of the field of view of the cameras.  
18 On one ISIT deployment the bait was enclosed in 5 cylindrical traps (diameter 100 mm, length 350 mm) with tapering  
19 wire mesh entrances. The onboard computers controlled video recording and other operations. At the end of the  
20 experiment the landers were recalled to the surface by acoustic commands, which caused the landers to drop ballast  
21 weights and float up under buoyant moorings. Full descriptions and explanations of the individual landers (see  
22 references above) and the operation of autonomous landers in general (Priede and Bagley 2000) have been published  
23 previously.

1 Filming and video analyses

2 The cameras on all three landers made digital video recordings. Sprint and FRESP recordings were of a total duration of  
3 61 min, in 1 min recording sequences, illuminated during recording by twin 75 or 50 W lamps respectively. ISIT  
4 recorded in 3 min sequences, with illumination by a single 25 W lamp for one 15 s period per recording sequence. Full  
5 details of the camera systems have been provided previously (Bailey et al. 2002; Battle et al. 2002; Bailey et al. 2003).

6  
7 For analysis of routine swimming activity, digitised video sequences of eels swimming in a straight line and  
8 close (<30 cm) to the scale reference, were played back frame-by-frame on a PC. The x,y coordinates of the tip of the  
9 eel's snout and tail were selected manually from each frame and recorded using a program in Visual Basic 4.0 (Microsoft  
10 Inc. USA). Digitising "noise" was removed from the coordinate data using moving averages, with the smooth-width  
11 optimised according to the criteria of Wakeling and Johnston (1998). The displacement of the tip of the snout in the x  
12 and y directions was calculated from the smoothed coordinates and differentiated with respect to time to give over-  
13 ground swimming velocity in each direction. Current velocity in each direction was then deducted from swimming  
14 velocity to give velocity through the water. Total (resultant) over-ground ( $U_g$ ,  $m \cdot s^{-1}$ ) and through-water ( $U_w$ ,  $m \cdot s^{-1}$ )  
15 velocities were then calculated from the x and y values. Length-specific velocities were calculated using measurements  
16 of total length ( $L$ , m) taken from the video recordings and are denoted by  $\hat{U}_g$  and  $\hat{U}_w$  (see also Appendix A: Glossary).

17  
18 Mean tail beat frequency ( $F$ , Hz) was calculated for each sequence from the period for complete tail beat cycles  
19 and used to provide an independent estimate of through-water velocity using the formula below (Videler 1993).

20

21 1) 
$$\hat{U}_w = 0.55 \cdot F$$

22

23 Power output required for steady swimming ( $P$ ,  $W \cdot kg^{-1}$ ) was estimated using the following formula (Alexander  
24 1999), where  $M$  is total wet weight (kg) of the observed animal estimated from the measured length of the eel and the  
25 length-weight relationship obtained from trawl samples (see results).

26

1 2) 
$$P = \frac{0.1 \cdot M^{0.67} \cdot U_w^3}{M}$$

2

3 Velocities and accelerations during burst swimming are denoted by  $U_{burst}$  ( $m \cdot s^{-1}$ ) and  $A_{burst}$  ( $m \cdot s^{-2}$ )  
 4 respectively. These data were obtained from the digitised positions of the eel centre of mass in 6 video sequences of  
 5 spontaneous escape responses, using a purpose-designed program in Mathematica (Wolfram Scientific, USA). The  
 6 estimated inertial power ( $P_{inert}$ , W) required to support the movements observed was calculated from fish mass (+ virtual  
 7 mass,  $M \cdot 0.2$ ),  $A_{burst}$  and  $U_{burst}$  (Bailey et al. 2003).

8

9 3) 
$$P_{inert} = M \cdot U_{burst} \cdot A_{burst}$$

10

11

12 All methods were identical to those used by Bailey (2003), with the exception that total power output could not  
 13 be calculated because no data was available on the hydrodynamic efficiency of burst swimming in eels.  
 14

15 Respirometry

16 Closed-box respirometry measurements of 4 fish were made in a single incubation at 1500 m (see Results for details).  
 17 The FRESF lander trapped the eels within the respirometry chamber and measured the chamber water oxygen  
 18 concentration ( $C_w O_2$ ,  $ml \cdot l^{-1}$ ) at 44 min intervals using an oxygen electrode (SBE-23B, Seabird Inc., USA). The  
 19 electrode was recalibrated by reference to the ambient oxygen concentration immediately before and after each chamber  
 20 measurement. Control measurements without animals showed that the oxygen consumption by microfauna and the  
 21 oxygen electrode were negligible. Full details of the equipment used are provided by Bailey et al (2002).

22

23 The total oxygen consumption rate of all fish within the chamber ( $\square C_w O_2 \cdot VOL_{resp} \cdot t$ ,  $ml \cdot h^{-1}$ ) was used to  
 24 estimate the oxygen consumption by individuals ( $VO_2$ ,  $ml \cdot h^{-1}$ ). As the fish were lost from the chamber during lander  
 25 recovery the wet mass of the trapped eels ( $M$ , kg) was calculated from  $L$  (measured in the video recordings) and the

1 length-weight relationship of trawl-caught fish. Average body mass specific oxygen consumption ( $MO_2$ ,  $\text{ml} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$ )  
2 was calculated from  $VO_2$  using the average value of  $M$ .

### 3 Trawling and sample processing

4 Fish were captured using a Semi-Balloon Otter Trawl (Haedrich and Merrett 1988), fished on a single warp.  
5 Immediately following recovery of the net all fish were placed on ice, identified to species level, weighed and measured,  
6 and placed in a coldroom at 2-4°C until sampling. All animals were given a unique ID code, allowing assays to be  
7 undertaken blind but ensuring that the animal data could be linked to the trawl information (date, depth etc.). Muscle  
8 samples were collected within 3 h of trawl recovery (a maximum of approximately 7 hours after capture for animals  
9 caught at the beginning of the deepest trawls).

### 10 Determination of metabolic enzyme activities

11 The activities of lactate dehydrogenase (LDH, EC 1.1.1.27 lactate:NAD<sup>+</sup> oxydoreductase), malate dehydrogenase  
12 (MDH, EC 1.1.1.37, L-malate:NAD<sup>+</sup> oxydoreductase), pyruvate kinase (PK, EC 2.7.1.40, ATP:pyruvate  
13 phosphotransferase) and citrate synthase were measured in the white muscles sampled from the epaxial region (n=25-29).  
14 Muscles were dissected from freshly caught specimens and frozen (-80°C) aboard ship until assays were carried out.  
15 Muscles were homogenised with an electronic homogeniser (CATX620) in cold Tris-HCl buffer (10 mM), pH 7.5 at 4°C.  
16 Homogenates were centrifuged (2500 g, 4°C, 15 min) and supernatants preserved for the assays. All assays were  
17 performed at 4°C using standard methods (Childress and Somero, 1979) that were adapted to a 96-well microplate reader  
18 (Titertek Multiskan, Labsystems). Chemicals were from Sigma unless specified. All assays were performed in triplicates.

19

20 *LDH assay:* LDH activity was calculated from the consumption of NADH with pyruvate as substrate. Diluted  
21 samples (20  $\mu\text{l}$ ) were added to a 180  $\mu\text{l}$  mixture containing 100 mM KCl, 2 mM sodium pyruvate and 0.15 mM NADH in  
22 80 mM Tris-HCl buffer, pH 7.5 (4°C). NADH consumption was monitored at 340 nm. *MDH assay:* Oxaloacetate (20  
23  $\mu\text{l}$ , 0.5 mM) was added to 180  $\mu\text{l}$  of 100 mM Tris-HCl buffer (pH 8.0, 4°C) containing 100 mM KCl and 0.2 mM  
24 NADH. NADH consumption was monitored at 340 nm. *PK assay:* In this assay, the conversion of phosphoenolpyruvate  
25 into pyruvate was followed by the LDH-catalysed conversion of pyruvate into lactate and the concomitant consumption

1 of NADH. For this, samples (20  $\mu$ l) were added to 180  $\mu$ l of a Tris-HCl buffer (80 mM, pH 7.5 at 4°C) solution  
2 containing 10 mM MgSO<sub>4</sub>, 0.1 mM fructose 1,6-diphosphate, 1 mM phosphoenolpyruvate, 5 mM ADP, 20 U · ml<sup>-1</sup>  
3 rabbit muscle LDH (Roche, Basel) and 0.15 mM NADH. *CS assay*: Twenty microlitres of oxaloacetate (0.5 mM) was  
4 added to a 180  $\mu$ l of a solution containing acetyl-coenzyme A 0.2 mM and 0.1 mM DTNB in Tris-HCl (pH 8.0 at 4°C)  
5 and the sample. The decarboxylation of acetylCoA was followed at 412 nm.

## 6 Statistics

7 All animals were pooled across cruises. Scaling relationships were determined using linear and power law least-squares  
8 regressions as appropriate. Depth and inter-specific differences were determined using ANOVA, with and without fish  
9 total length ( $L$ , m) as a covariate.

10

## 11 **Results**

12 *Synphobranchus kaupii* were abundant (>50 individuals) in all trawls in the Porcupine Seabight from 775 m (the  
13 shallowest undertaken) to 2023 m with occasional individuals being captured at depths of up to 2500 m (Figure 2). The  
14 maximum haul was 1086 individuals at 1200 m (an estimated abundance of 11.4 individuals per 1000 m<sup>2</sup>). Mean total  
15 length ( $L$ , m) of the fish caught in the trawls was 0.34 m, with mean total wet mass ( $M$ ) of 0.05 kg.  $L$  increased  
16 significantly with increasing depth ( $L = -0.0859 + 0.0003 \cdot \text{depth (m)}$ ,  $r^2 = 0.48$ ,  $F_{2944} = 2745$ ,  $p < 0.001$ ), so that animals  
17 living at 2000 m were twice the size of those at 1000 m (Figure 2). Length-weight relationships were determined from  
18 pooled trawled animals and took the form  $M = 1.28L^{3.6}$  ( $r^2 = 0.94$ ,  $F_{1255} = 18058.3$ ,  $p < 0.001$ ). There were no significant  
19 differences between the mean length of fish caught by trawl or observed by camera at any depth where both types of data  
20 were obtained.

## 21 Foraging behaviour

22 The peak number of eels visible in the field of view of the baited cameras was highly variable between deployments from  
23 11 to 50 eels, with the number visible in the first light sequence (<12 minutes after landing) averaging  $16.5 \pm 7.5$  ( $\pm 1$   
24 s.e.) individuals. The time to peak numbers was also variable, but always within the first hour of the arrival of the lander

1 on the seafloor. The number of eels present reduced over time and the number of eels in the field of view of the camera  
2 was significantly lower at the end of the 15 s video sequences than at the start (n = 6 deployments, Paired t-tests,  $df \geq 17$ ,  
3  $t \geq 2.1$ ,  $p < 0.05$ ). A small number of other large scavenging animals co-occurred with *Synaphobranchus kaupii*,  
4 including the hagfish *Myxine ios*, and unidentified sharks and crabs. The tube traps obtained large numbers of  
5 amphipods (*Eurythenes gryllus*).

## 6 Swimming speeds

7 Over-ground ( $U_g$ ) and through-water ( $U_w$ ) routine swimming velocities were determined from 32 video sequences.  
8 Animal total length ( $L$ ) ranged from 0.13 to 0.58 m (it was not possible to determine whether any animal was filmed  
9 more than once). Maximum and mean measured values for each sequence are denoted by the subscripts  $_{max}$  and  $_{mean}$   
10 respectively. Length-specific velocities were calculated and are denoted by  $\hat{U}$ . For example “maximum length-specific  
11 through-velocity” is denoted by  $\hat{U}_{w max}$ . The average values of  $U_{w mean}$  and  $\hat{U}_{w mean}$  were  $0.14 \pm 0.06 \text{ m} \cdot \text{s}^{-1}$  and  $0.55 \pm 0.03$   
12  $L \cdot \text{s}^{-1}$  ( $\pm 1$  s.e.) respectively. These velocities, tailbeat frequency ( $F$ , Hz) and power output ( $P$ , W) scaled significantly  
13 with body length ( $L$ , m). See Figure 3 for details and scaling relationships. There was no relationship between fish  
14 length and specific power output ( $P_{spec}$ ,  $\text{W} \cdot \text{kg}^{-1}$ ).

15  
16 Velocities and accelerations during burst swimming are all “through-water” and are denoted by  $U_{burst}$  ( $\text{m} \cdot \text{s}^{-1}$ )  
17 and  $A_{burst}$  ( $\text{m} \cdot \text{s}^{-2}$ ) respectively (Figure 4). Average peak values of  $U_{burst}$  and  $A_{burst}$  were  $0.69 \pm 0.16 \text{ m} \cdot \text{s}^{-1}$  and  $3.06 \pm 0.71$   
18  $\text{m} \cdot \text{s}^{-2}$  ( $\pm 1$  s.e.) respectively, and increased with fish length but not significantly so. When compared to data for  
19 *Antimora rostrata* using ANOVA (with and without  $L$  as a covariate), there was no significant difference between the  
20 species for either variable. The estimated inertial power ( $P_{inert}$ ) required to support the movements observed was  
21 calculated from the product of fish mass (+ virtual mass),  $A_{burst}$  and  $U_{burst}$  (Bailey et al. 2003).  $P_{inert}$  scaled significantly  
22 with fish length ( $P_{inert} = 15.69 \cdot L^{6.4}$ ,  $r^2 = 0.75$ ,  $F_4 = 11.69$ ,  $p = 0.027$ ), but given the small amount of data available and  
23 the assumptions intrinsic in the calculation this relationship should be treated with some caution.

24

## 1 Metabolic rate measurements

2 One incubation was performed, with 4 eels in the trapping respirometry chamber ( $L = 0.39 - 0.59$  m). The total rate of  
3 oxygen consumption ( $\Delta C_w O_2 \cdot VOL_{resp} \cdot t$ ,  $ml \cdot h^{-1}$ ) of all the eels in the trap was  $11.8 \text{ ml} \cdot h^{-1}$ , giving a mean  $VO_2$  for the  
4 4 individuals of  $3.0 \text{ ml} \cdot h^{-1}$ . The estimated total mass of the eels was  $0.38 \text{ kg}$ , giving a mean  $MO_2$  of  $31.6 \text{ ml} \cdot \text{kg}^{-1} \cdot h^{-1}$ .  
5 The fish were active within the chamber during video recordings during incubation.

## 6 Metabolic enzymes

7 Mean metabolic enzymes activities measured on white muscle isolated from 23-29 specimens are shown in Table 1. A  
8 marked scaling of all four enzymatic activities was observed (Figure 5). In all cases, the measured activities decreased  
9 exponentially with fish length. The scaling equations of CS, LDH, MDH and PK were as follows:  $A_{CS} = 0.22 \cdot L^{-1.37 \pm 0.43}$   
10 ( $r^2 = 0.60$ ;  $p < 0.001$ );  $A_{LDH} = 54.54 \cdot L^{-1.19 \pm 0.25}$  ( $r^2 = 0.43$ ;  $p < 0.001$ );  $A_{MDH} = 8.27 \cdot L^{-0.93 \pm 0.40}$  ( $r^2 = 0.18$ ;  $p = 0.027$ );  $A_{MDH}$   
11  $= 0.015 \cdot L^{-1.46 \pm 0.38}$  ( $r^2 = 0.37$ ;  $p = 0.002$ ), where  $L$  is total length (m) and  $A$  is activity in International units  $\cdot$  g wet  
12 weight $^{-1}$ . There was no significant correlation between depth of capture and the activities of the four enzymes when fish  
13 length was taken into account.

## 14 **Discussion**

### 15 Activity levels and foraging behaviour

16 *Synphobranchus kaupii* arrive at bait more quickly and in greater numbers than other scavenging animals in the  
17 Porcupine Seabight and abyssal plain as described by Priede et al (1994) and Collins et al (1999). With average through-  
18 water swimming speeds of  $0.15 \text{ m} \cdot \text{s}^{-1}$  *S. kaupii* swam slightly slower than the morid *Antimora rostrata* and at similar  
19 speeds to the grenadier *Coryphaenoides armatus* (Collins et al. 1999). However, the present study included fish smaller  
20 than the *C. armatus* and *A. rostrata* investigated above, and when length-specific velocities are compared the average  
21 swimming speed attained by *S. kaupii* ( $0.55$  body lengths  $\cdot$   $\text{s}^{-1}$ ) was 10% higher than that of *A. rostrata* and almost three  
22 times higher than the mean length-specific velocity of *C. armatus*. The above comparisons are between video analysis of  
23 animals close to the bait (the present study) and acoustic tracking of fish at ranges of 30 to 500 m (Collins et al. 1999),  
24 however new video data appear to support these conclusions (S. Unsworth, unpublished data). The above comparisons

1 show that *S. kaupii* and *A. rostrata* have similar routine activity levels, and comparisons of their absolute burst  
2 performances (peak velocity or acceleration) are also similar.

3  
4 Comparisons with laboratory studies of European and American eels (*Anguilla anguilla* and *Anguilla rostrata*)  
5 show that *S. kaupii* swam with similar tail-beat frequencies and through-water velocities (Gillis 1998; Août and Aerts  
6 1999) while McCleave and Arnold's (1999) study of free-swimming European eels in the North Sea recorded greater  
7 length-specific and absolute through-water swimming speeds once fish length is taken into account. Differences in water  
8 temperature and the lack of overlap in fish size between this and the present study make these data hard to compare, but  
9 it would appear that the differences in performance are larger than can be explained by temperature.

10  
11 Although slow-moving in comparison with *Anguilla anguilla*, *Synphobranchius kaupii* is the most active  
12 benthopelagic deep-water fish yet studied. These performance levels were associated with high specific white muscle  
13 lactate dehydrogenase activities when compared to some other studies in deep-sea scavenging fish (Sullivan and Somero  
14 1980; Siebenaller et al. 1982). The specific activities of white muscle pyruvate kinase, malate dehydrogenase and citrate  
15 synthase were all similar to the values for macrourids presented by Siebenaller et al (1982), although differences in  
16 technique, and in particular the higher temperature used in the previous study make detailed comparisons difficult.  
17 Drazen's (2002) CS and LDH activity measurements in Pacific *Coryphaenoides armatus* were similar to those recorded  
18 in the present study, while *C. acrolepis* CS activities were lower than those presented here for *S. kaupii*.

19  
20 In direct comparisons of white muscle, using identical techniques, *S. kaupii* had higher activities for all 4  
21 enzymes than other deep-living species including *C. armatus* and *A. rostrata* (B. Genard, unpublished). At present there  
22 is no evidence that these high enzyme activities support high performance from white muscle during burst swimming, but  
23 some use of white muscle during routine activity may account for the high routine swimming speeds observed. The  
24 likely high energetic cost (Août and Aerts 1999) of the rapid rearward swimming observed in this species is another  
25 potential reason why high LDH activities are required.

1 Comparisons of the metabolic rate of *S. kaupii* with rates from other deep-sea fish reveal that the *in situ* oxygen  
2 consumption rates of the trapped eels were higher than those of the hagfish *Eptatretus deani* and the deep-sea grenadiers  
3 *Coryphaenoides acrolepis* and *C. armatus* measured previously (Smith and Hessler 1974; Smith 1978; Bailey et al.  
4 2002). The comparisons with *C. acrolepis* and *E. deani* are particularly interesting as the metabolic rate measurements  
5 were obtained at a similar depth (1230 m) on the continental slope of the eastern Pacific, and at a similar temperature  
6 (Smith and Hessler 1974). The metabolic rates of these fish were only 2.4 and 2.2 ml · kg<sup>-1</sup> · h<sup>-1</sup> respectively, compared  
7 to 31.6 ml · kg<sup>-1</sup> · h<sup>-1</sup> for the eels measured here. The difference in mass, and likely effects of activity and post-prandial  
8 Specific Dynamic Action (SDA) on the metabolism of the eels could account for the difference between *C. acrolepis* and  
9 *S. kaupii*. As noted above, muscle CS activities are also lower in *C. acrolepis* than in *S. kaupii*. The order of magnitude  
10 difference in metabolic rate between *S. kaupii* and of *E. deani* is harder to explain as these animals were of similar sizes.  
11

12 For all these short term, *in situ*, experiments the true nutritional state of the fish cannot be known and so SDA  
13 might be present even in a fish that was not fed by the experimenter. The eels in the present study were active in the  
14 chamber, so these were not resting metabolic rates. High metabolic rates are not unprecedented in deep-living fish.  
15 Koyama et al (2002) undertook respirometry in a repressurised demersal fish (*Ebinania brephocephala*,  $M = 0.061.1$  kg)  
16 from 500 m. While on a maintenance diet this fish had a metabolic rate of 100 ml · kg<sup>-1</sup> · h<sup>-1</sup>, higher than that measured  
17 for *S. kaupii*, even when body size is taken into account. Studies in orange roughy (*Hoplostethus atlanticus*), based on  
18 food consumption, indicate metabolic rates of 110-140 ml · kg<sup>-1</sup> · h<sup>-1</sup> for juveniles and adults respectively (Bulman and  
19 Koslow 1992). These estimates are also higher than the oxygen consumptions measured here.  
20

21 The above comparisons are with deep-living but taxonomically distant species. European eels, *Anguilla*  
22 *anguilla*, of similar size to the *S. kaupii* used here, have been acclimated to similar pressures to those of the present study  
23 (101 ATA or equivalent to ~1000 m) by Sébert and his co-workers (1995). Once acclimated to elevated pressure the  
24 metabolic rates of the eels were below those recorded under atmospheric pressure (Sébert et al. 1995) and also lower than  
25 *S. kaupii*'s, given the difference in experimental temperatures. However, the oxygen consumption value reported in the  
26 present study falls within the published values for routine and active metabolic rates in *A. anguilla* (Froese and Pauly  
27 2003) indicating that deep-sea life has done little to depress metabolism in *S. kaupii*. *Synaphobranchus kaupii* has a

1 metabolic rate more similar to shallow-water European eels than to the deep-sea fish that live at the same depth in the  
2 Pacific Ocean (where synphobranchid eels are not dominant). There are clearly limitations to the resolution of the  
3 respirometry technique used here, with only a single measurement in four active animals of unknown nutritional state,  
4 but the basic finding that these eels have relatively high metabolic rates for demersal deep-sea fish is difficult to dispute.

5  
6 We hypothesise that some elevation of activity capacity and metabolism exists and is related to the habitat and  
7 ecology of *S. kaupii*. The trawl catches suggest that in the Porcupine Seabight *S. kaupii* are most abundant at 1000-1500  
8 m, an area associated with relatively strong current regimes and benthic communities such as sponge beds and coral reefs  
9 which are dependent on this hydrodynamic regime (Rice et al. 1990; Flach et al. 1998; De Mol et al. 2002; Howell et al.  
10 2002; Huvenne et al. 2003). Our data support these findings, showing that current velocities in excess of  $0.2 \text{ m} \cdot \text{s}^{-1}$  are  
11 common in this area. Observations of *S. kaupii* made from a submersible in the Bay of Biscay (NE Atlantic) by Uiblein  
12 et al (2002) showed that they were most common in turbulent waters, and where debris had accumulated on the bottom.  
13 *Synphobranchus kaupii* spent a greater proportion of their time swimming than the other species observed (Uiblein et al.  
14 2003), and the proportion moving was highest in areas that appeared to less food-rich (Uiblein et al. 2002). Use of  
15 anaerobiosis while burrowing (MacAvoy et al. 2002) is an alternative explanation for high LDH activities, though the  
16 evidence for high levels of routine activity for *S. kaupii* in this system is convincing.

17  
18 As an olfactory forager *S. kaupii* is dependent on currents to allow it to detect food odours, but the observed  
19 high degree of olfactory system development (Wagner 2002) is only adaptive if co-evolved with the ability to travel for  
20 long distances up-current in order to reach food, and before the food has been consumed by other animals. Strong  
21 currents disperse odour over a wide area, reducing the time between the arrival of carrion on the seafloor and detection  
22 by olfactory scavenger, but the disadvantages in terms of time to reach the bait outweigh the advantages unless fish can  
23 swim at more than twice the current velocity (Bailey and Priede 2002).

1 Scaling and ontogenetic changes

2 *Synphobranchus kaupii* is notable for the changes in distribution and muscle biochemistry undergone during ontogeny.  
3 Larger eels also live deeper, doubling in size between 1000 and 2000 m, and therefore probably experience progressive  
4 changes in selective pressure due to the changing physical and biological environment with age. It is likely that these  
5 changes are associated with the unusual scaling relationships observed.

6

7 With increased size it is common for muscle mass specific citrate synthase activity to fall, and this is seen in *S.*  
8 *kaupii*. Often in active fishes this change in muscle aerobic capacity are associated with a progressive increase in lactate  
9 dehydrogenase activity (Childress and Somero 1990; Somero and Childress 1990). In *S. kaupii* lactate dehydrogenase,  
10 malate dehydrogenase and pyruvate kinase activity all exponentially reduce with increases in body size. The  
11 consequences of this unusual change in muscle metabolism are not clear, as no unusual decreases in fish performance  
12 were detected from our video observations of routine and burst activity. Scaling of routine swimming performance is  
13 entirely conventional and similar to that reported previously (Brett 1965).

14

15 Similar ontogenetic changes in muscle biochemistry to those observed here have been reported where changes  
16 in habitat and behaviour occur with ontogeny (Siebenaller 1984), or where mobilisation of resources for reproduction  
17 competes with muscle maintenance (Garenc et al. 1999). As larger *S. kaupii* tend to live deeper the observed reductions  
18 in swimming performance and muscle metabolic power are likely to reflect both ontogenetic changes and adaptation to a  
19 progressively deeper habitat. However, we found no significant reduction of metabolic enzyme activities with increasing  
20 depth of capture, suggesting that the fish age rather than its depth of living is responsible for this fall in activity. The  
21 strong relationship between depth and fish length make these variables hard to disentangle as causal factors.

22

23 The unusual changes in muscle enzyme activity observed must be related to muscle use, and to the selective  
24 pressures on locomotion related to foraging and predator-prey relationships. Such selective pressures are affected by the  
25 abundance and types of predators and prey in the environment and any factors affecting their interaction frequency.  
26 *Synphobranchus kaupii* is a predator as well as a scavenger, and the characteristics and frequency of locomotor efforts  
27 during prey capture are strongly affected by the sizes of prey taken. Fish like *S. kaupii* that take progressively larger prey

1 as they grow larger (Gordon and Mauchline 1996) often show reductions in the increase in LDH activity during  
2 ontogeny, and may even show negative scaling (Garenc et al. 1999; Sherwood et al. 2002), possibly because fewer  
3 attacks are required for a given energy intake (Sherwood et al. 2002). Larger prey are likely to have higher burst  
4 swimming speeds, and while LDH is often (but not always) a correlate of burst activity capacity (Gibb and Dickson  
5 2002; Odell et al. 2003) this enzyme is not a direct factor affecting ATP supply during the short duration of fast-start  
6 swimming (much less than 1 s in most situations). The ontogenetic changes in white muscle enzyme activity here do not  
7 appear to affect peak performances during burst activity in *S. kaupii*. These findings suggest that changes in the  
8 frequency and duration of attacks are more important than the peak power outputs required in determining the optimum  
9 LDH activity in this species, and these changes could be brought about by progressive utilisation of larger prey items.

10  
11 A powerful factor affecting predator-prey interactions is light level (James and Heck Jr. 1994; Childress 1995).  
12 Uiblein et al (2002) understandably discounted light level as an important factor affecting *S. kaupii* below 1000 m, as  
13 downwelling light was expected to be absent or extremely weak. In the Porcupine Seabight only the smallest individuals  
14 of *S. kaupii* inhabit depths where downwelling light penetrates (Denton 1990; Herring 2002). However, many deep-sea  
15 animals have large, functional eyes (Wagner et al. 1998; Collin et al. 2000; Warrant 2000) and new data for the  
16 Porcupine Seabight reveals abundant but spatially heterogeneous benthic bioluminescence (E. Battle, unpublished).  
17 Although the effects of this bioluminescence on *S. kaupii* are not known, eels living as deep as 1500 m continued to react  
18 to the artificial light provided by the landers, and avoided the illuminated area. It appears likely that during ontogeny the  
19 eels move into deeper water, away from bioluminescent and downwelling light, resulting in some of the reduction in  
20 muscle metabolic power observed. Certainly some decline in eye function with ontogeny in *S. kaupii* is indicated by a  
21 progressive reduction in the length of the Rod Outer Segments of the retina (Fröhlich and Wagner 1996).

## 22 23 Summary

24 The demersal deep-sea environment contains diverse fish assemblages, with a wide range of behavioural repertoires.  
25 This study demonstrates that the eel *Synaphobranchus kaupii* had swimming and muscle metabolic activities that were  
26 high for a deep-sea fish, probably in order to allow olfactory foraging in a high-current environment with abundant

1 bioluminescence. These data were supported by a single respirometry experiment in four fish that, although only a  
2 preliminary finding, showed high levels of oxygen consumption.

3

4           Scaling of energy supply to white muscle indicated an exponential decrease muscle metabolic capacity with  
5 growth. As no reduction in fish performance was observed we hypothesise that changes in muscle enzyme activity  
6 reflect ontogenetic shifts in the prey taken by this species resulting in reductions in the frequency and duration of feeding  
7 efforts. Acting in conjunction with the reductions in benthic light level which the fish experience as they move deeper  
8 during ontogeny, these changes are likely to create progressive changes in the selective pressures on the ability to sustain  
9 and recover from exercise.

10

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1 Table 1. Mean metabolic enzymes activities in white muscle of eels, *Synaphobranchus kaupii*.

Enzyme	Activity, Units · g wet weight <sup>-1</sup> (mean ± 1 s.e.)	N
Citrate synthase	0.61 ± 0.08	25
Lactate dehydrogenase	128.66 ± 11.46	28
Malate dehydrogenase	16.06 ± 1.89	26
Pyruvate kinase	2.89 ± 0.33	25

2

3 Specimens were obtained by OTSB trawling in the Porcupine Seabight, NE Atlantic. All enzyme activities were

4 measured at 4°C as described in the methods; values are presented as means with their error. N, number of specimens.

## 1 **Figure Legends**

2 Figure 1. Chart of the Porcupine Seabight (PSB) and Porcupine Abyssal Plain (PAP), North Atlantic. Lander operations  
3 and trawling were carried out in two main areas, the Belgica Mounds (BM) and Goban Spur (GS). These locations are  
4 denoted on the chart by the areas enclosed by the dotted lines. Bathymetric contours are at 500 m intervals, beginning at  
5 500 m depth. Progressively darker shading also indicates greater depth.

6

7 Figure 2. Mean lengths (black bars) and abundances (white bars) of the eel *Synaphobranchus kaupii* captured per trawl,  
8 divided into 500 m depth classes. Error bars are 1 S.E. The number of trawls from which the data were obtained is  
9 indicated above each bar. The greatest numbers of *S. kaupii* were captured between 1001 and 1500 m (average of 176.5  
10 eels · trawl<sup>-1</sup>), with the biggest single haul being 1086 individuals at a depth of 1200 m. No trawls were carried out below  
11 775 m. The average length of the eels captured increased with depth of occurrence (see text), and the overall mean size  
12 of eel was 0.34 m.

13

14 Figure 3. Scaling of routine swimming performance in the deep-sea eel *Synaphobranchus kaupii* filmed in the Porcupine  
15 Seabight, N. Atlantic. Parameters presented are A) tailbeat frequency ( $F$ , Hz), B) peak through-water velocity ( $U_w$ , m · s<sup>-1</sup>)  
16 and power output ( $P$ , W · kg<sup>-1</sup>). All three parameters scaled significantly with body size. Scaling relationships and  
17 statistics were:  $F = 0.46 \cdot L^{-0.53}$ ,  $r^2 = 0.49$ ,  $F_{30} = 29.04$ ,  $p < 0.001$ ;  $U_w = 0.25 \cdot L^{0.46}$ ,  $r^2 = 0.42$ ,  $F_{30} = 21.46$ ,  $p < 0.001$ ;  $P =$   
18  $0.002 \cdot L^{3.79}$ ,  $F_{30} = 160.39$ ,  $p = 0.002$ .

19

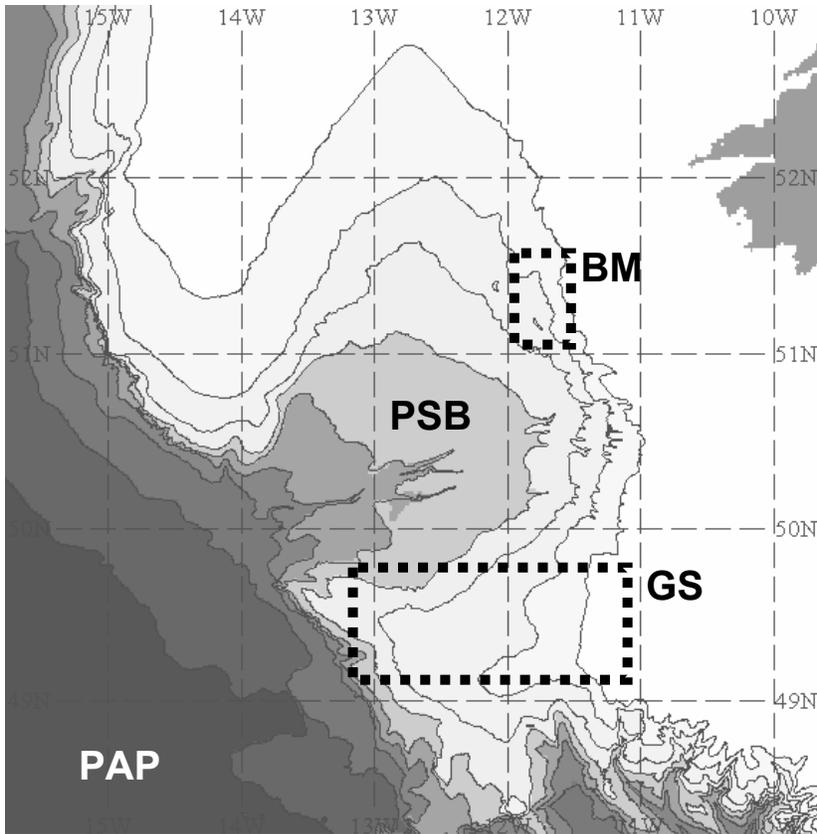
20 Figure 4. Velocity ( $U_{burst}$ ) and acceleration ( $A_{burst}$ ) of *Synaphobranchus kaupii* during spontaneous burst swimming  
21 filmed *in situ* at 1500 m. In this example the animal is moving at a velocity (solid line) of close to 0.17 m · s<sup>-1</sup>, before  
22 being startled and making an escape response. Acceleration (dotted line) peaks at 4.7 m · s<sup>-2</sup>, bringing the fish to a peak  
23 velocity of 1.0 m · s<sup>-1</sup>. The fish then rapidly decelerates before swimming away from the stimulus (another eel) at a  
24 speed of approximately 0.55 m · s<sup>-1</sup>, resuming routine swimming approximately 1.1 s after initiating its escape response.

25

26 Figure 5. Relationships between fish length ( $L$ , m) and white muscle enzyme activities for *Synaphobranchus kaupii*  
27 captured by Semi-balloon Otter Trawl in the Porcupine Seabight, N. Atlantic. All the presented relationships were

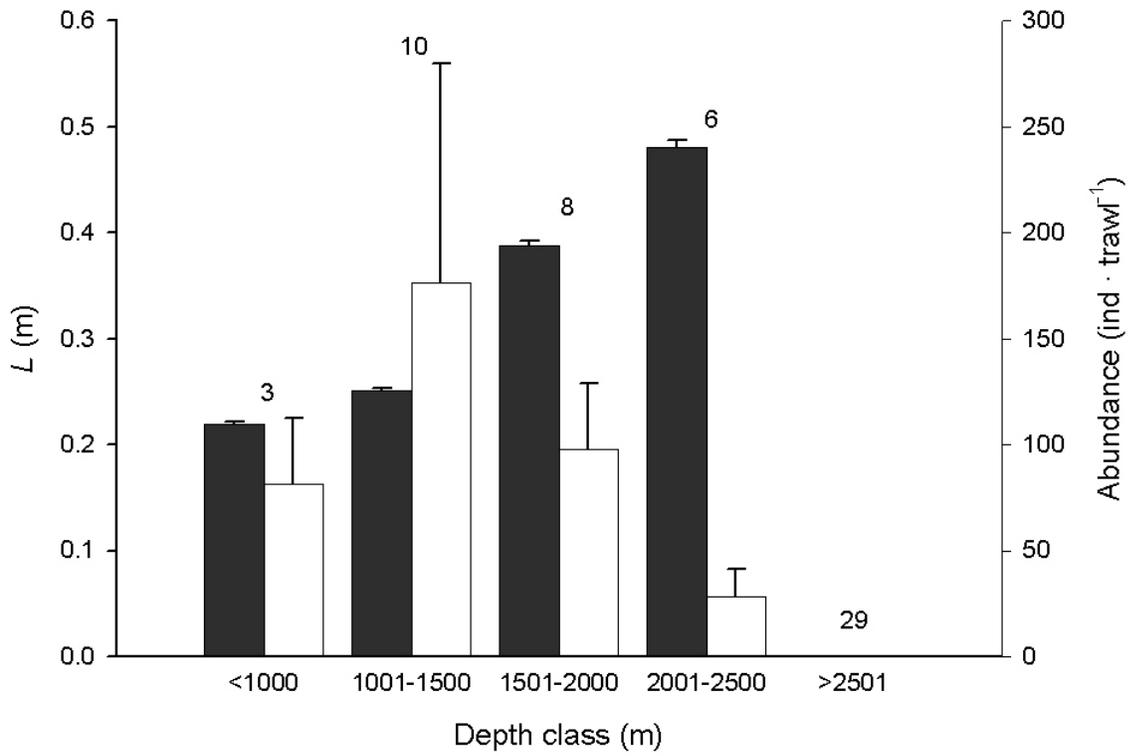
- 1 significant and are for A) Citrate synthase (CS); B) Lactate dehydrogenase (LDH); C) Pyruvate kinase (PK); D) Malate
- 2 dehydrogenase (MDH). See text for scaling relationships.

1 **Figure 1**



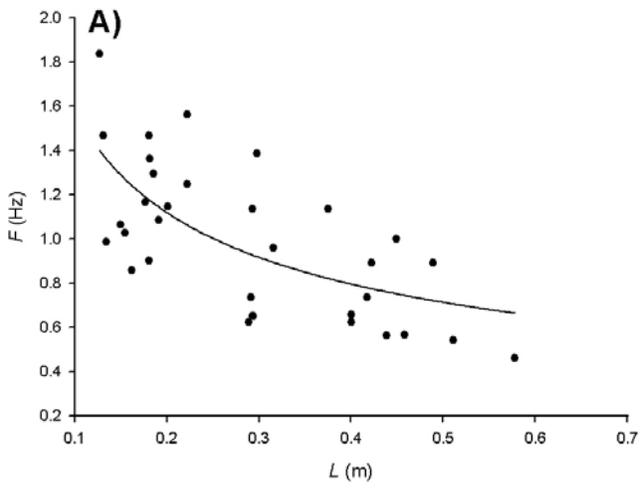
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1 Figure 2

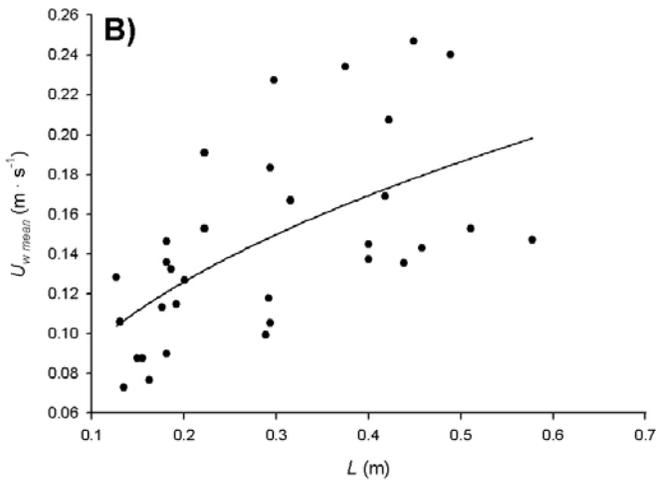


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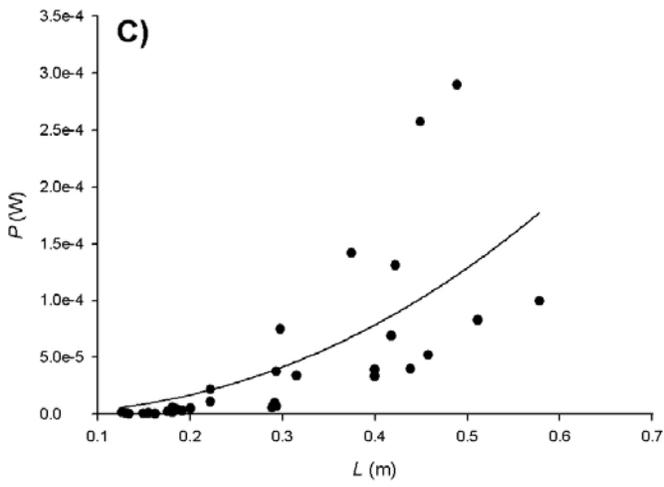
1 **Figure 3**



2

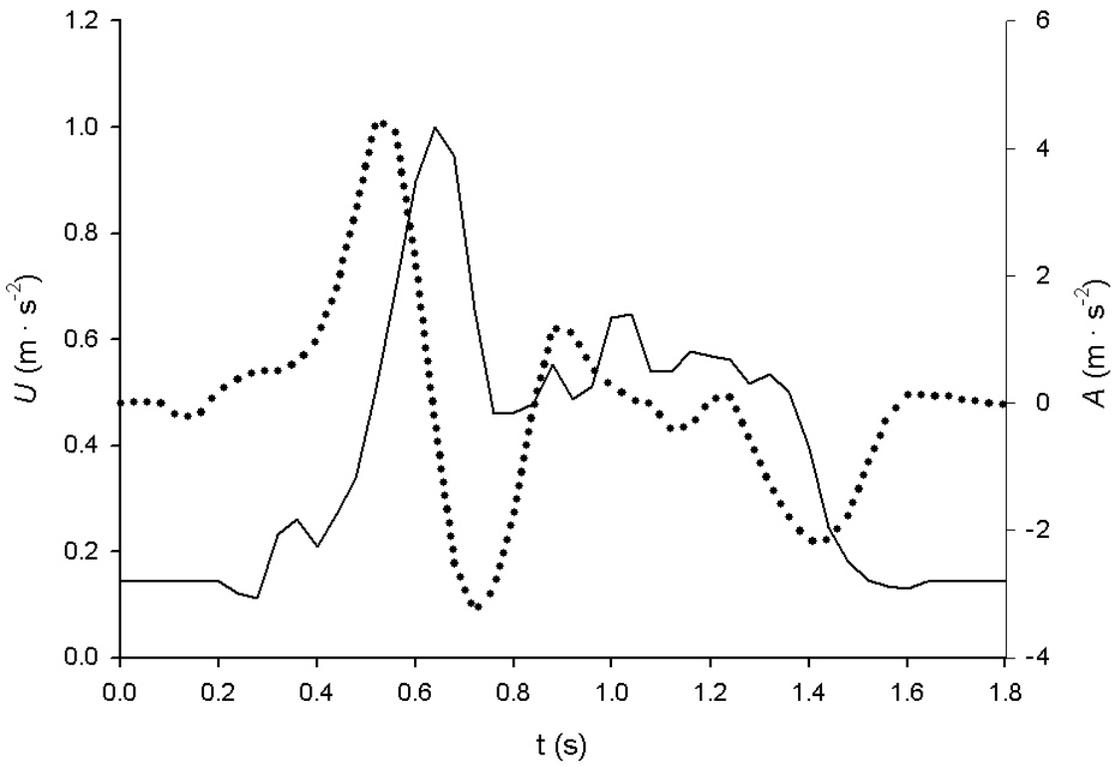


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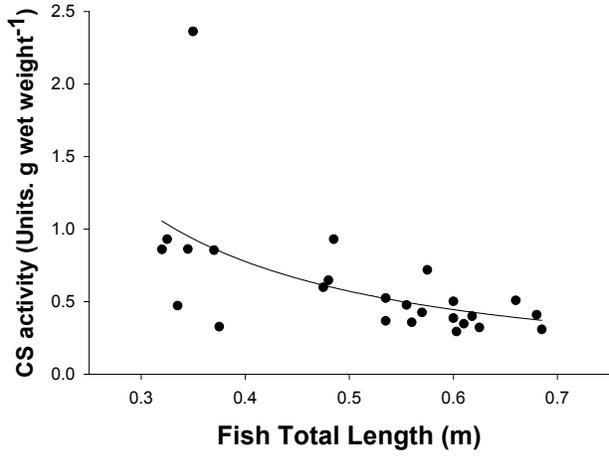
4

1 Figure 4



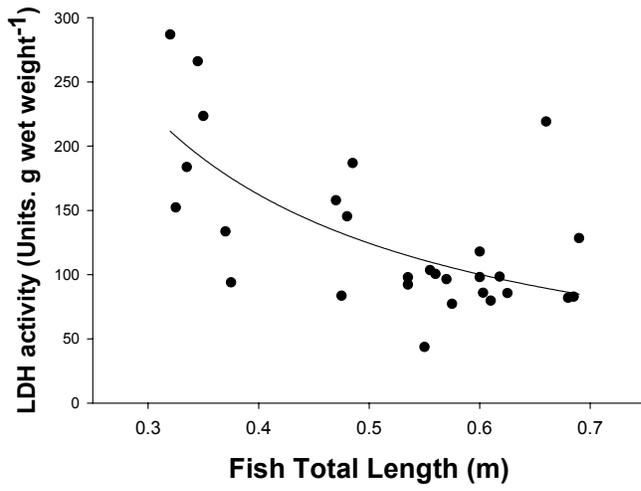
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1 **Figure 5A)**



2

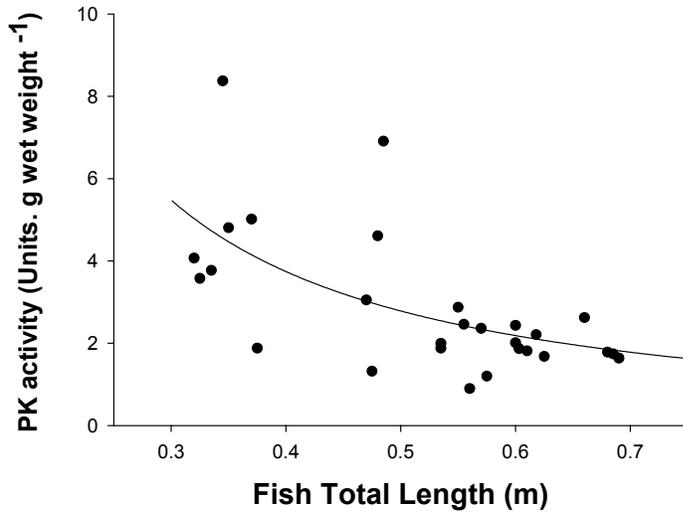
3 **B)**



4

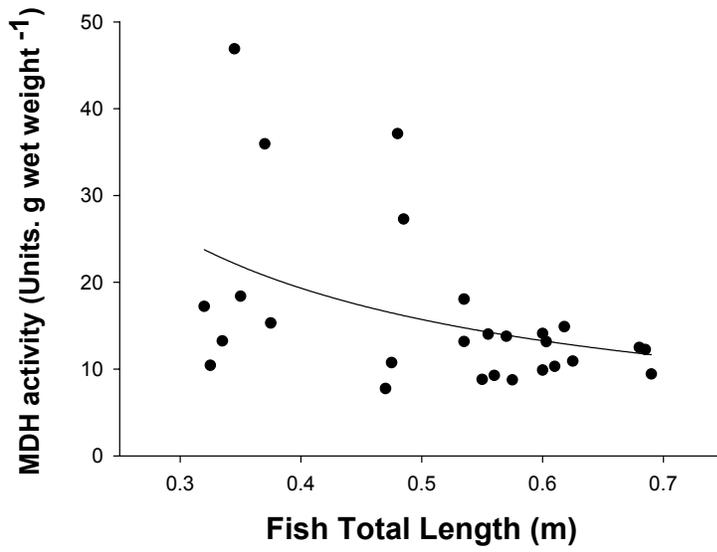
5

1 C)



2

3 D)



4

1 **Appendix A: Glossary**

2  $L$ , fish maximum length (m);  $M$ , fish wet mass (kg);  $F$ , tail-beat frequency (Hz);  $U$ , swimming velocity ( $\text{m} \cdot \text{s}^{-1}$ );  $U_g$ ,  
3 over-ground routine swimming velocity ( $\text{m} \cdot \text{s}^{-1}$ ),  $\hat{U}_g$ , length-specific over-ground routine swimming velocity ( $L \cdot \text{s}^{-1}$ );  $U_w$ ,  
4 through-water routine swimming velocity ( $\text{m} \cdot \text{s}^{-1}$ ),  $\hat{U}_w$ , length-specific through-water routine swimming velocity ( $L \cdot \text{s}^{-1}$ );  
5  $P$ , power output of routine swimming (W);  $P_{spec}$ , body mass specific power output of routine swimming ( $\text{W} \cdot \text{kg}^{-1}$ );  $U_{burst}$ ,  
6 peak swimming velocity of burst swimming ( $\text{m} \cdot \text{s}^{-1}$ );  $A_{burst}$ , peak acceleration during burst swimming ( $\text{m} \cdot \text{s}^{-2}$ );  $P_{burst}$ ,  
7 peak power output of burst swimming (W);  $t$ , respirometry incubation time (h);  $VOL_{resp}$ , respirometer volume (l);  $C_wO_2$ ,  
8 respirometry chamber oxygen concentration ( $\text{ml} \cdot \text{l}^{-1}$ );  $\Delta C_wO_2$ , change in respirometry chamber oxygen concentration ( $\text{ml}$   
9  $\cdot \text{l}^{-1} \cdot \text{h}^{-1}$ ).  $VO_2$ , individual eel oxygen consumption ( $\text{ml} \cdot \text{h}^{-1}$ );  $MO_2$ , mass specific oxygen consumption ( $\text{ml} \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$ );  
10 CS, citrate synthase; LDH, lactate dehydrogenase; MDH, malate dehydrogenase; PK, pyruvate kinase,  $A_{CS}$ , citrate  
11 synthase activity (International Units  $\cdot \text{g wet weight}^{-1}$ );  $A_{LDH}$ , lactate dehydrogenase activity (International Units  $\cdot \text{g wet}$   
12  $\text{weight}^{-1}$ );  $A_{MDH}$ , malate dehydrogenase activity (International Units  $\cdot \text{g wet weight}^{-1}$ );  $A_{PK}$ , pyruvate kinase (International  
13 Units  $\cdot \text{g wet weight}^{-1}$ ).