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Pressure resistance of aerobic metabolism in eels from different water environments

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Abstract

Eels from different locations were tested comparing their energetic capacities to migrate by studying muscle (red and white) aerobic metabolism. As the migratory activity corresponds to a lengthy swimming activity at depth, their pressure resistance was evaluated by considering fish response to compression, mitochondrial respiration measured under pressure (101 ATA) and cytochrome *c* oxidase after 3 days under pressure. The results show that only fish from two of the sites have the metabolic capacities to cope with the high pressure encountered during migration.
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1. Introduction

The eel has a particular life cycle, growing in the rivers and lakes then migrating for 6000 km to reproduce somewhere in the ocean, probably in the Sargasso Sea (Tesch, 2003). The migratory activity corresponds to important changes in the fish environment, mainly the transfer from fresh temperate water to cold sea water. Such a transfer is accompanied by a long swimming activity performed at depths estimated between 600 and 1000 m or perhaps less (McCleave and Arnold, 1999; Tesch, 2003). The swimming activity obviously involves muscle, mainly red muscle i.e. aerobic metabolism. Recent studies published in this journal (Sébert and Theron, 2001; Theron and Sébert, 2003) have shown the potential effects of 101 ATA (corresponds to a 1000 m depth) hydrostatic pressure on mitochondrial respiration. All fish are not equal when confronted by pressure (Somero, 1991; Macdonald, 1993; Randall and Farrell, 1997; Sébert, 1997, 2003) and it appears that eels have developed strategies allowing them to optimise their energy metabolism in order to reduce the deleterious effects of pressure (Sébert and Theron, 2001; Sébert et al., 1998; Sébert, 2003). However, regarding the eel, *Anguilla anguilla*, a recent study seems to show that, due to the energetic constraints of the migratory activity (Van Ginneken and Van den Thillart, 2000; Boëtius and Boëtius, 1980; Svedäng and Wickström, 1997), they do not all have the capability to migrate, as it depends on their

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locations (Tsukamoto et al., 1998; Vettier et al., 2003). Such an observation cannot be ignored when considering the dramatic decline in the eel population in Europe (number of European eels has dropped 99% since 1978) and everywhere in the world. Overfishing (elvers and adults) may be a cause but we cannot exclude the fact that pollution or other environmental factors encountered during the life cycle alter the fitness of the fish and/or modify its genetic abilities. Consequently, as mitochondrial respiration appears to be a good index for migratory capabilities (Sébert, 2003), we have studied the aerobic energy metabolism of European eels from different water environments in order to test their pressure resistance.

2. Material and methods

2.1. Animals

Fish were obtained from different locations corresponding to different water environments: Loire river, Certes marsh, Sainte Eulalie current in France, and Balaton lake in Hungary. At their arrival in Brest, the fish were stored in polyethylene tanks fed with running aerated tap water. One week after, the fish were slightly anaesthetised (*Eugenia caryophyllata,* clove oil, 1 ml for 10 l of water; ethanol, 10 ml for 10 l of water) in order to perform the morphometric measurements shown in Table 1.

2.2. Morphometric data

Body length, BL, and body mass, BM, horizontal and vertical eye diameters (EDh, EDv, mm) and pectoral fin length (PFL, mm) were measured. BL was measured by positioning the fish in a graduated gutter and eye diameters using a calliper-square. Different indexes were calculated from these data: Body Mass Index ($BMI = BM \times BL^{-2}$), Condition Factor $CF = (BM/BL^3) \times 10^5$, Ocular Index $OI = 100 \times [(ODh + ODv)/4]^2 \times (\pi/BL)$ and Pectoral Fin Index $PFI = 100 \times (PFL/BL)$ as proposed by Fulton (in Ricker, 1975), Pankhurst (1982); Durif (2003), respectively. The density was determined from the body mass and the volume displaced by the eel when completely immersed. Body surface was determined by covering the fish with aluminium paper, then weighing it. Water content of muscle and gills was calculated after

Table 1
Eel morphometric and metabolic data at atmospheric pressure (1 ATA)

	LOIRE	BALATON	Ste EULALIE	CERTES
N	12	13	18	13
Sex	F	F	F	M
Stage	Silver	Yellow	Silver	Silver
Length (cm)	72.1 ± 1.5	48.4 ± 5.9	62.7 ± 1.7	40.1 ± 17.9
Body mass (g)	659 ± 36	154 ± 6	430 ± 39	98 ± 15
BMI (kg m^{-2})	1.26 ± 0.03	0.66 ± 0.02*	1.05 ± 0.04*	0.57 ± 0.03*
Condition factor	0.17 ± 0.00	0.14 ± 0.00*	0.17 ± 0.00	0.14 ± 0.00*
Body surface (cm^2)	924 ± 34	351 ± 8.6	691 ± 40	262 ± 25
Density (g L^{-1})	ND	1.01 ± 0.01	1.04 ± 0.01*	1.15 ± 0.03
Ocular index	9.85 ± 0.24	4.4 ± 0.3*	11.2 ± 0.4*	10.3 ± 0.7
Pectoral fin index	5.1 ± 0.5	4.6 ± 0.1	5.5 ± 0.1	5.7 ± 0.1
Muscle water content (%)	62.4 ± 0.9	67.2 ± 1.9*	65.6 ± 6.5	66.9 ± 1.2*
Gill water content (%)	76.7 ± 1.1	80.8 ± 0.4*	80.9 ± 5.4	81.4 ± 0.5*
Red muscle color	Orange	Red	Orange	Red/orange
Hematocrit (%)	ND	31.4 ± 1.8	36.1 ± 1.0*	22.4 ± 1.2*
Eye surface/BS	7.7	6.1 ± 0.4	10.4 ± 0.5	16.6 ± 1.5
MO_2 (mmol/h/kg)	1.6 ± 0.2	1.2 ± 0.04	0.9 ± 0.01	0.9 ± 0.01
MO2/BS (mmol/h/m^2)	12.2 ± 1.4	5.3 ± 0.3*	5.1 ± 0.2*	4.3 ± 0.28*

*means that the considered parameter is significantly different ($P < 0.05$ or best) from what is observed in eels from the Loire (see Section 4). Note the high density and the low hematocrit in eels from Certes.

drying pieces (48 h at 90 °C) of these tissues (after the animal was sacrificed). The hematocrit, Ht, was measured in the conventional way after blood sampling during animal sacrifice.

2.3. Protocol

All the experiments were performed at 15 °C. The eels were placed in an experimental tank (14.9 l), connected to a high-pressure water circulation system, and the tank was placed in a hyperbaric chamber (Sébert et al., 1990). The water circulation system allowed a continuous renewal of the water, so that temperature and oxygen concentrations could be controlled.

After one day at atmospheric pressure, the hyperbaric chamber was compressed at a rate of 10 atm/min to 101 ATA: the fish were maintained at this pressure for 3 days. During the compression period, the pressure at which the fish exhibited strong motor activity (convulsions) was noted as the pressure threshold (Ptr). During the experiments water oxygen partial pressure (Pw_{O_2}) and temperature (*T*w) in the experimental tank were regularly monitored; water flow was approximately $30\,l\,h^{-1}$. Animal oxygen consumption, MO2, was measured by the confinement method stopping water flow and following the decrease in Pw_{O_2} (Sébert and Barthélémy, 1985). The maximal value obtained at the end of the compression was considered to be the maximal O2 consumption, M_{O2}^{max}. After 3 days at this pressure, the chamber was decompressed at the same rate of 10 atm/min. Immediately after decompression the eels were killed by decapitation and their blood was collected in glass capillaries to determine the hematocrit. Three sections of the eel (about 2 cm length, starting from mid dorsal fin towards the tail) were frozen in liquid nitrogen then stored at −80 °C for further analysis. Red muscle (the colour of which was noted) and white muscle were sampled to perform direct tissue oxygen consumption measurements and finally white muscle and gills were sampled and weighed before and after desiccation in order to determine the water content and then the dry weight. The same procedures were used for the control group, which was kept in the same experimental tank under the same environmental conditions (water temperature and oxygen content, light, noise, time) but at atmospheric pressure (1 ATA). However, the red muscle sample of the control group was also used for the direct measurement of oxygen consumption under pressure.

2.4. Measurements

2.4.1. Fibre oxygen consumption

After decapitation, the red muscle was dissected along the left lateral line and the white muscle was dissected on the left side, at about 30% of total length, close to the vertebral column. Dissection was completed within 4 min. The muscle samples were immediately placed in an ice-cold extraction medium (Sébert and Theron, 2001). Muscle fibres were permeabilised using a saponin solution (0.2 mg/ml) to alter the cell membrane but not the mitochondrial membrane, so as to perform mitochondrial respiration measurements (Sébert and Theron, 2001).

When permeabilisation was completed, respiration was measured in a thermostated glass vessel following its oxygen content decrease, using a Strathkelvin Instrument® O_2 microelectrode (accuracy: ±0.2% saturation). A vessel was specially designed, using an electrode with pressure compensation (YSI 5739) to measure oxygen consumption under pressure and its control at atmospheric pressure (Sébert and Theron, 2001). For both conditions the rates of oxygen consumption were measured on freshly permeabilised fibres using pyruvate plus malate and ADP at saturating concentrations (final concentrations were, respectively, 12 and 6 and 5 mM).

2.4.2. Cytochrome Oxydase (COX) activity

The method was adapted from Simon et al. (1992). Tissue extracts were prepared from the previously frozen sections of eels. Superficial red muscle samples and white muscle samples were dissected, still frozen on a bed of liquid nitrogen. The tissues were homogenized in 100 mg/1 ml of extraction buffer (Tris, 0.1 M; EDTA, 2 mM; DTE, 2 mM; pH7.4) at 4 °C, using a Polytron (four times acceleration, within 5 s, to 10000 rpm then deceleration within 5 s). The obtained extracts were then centrifuged at 11000*g* for 20 min at 4 °C. Filtrated supernatants were directly used for COX activity determination. COX activity was determined by spectophotometry at 550 nm in sodium phosphate buffer (0.33M pH7 at

15 °C) with 50 μmol L^{-1} reduced Cytochrome *c* at saturating concentrations.

2.4.3. Energetic nucleotide contents

Energetic nucleotides (ATP, ADP and AMP) were extracted with an acid solution of Trichloroacetic Acid following the technique used by Sébert et al. (1987). The extracts were immediately analysed using a HPLC method associated with spectophotometry UV detection (254 nm) as previously described by Cann-Moisan et al. (1988). The energy charge was computed as $EC = \{[ATP] + 0.5\ [ADP]\} / \{[ATP] + [ADP] + [AMP]\}$.

Protein contents were determined using the indirect Lowry method (Lowry et al., 1951).

Data analysis. The results are expressed as the mean ± SEM. The statistical significance of the results has been tested at the 5% level using the Student t test.

3. Results

The morphometric data and the general response to high pressure (as evaluated from pressure threshold and maximal oxygen consumption) are shown in Table 1 and 2, respectively. Eels from Certes and Balaton have a significantly lower condition factor CF, body mass index BMI, and hematocrit Ht than eels from the Loire or Sainte Eulalie. In the same manner, their global sensitivity to compression is higher with a lower P_{tr} (significant for Balaton) and a higher MO_2 at the end of compression (MO_2^{Max}). The effects of pressure on red muscle (Table 3) also display a distinction between eels from the Loire and Sainte Eulalie and the others. Although the values of oxygen consumption at 1 ATA are similar for the four sites tested, it can be observed that when fibres are directly exposed to 101 ATA hydrostatic pressure, only red fibres from the Loire eels significantly increase their oxygen consumption whereas fibres from Balaton and Sainte Eulalie show a decrease. In contrast, only eels from Loire and Sainte Eulalie increase MO_2 of red fibres after 3 days under pressure (NS for Sainte Eulalie). In the same manner, COX activity which is high at 1 ATA for eels from the Loire and Sainte Eulalie does not increase after 3 days at 101 ATA which is not the case for the other two sites. Consequently, the MO_2/COX ratio increases in the Loire (significant) and Sainte Eulalie eels but decreases for the other two sites. Red muscle appears to be the most sensitive tissue because no significant traits are observed for white muscle (Table 4) although, for this muscle, eels from Certes seem more similar to the Loire than Sainte Eulalie. It is interesting to note that respiration and COX activity in white muscle are significantly lower in those white muscle which have significantly higher adenylate contents than red muscle. Whatever the site or the muscle, there are no significant pressure effects on protein contents.

4. Discussion

Morphometric data clearly show that the studied eels are not similar. The determination of Ocular Index (Pankhurst, 1982) and Pectoral Fin Index (Durif, 2003) does not leave any doubt concerning the fact that only Balaton eels are at the yellow stage, which

Table 2
Pressure sensitivity of the fish

	LOIRE	BALATON	Ste EULALIE	CERTES
N	6	6	6	6
Pressure treshold (bars)	67.5 ± 5.5	41.7 ± 1.7*	67.0 ± 4.0	59.0 ± 1.0
MO_2^{max} (mmol/h/kg)	2.5 ± 0.5	3.7 ± 0.1*	2.5 ± 0.2	3.8 ± 0.3*

MO_2^{max} is the maximal animal oxygen consumption observed just after compression and is an index of pressure sensitivity as the pressure threshold, which corresponds to the pressure at which the fish exhibit a strong motor activity. Note that eels from the Loire and Sainte Eulalie have low MO_2^{max} and high Pressure thresholds. *means that the considered parameter is significantly different ($P < 0.05$ or best) from what is observed in eels from the Loire (see Section 4).

Table 3
Energetic features of red muscle fibers

	LOIRE ($N = 6$)		BALATON ($N = 6$)		STE-EULALIE ($N = 9$)		CERTES ($N = 6$)	
	1 ATA	101 ATA	1 ATA	101 ATA	1 ATA	101 ATA	1 ATA	101 ATA
MO2 3 d (μmol/min/g)	0.30 ± 0.01	0.66 ± 0.10*	0.29 ± 0.05	0.28 ± 0.04	0.34 ± 0.02	0.39 ± 0.04	0.41 ± 0.05	0.39 ± 0.05
COX (mU/g)	50.0 ± 8.7	52.1 ± 11.3	18.7 ± 4.1	27.5 ± 1.4	60.3 ± 5.8	63.2 ± 4.8	39.1 ± 3.6	50.6 ± 6.3
1000*MO2/COX (μmol/min/mU)	7.3 ± 2.4	13.3 ± 1.1*	18.3 ± 3.1	11.5 ± 2.8	5.9 ± 0.4	6.2 ± 0.7	10.0 ± 1.2	8.0 ± 1.1
MO2 101ATA (μmol/min/g)	0.21 ± 0.01	0.27 ± 0.03	0.24 ± 0.02	0.17 ± 0.02	0.29 ± 0.04	0.22 ± 0.03	0.23 ± 0.02	0.23 ± 0.02
Δ101/1ATA (%)		25.0 ± 3.3*		− 19.0 ± 5.0*		−22.0 ± 6.0*		7.2 ± 15.6
ATP (μmol/g)	1.81 ± 0.17	2.20 ± 0.30	1.45 ± 0.18	1.94 ± 0.34	1.39 ± 0.14	1.24 ± 0.15	1.19 ± 0.26	1.50 ± 0.27
AS (μmol/g)	2.20 ± 0.19	2.64 ± 1.32	1.91 ± 0.26	2.39 ± 0.37	1.95 ± 0.16	1.75 ± 0.16	1.86 ± 0.27	2.04 ± 0.26
EC	0.90 ± 0.01	0.91 ± 0.00	0.87 ± 0.01	0.90 ± 0.01*	0.85 ± 0.01	0.84 ± 0.01	0.80 ± 0.02	0.85 ± 0.02
Proteins (mg/g_{ww})	17.9 ± 1.1	15.8 ± 2.3	19.1 ± 0.9	21.7 ± 1.1	21.2 ± 0.5	22.6 ± 1.6	16.7 ± 0.9	17.1 ± 0.9

MO2 3d, oxygen consumption of red muscle fibers measured at 1 ATA after the fish was exposed for 3 days at 101 ATA; MO2 101 ATA, oxygen consumption of red muscle fibers measured at 1 ATA and 101 ATA; COX, maximal activity of Cytochrome *c* Oxydase; Δ101/1ATA, % variation of fibers respiration at 101ATA when compared at 1 ATA; AS, adenylate sum (ATP + ADP + AMP). Note that only eels from the Loire and Sainte Eulalie improve their respiration after 3 days at 101 ATA. In contrast, only eels from the Loire and Certes improve their respiration under pressure. Some of the results for Balaton are from Vettier et al. (2003). *means that the considered parameter is significantly different ($P < 0.05$ or best) from what is observed in eels from the Loire (see Section 4).

Table 4
Energetic features of white muscle fibers

	LOIRE ($N = 6$)		BALATON ($N = 6$)		STE EULALIE ($N = 9$)		CERTES ($N = 6$)	
	1 ATA	101 ATA	1 ATA	101 ATA	1 ATA	101 ATA	1 ATA	101 ATA
MO2 3 d (μmol/min/g)	0.12 ± 0.01	0.12 ± 0.00	0.10 ± 0.01	0.11 ± 0.01	0.13 ± 0.01	0.14 ± 0.01	0.09 ± 0.01	0.15 ± 0.01
COX (mU/g)	3.4 ± 0.6	3.3 ± 0.8	1.3 ± 0.2	1.4 ± 0.2	1.7 ± 0.3	2.1 ± 0.5	2.9 ± 0.5	4.0 ± 0.8
1000*MO2/COX (μmol/min/mU)	45.0 ± 11.9	43.0 ± 12.0	85.3 ± 11.2	78.9 ± 10.2	98.4 ± 16.6	105.4 ± 23.4	38.9 ± 8.8	41.0 ± 9.2
ATP (μmol/g)	4.3 ± 0.5	3.8 ± 0.9	4.3 ± 0.6	4.8 ± 0.3	2.7 ± 0.3	3.1 ± 0.2	3.3 ± 0.4	4.1 ± 0.5
AS (μmol/g)	5.2 ± 0.6	4.6 ± 2.3	5.1 ± 0.7	5.8 ± 0.3	3.6 ± 0.3	4.1 ± 0.3	4.6 ± 0.3	5.0 ± 0.5
EC	0.91 ± 0.01	0.91 ± 0.00	0.92 ± 0.01	0.91 ± 0.01	0.86 ± 0.01	0.88 ± 0.01	0.86 ± 0.02	0.89 ± 0.02
Proteins (mg/g_{ww})	26.4 ± 0.8	26.4 ± 2.0	26.2 ± 2.8	28.5 ± 2.2	28.2 ± 0.8	29.5 ± 0.9	22.2 ± 2.3	24.5 ± 1.5

MO2 3d, oxygen consumption of white muscle fibers measured at 1 ATA after the fish was exposed for 3 days at 101 ATA; COX, maximal activity of Cytochrome *c* Oxydase; AS, adenylate sum (ATP + ADP + AMP). Note the lower values in respiration and COX activity when compared to red muscle. In contrast, note the higher value in ATP content for the same comparison. Some of the results for Balaton are from Vettier et al. (2003).

explains the low performance of these eels, in terms of aerobic capacities, and their probable unability to migrate (Vettier et al., 2003). Although known for its deleterious effects, parasitism by *Anguillicola crassus* (Molnar et al., 1991; Sures et al., 2001) does not seem to be responsible for this fact because eels from Sainte Eulalie, although infested, show a good resistance to compression (Table 2).

As the results from white muscle do not allow us to classify the sites, and furthermore red muscle is responsible for the swimming activity during migration, we will focus the discussion on red muscle. The main parameters considered at 101 ATA are very specific in their sensitivity to pressure effects. Thus their use is justified by comparing them with results obtained in trout in the same conditions, as trout is a fish which has a very low resistance to high pressure (Sébert, 2003). For example, the pressure threshold (Ptr), which is the pressure at which the fish reacts to compression with strong motor activities, is very low in trout; in the same manner, maximal oxygen consumption, which is the value observed at the end of the compression and is an index of pressure sensitivity, is very high in trout (Sébert and Macdonald, 1993). The respiration of red muscle fibres directly measured under pressure (Cohen, 1983) or after the fish were exposed to high pressure for 3 days together with maximal COX activity has been shown to be a good index for pressure tolerance (Theron et al., 2000; Sébert and Theron, 2001; Vettier et al., 2003). On this basis, the results show that eels from the Loire have the greatest capacities to migrate (high COX activity, high Ptr, low maximal MO2, improvement of respiration under pressure) whereas those from Balaton are probably unable to perform the swimming activities required during migration. This is in agreement with the previous results obtained in the trout which show a dramatic fall in COX activity, energy charge and respiration under pressure, a low pressure threshold and a high maximal MO_2 (Sébert et al., 1987; Sébert and Theron, 2001). In fact, Vettier et al. (2003) have estimated that swimming towards the Sargasso sea (Boëtius and Boëtius, 1980; Van Ginneken and Van den Thillart, 2000) could represent about 60% of the maximal aerobic capacities of Balaton eels which leaves very little room for other processes requiring energy during migration (osmoregulation, gonads development, reproduction…). Due to these results, the Loire river can really be considered as a reference site. It must be pointed out that the features of aerobic metabolism at 1 ATA does not pre-empt such a conclusion. For example, the energy charge EC is not different when comparing Loire and Balaton eels. In contrast, EC is higher in Loire eels than in Certes or Sainte Eulalie. It must be noted that when the values of MO_2 or COX activity are standardised to the protein contents, this does not induce any changes in the conclusions.

The processes for aerobic energy production (respiratory chain and oxidative phosphorylation) are located in the inner membrane of the mitochondrion. It could thus be reasonably hypothetized that the alterations observed under pressure are due to the effects of pressure on cell membranes, mainly by decreasing membrane fluidity, although such a concept does not fully explain the many effects of membrane composition on membrane function (Hulbert and Else, 1999). These effects are well known (Macdonald, 1984) and such a hypothesis has been raised to explain the differences between the trout and eel responses (Sébert and Theron, 2001). However, in their paper, Sébert and Theron have suggested that in trout, pressure effects on membrane (decrease in fluidity) and enzyme complexes were not compensated for. In contrast, during the silvering process which is the preparatory stage before migration, the eel is supposed to reach a supra-functioning capacity of mitochondria at 1 ATA in order to cope with the effects of high pressure encountered during migration (Sébert and Theron, 2001). This process probably combines with a higher membrane fluidity, which is sometimes considered as a pacemaker for energy metabolism, the intensity of which is in relationship with phospholipid polyunsaturation (Hulbert and Else, 1999). Our results seem to demonstrate that this preparation (changes in the functioning of the respiratory chain and oxidative phosphorylation together with membrane modifications; see Sébert, 2003) leading to energy production optimisation under pressure is not at the same stage in all the sites despite similar silvering indexes (OI, PFI) except for Balaton. A possible explanation is the membrane composition. In fact, as previously reported, pressure resistance and acclimation depend, to a great extent, on membrane

fluidity which is maintained (homeoviscous regulation) via the integration of more polyunsaturated fatty acids (PUFA) in the membrane phospholipids (see Bell et al., 1986; Sébert, 2003 for reviews). A possible explanation to the low pressure resistance of Certes'eels to hydrostatic pressure per se could be that, as they normally live in brackish water, they may be less able to recruit and/or to desaturate fatty acids (Watanabe, 1982; Bell et al., 1986; Greene and Selivonchick, 1987). If we consider that the more advanced the silvering process, the more ready the fish is to migrate, we must conclude that fish from different sites are different. In this sense, although not significantly different from Certes'eels, those from Sainte Eulalie are similar to the Loire eels because they have many common responses (see Tables 3 and 4). Included in the common traits is the high COX activity at 1 ATA. This activity is dependent on membrane fluidity (Vik and Capaldi, 1977; Wodtke, 1981) which is known to decrease at the beginning of pressure exposure (See Sébert, 2003). Consequently it may well be that membrane fluidity is higher in the Loire and Sainte Eulalie eels.

In conclusion, our results show that the environmental conditions of the eel can modify the physiological processes and thus counteract the pressure effects on aerobic metabolism and probably the capability of the fish to migrate.

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