Fish at high pressure: a hundred year history∗

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Abstract

Two main periods can be considered in the history of fish metabolism under pressure. The first period (roughly from 1870 to 1970) was mainly descriptive: survival times and behavior were studied and some authors described an increase in oxygen consumption under pressure; later, the counteracting effects of high temperature on pressure were mentioned. The second period (from 1970 onwards) was more integrative and two major ways were explored. The first was to use shallow-water fish, experimentally exposed to hydrostatic pressure, which can induce a metabolic state resembling histotoxic hypoxia. The second way was to use deep-living fish which have, when compared to surface fish, muscle enzymes with higher structural stability, lower activity (in relationship with habitat depth) and kinetics that are less sensitive to pressure increase. Using this approach, it was also shown that muscle composition and function were somewhat different at depth and that deep fish are well adapted to pressure partly by maintaining membrane fluidity (homeoviscous theory). Since about 1990, the two above-mentioned approaches have still been pursued but by fewer researchers. Studies on deep-living fish are mainly concerned with enzyme kinetics whereas shallow water fish are used mainly for cellular energetic studies. Regarding this topic, it has been shown that yellow freshwater eels are able to acclimate to high-pressure effects, by optimizing membrane fluidity and composition (as achieved by deep-living fish), by improving oxidative phosphorylation (increase of P/O ratio) and the glycolytic pathway. © 2002 Elsevier Science Inc. All rights reserved.

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1. Introduction

High pressure has scarcely been studied although it is both a thermodynamic and an environmental factor (80% of the biosphere is beyond 1000 m, i.e. 100 atmospheres; Siebenaller, 1991; Macdonald, 1997). This is probably due to the cost of the material required but also to the technical difficulties often encountered. Today, there are some research teams working on the biological effects of pressure and only a few of them are concerned with living organisms such as fish. Using fish as a model (Barthélémyn, 1985) provides many advantages, mainly (1) fish are ectothermic and consequently it is possible to study interactions between temperature (and thus metabolism) and pressure and (2) fish breathe water, the density of which is few modified by pressure: the problem due to the inhalation of gases by mammals under pressure is thus cancelled because it is possible to separate hydrostatic pressure (HP) effects from high gas pressure effects. For example, during compression (hydrostatic pressure) fish exhibit abnormal activities along with excitation,
followed by uncoordinated movements, seizures and finally immobility. These symptoms can be compared to observations of mammals under pressure (and thus submitted to hydrostatic pressure and gas pressure) and named High Pressure Neurological Syndrome (HPNS, see Brauer et al., 1982, 1985 for review). Such a comparison raises the hypothesis that HPNS in mammals breathing gas under pressure could be due to the effects of hydrostatic pressure per se. Despite its evident interest, the number of publications involving fish under pressure is relatively low. The aim of this review is to present historical data and an overview of results and concepts rather than to report on all the results obtained from one topic. Such reviews or multi-author books have already been published (Siebenaller and Somero, 1989; Siebenaller, 1991; Somero, 1991, 1992; Sébert and Macdonald, 1993; Macdonald, 1993; Randall and Farrell, 1997; Sébert, 1997) and we will restrict ourselves to fish metabolism that has been the subject of most studies.

2. The descriptive period (1870–1970)

Undoubtedly, Regnard and Bert were the first to expose fish to pressure. Regnard (1884, 1885) has described the excitation of the goldfish’s nervous system at low pressure and then its inhibition when pressure increases leading to immobility. Having devised a system which allowed observations to be made inside the hyperbaric apparatus, he concluded that what was observed after fish decompression was due to pressure effects and not to decompression. Bert (1878) observed the same effects in glass eels but it is difficult to know if the fish were exposed solely to hydrostatic pressure or to both gas and hydrostatic pressures. Bert was the first to note that the duration of pressure exposure and the rate of compression were important parameters in determining the symptoms and their intensity. The interpretation of these observations led to several hypotheses. An interesting observation by Regnard (1885) was that, due to pressure, water penetrates the muscle tissue, which becomes rigid and unexcitable. Pelster (1997) mentions that the accumulation of low density material (like water, lipid or gas) decreases fish density and ensures buoyancy at depth. Bert (1878) rightly considered that fish living at 2000 m depth could have a ‘volume decrease’ and thus sustain hydrostatic pressure (HP), while reciprocally, fish trawled from the bottom to the surface (decrease in pressure together with a temperature increase) could exhibit a volume increase explaining their death, a point which will be raised later. Until 1920–1930, studies of fish under pressure remained mainly descriptive in terms of behavior and survival times. The first real physiological experiments were performed by Fontaine (1928, 1929), who measured oxygen consumption (M.O2) of Pleuronectes platessa, Ammodiles lanceolatus, Gobius minutus, and observed that fish exposure to 101 ATA (1000 m depth) induced an increase in M.O2 with a peak level at the end of compression then a slow decrease, with M.O2 always remaining higher than control value at atmospheric pressure (Fig. 1). Like Paul Bert, Fontaine noted the importance of the compression rate on the intensity of the response. The same pattern of M.O2 evolution during pressure exposure was observed later by Naroska (1968). From these different studies there appeared an important fact which is still under study: temperature is able to counteract the pressure effects. This was an observation made by Fontaine (1930) considering protoplasm viscosity. This hypothesis has been reconsidered and explained by Marsland (1944), who observed in Fundulus an expansion of the melanophores under pressure and a contraction on pressure release. Marsland and Brown (1942) were the first to highlight a possible mechanism concerning pressure effects and the opposite action of temperature. This mechanism, which was the second important idea of the period, is based on the effects of pressure on sol-gel equilibria (Kinne,
1970): this was not yet the concept of pressure effects on membrane fluidity and other membrane physico-chemical parameters, but the idea was put forward. It must be noted that in his review, Fontaine (1930) reported studies by Bridgmann (cited) who showed that: (1) liquid viscosity increases with pressure; (2) the pressure effect is more pronounced on viscosity than other physical parameters; and (3) generally, the increase in viscosity is proportional to the complexity of the liquid molecules under study. Bridgmann also reported coagulation of the white of eggs at high pressure (see numerous studies concerning pressure effects on proteins; e.g. Balny et al., 1997). All these observations, along with the limited technical means available at that time, appear to be fundamental in understanding many physiological effects observed later. Thus, for example, when Ebbecke (1944) and others before him wrote that surface fish were unable to cope with high pressures (2000 m depth and more), Schlieper (1968), integrating the previous ideas, concluded that ‘deep-sea animals would perhaps cope more successfully with the tremendous pressure at temperatures higher than the normal temperatures of 2–4 °C at the bottom of the deep sea’. The descriptive period ended with the reviews by Flügel (1970) and Flügel and Schlieper (1970). It appears that the main part of the studies about pressure was performed on invertebrates, was descriptive and also concerned pressure tolerance and/or heart rate variations vs. temperature, salinity, pH, O2 partial pressure. Tolerance seems to decrease with the increase in organism complexity (Ebbecke, 1944). A recent study also seems to show that, likewise, pressure acclimatization is faster in simpler animals (Sébert et al., 1995a). The review by Gordon (1970) does not provide more information on fish metabolism under pressure but reports on some studies concerning the nature of lipids in deep-sea fish which differ from surface fish (Lewis, 1962, 1967). However, although the causative factors were thought to originate from different feeding, the fundamental biochemical difference still remains to be determined (Gordon, 1970). Thus, at the end of the descriptive period, although there was a considerable amount of information and observations, they were not integrated in such a way as to propose mechanisms and to provide physiological explanations. The following period, the integrative one, confirmed most of the results previously obtained and proposed mechanisms in physiological and/or biochemical terms.

3. The integrative period (since about 1970)

During this period, two technical approaches were used. The first involved studying deep-living fish and comparing them, in some cases, to congeneric shallow-water fish. The second consisted in studying shallow-water fish exposed to high pressure in hyperbaric chambers. A conceptual difference exists between these two approaches: whereas the first studied fish adapted to pressure (but also to the other environmental factors at depth) the second, in fact, studied the pressure effects and eventual acclimatization to them.

Using deep-sea fish, the expedition of Alpha-Helix (Kona expedition) and then the Challenger cruise (together with other smaller expeditions) provided many results. The metabolism of fish living at depth has been extensively reviewed (Torres et al., 1979; Somero et al., 1983; Childress and Mickel, 1985; Siebenaller and Somero, 1989; Somero, 1991, 1992; Sébert and Macdonald, 1993). These reviews justify the fact that only the major points will be considered in this paper.

A ‘deep-water environment, which is the prevalent condition of the biosphere, is typified by low temperatures, elevated hydrostatic pressure, absence of non biological light and relatively low influx of utilizable organic material derived from primary production in surface water’ (Siebenaller and Somero, 1989). All these environmental factors can influence metabolism directly or indirectly and consequently, pressure effects cannot be isolated. The main results obtained from fish living at depth show that metabolic rates are much lower than in shallow water fish and decrease with the depth of capture and thus the temperature. Torres and Somero (1988) noted that species living at 1000 m respire at a rate of two orders of magnitude less than species living at the surface (Fig. 2). This reported low metabolic rate is generally interpreted as a decrease in locomotor activity and is concomitant with the known decrease in blood oxygen carrying capacity (Blaxter et al., 1971; Graham et al., 1985). However, Roer et al. (1984) noted that ‘there might have been little or no difference between the metabolic rates of the deep and shallow species’ as shown in Fig. 2 where oxygen consumption from different species, corrected for temperature, was reported vs. depth. No
Fig. 2. Oxygen consumption in relation to depth. Circles correspond to deep-sea fishes with M.O₂ measurements in situ (pelagic fishes: Coryphaenoides, Eptatetus, from Smith (1978), Smith and Hessler (1974); demersal fishes: Sebastolobus, from Smith and Brown (1983)) or at habitat pressure (Melanostigma, from Belman and Gordon (1979); Batrachoccus, Cottinella, Abyssocottus, from Roer et al. (1984)) with water temperature between 3 and 5 °C. Squares and triangles are from Simon et al. (1989) at 17 °C (triangles) or corrected to 4 °C using Q₁₀ = 2 (squares) and concern the yellow eel.

important differences were observed. At the same time, muscle biochemistry was extensively studied in terms of metabolism. In fact, the low metabolic rate of fish living at depth was regarded as the consequence of a multifactorial environment (low level of food, lifestyle, predator–prey interactions, presence or absence of support and refuge) rather than pressure and/or temperature. What are the biochemical determinants of low metabolic rate? Many studies have been performed on white muscle, the major locomotor muscle of fish, generating power required for swimming (Siebenaller and Somero, 1989). The above mentioned reviews and the report from the Kona expedition (Hochachka, 1975) show that deep-living fish in comparison with shallow water fish, have: (1) a higher structural stability of their enzymes (proteins) under pressure; (2) lower enzyme activities related to the lower metabolic rates: it must be kept in mind that deep fish generally have a higher muscle water content which can ultimately produce a dilution effect (see Yancey et al., 1992 for example); and (3) enzyme kinetics that are relatively unaffected by pressure as demonstrated from Km measurements. These main results, schematically illustrated in Fig. 3, were observed in different enzymes concerned with aerobic and anaerobic pathways, but also for ATPases, mainly Na⁺/K⁺ ATPase. Briefly, it seems that fish living at depth have selected pressure-resistant enzymes. However, the efficiency of selecting pressure-resistant proteins would be extremely reduced if their function was impeded by a pressure-altered membrane environment, unless the proteins were adapted to function in such conditions. The role of membrane fluidity, as suggested during the descriptive period, is thus confirmed as regards deep-living fish which exhibit, at atmospheric pressure, a higher membrane fluidity than shallow water fish in relationship with the depth of occurrence. This ‘homeoviscous adaptation’ (Cossins and Macdonald, 1984, 1986, 1989; Gibbs and Somero, 1990) that, through a change in lipid saturation, maintains an optimal state of membrane fluidity in response to pressure increase or temperature variation. For the last 10 years, research has

Fig. 3. Schematic drawing of the main pressure effects. When depth (or pressure) increases, there is a general decrease in enzyme activities and oxygen consumption and an increase in membrane fluidity. This is true when comparing deep-water fishes (DWF) living at different depths and when exposing shallow water fish (SWF) to different pressures. In contrast, The Km* value varies differently depending whether the fishes are shallow or deep species. *Km is a parameter of enzyme reactions; this is the substrate concentration for which the rate of reaction is half the maximum (0.5 Vmax).
been preferentially directed towards the cellular and molecular levels, even if some of them concern the metabolism of the whole animal (Cowles and Childress, 1995; Stolbov and Silkin, 1997). For example, Childress (1995) has argued that predator–prey relationships, particularly visual interactions, are a major cause of reduced metabolism in deep-living fish (see also Gartner et al., 1997). However, the most significant part of the studies using deep-water fish over the last 10 years has concerned the G-protein adenyl cyclase system (G-protein mediated signal transduction), modulating intracellular cAMP levels (see Siebenaller and Murray, 1995). This system plays an important role in metabolism and other physiological functions. Pressure stimulates GTPase activity (increasing Vmax, reducing Km) but also reduces the stimulation of GTPase activity by A1 receptor agonists (see Gibbs, 1997 for review) and the time course, t1/2, of the binding (Siebenaller and Murray, 1999). Moreover, pressure appears to enhance the efficacy of GTP[S] by inhibiting ribosylation (Stevens and Siebenaller, 2000). As the system is embedded in the membrane, the role of the change in membrane lipid composition has been highlighted as in other studies (Bakes et al., 1995). The effects of pressure on biomembranes (Kato and Hayashi, 1999) and enzyme activities (Michels et al., 1996) are widely discussed, in an attempt to understand high pressure-induced biological phenomena, mainly metabolism.

Life around hydrothermal vents has also been studied. Fish living in these deep waters have been described (Cohen and Haedrich, 1983; Cohen et al., 1990; Weitzman, 1997) but information concerning their physiology is scarce and their adaptation to high temperature and pressure has rarely been investigated. One of the major interests in studying hydrothermal fish is that they live in the deep and are thought to encounter high temperatures which, from a thermodynamic point of view, enable them to counteract at least partly, the high pressure effects on biological membranes. However, it must be pointed out that only three endemic fish species are potentially exposed to high water temperature and it is difficult to know exactly what temperature and for how long. Dahlhoff et al. (1990) have shown that M4-LDH of Thermaces andersoni, the only hydrothermal vent fish undoubtedly exposed to high temperatures, exhibited only minimal perturbations (demonstrated from Km measurements) by elevated temperature under in situ pressure. This could be related to the fact that it is adapted to this particular milieu, having in mind that some fish have mitochondria able to detoxify sulfide (Bagarino and Vetter, 1990).

By using shallow water fish exposed to high pressure, only the pressure change as regards control fish at atmospheric pressure can be considered. The resulting physiological effects are studied, knowing that the available techniques allow few parameters to be measured at experimental pressure. The main results from this approach have been reviewed by Barthélémy (1985), Sébert and Macdonald (1993) and Sébert (1997). When freshwater fish (Anguilla anguilla and sometimes Oncorhynchus mykiss) are exposed to high hydrostatic pressure (101 ATA equivalent to a 1000 m depth) for some hours, the following metabolic events are observed. Firstly, there is an increase in oxygen consumption during compression (Fig. 1). This increase depends on the rate of compression, on the size of the fish and more generally on the level of the metabolic rate before compression (Sébert, 1993). M.O2 decreases continuously (from the maximum level observed at the end of the compression) despite the motor activity of the fish. The measurements performed on muscle tissue, after decompression, show a decrease in ATP and glycogen contents, in cytochrome oxidase activity and an increase in LDH activity, fatty acids stores and circulating lactate (Fig. 4). Thus, it has been concluded that hydrostatic pressure induces a state resembling histotoxic hypoxia via a decrease in membrane fluidity, thus altering aerobic metabolism (Sébert et al., 1993a). However, when exposure to pressure is maintained for several days (Johnstone et al., 1989) or weeks (Simon et al., 1989), it appears that shallow water fish such as the eel are able to acclimatize to pressure effects. The pressure acclimatization process is the ‘normalization’ of metabolism through membrane refluidification (homeoviscous adaptation, see Sébert et al., 1993b, 1994) that allows normal functioning of the respiratory chain and oxidative phosphorylation (Fig. 4 and Sébert, 1997 for review). The exploration of pressure/temperature interactions during the pressure acclimatization process shows that fish are insensitive to transient temperature changes (Sébert et al., 1995b). An interesting fact is that results observed on the whole animal or muscle samples are also observed at the mitochondrial level (Theron et al., 2001a).
It has been recently shown that normal energy production during pressure exposure is ensured by an improvement in oxidative phosphorylation: the P/O ratio significantly increases (Theron et al., 2000b). Using a new approach, Sébert et al. (1998) have shown that pressure also induces an increase in the anaerobic glycolytic flux together with a decrease in the transition time from aerobic to anaerobic metabolisms. It must be noted that the modifications in energy metabolism are accompanied by structural changes in gill and muscle (Simon et al., 1991; Dunel-Erb et al., 1996) leading to the hypothesis that yellow freshwater eels acclimated to high pressure acquire, during the acclimatization process, many of the physiological features of a deep-sea water fish. The possibility of a genetic de-repression by high pressure and/or pressure-induced mutant expression, as observed in bacteria (Bartlett et al., 1989; Chi and Bartlett, 1993), cannot be excluded in fish and needs further exploration.

4. General problems in interpreting results from pressure studies

As quoted by Gibbs (1997) and reported by numerous authors, the physiological parameters of deep-sea fish are greatly perturbed at atmospheric pressure because fish are often moribund, irrespective of whether or not they have a swimbladder. However, this does not seem to be a problem in biochemical studies as Whitt and Prosser (1971) reported: ‘The specimens were caught at a depth of approximately 7000 feet and were brought to the surface dead, but in good physical conditions’. Another problem is that congeneric fish species living at different depths are used to explain that members of the same genus have pressure-insensitive enzymes. This has not always been verified. In many cases, the choice of species may have been inappropriate. Gibbs (1997) suggested that intraspecific analysis may help in distinguishing between food limitation (inducing low metabolic rate and enzyme levels) and a relaxed locomotory selection (resulting in genetic differences) hypothesis. No putative pressure adaptative differences in enzyme properties could be distinguished from phylogenetic effects: researchers need to choose their study subjects wisely, with the help of molecular systematics, and be aware of potential artifacts (Gibbs, 1997).

Although the direct effects of pressure are generally ruled out as the primary cause of reduced...
Table 1

Comparison of oxygen consumption, M.O₂, measured at similar temperatures

<table>
<thead>
<tr>
<th>Animal</th>
<th>Pressure of measurement (meters)</th>
<th>Temperature, °C</th>
<th>M.O₂ mmol h⁻¹ kg⁻¹</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>DWF</td>
<td>In situ, (1200 m)</td>
<td>3.0</td>
<td>0.12</td>
<td>1</td>
</tr>
<tr>
<td>DWF</td>
<td>Surface</td>
<td>3.5*</td>
<td>0.37</td>
<td>2</td>
</tr>
<tr>
<td>DWF (cold adapted)</td>
<td>Surface</td>
<td>3.5*</td>
<td>0.62</td>
<td>2</td>
</tr>
<tr>
<td>DWF</td>
<td>1000</td>
<td>3.0</td>
<td>0.27</td>
<td>3</td>
</tr>
<tr>
<td>SWF</td>
<td>Surface</td>
<td>4.0*</td>
<td>0.41</td>
<td>4</td>
</tr>
<tr>
<td>SWF</td>
<td>1000 (30 days)</td>
<td>4.0*</td>
<td>0.26</td>
<td>5</td>
</tr>
<tr>
<td>DW Medusae</td>
<td>Surface</td>
<td>5.0</td>
<td>0.20</td>
<td>6</td>
</tr>
<tr>
<td>DW Cephalopods</td>
<td>Surface</td>
<td>5.0</td>
<td>0.20</td>
<td>7</td>
</tr>
<tr>
<td>DW Crustaceans</td>
<td>Surface</td>
<td>5.0</td>
<td>0.80</td>
<td>7</td>
</tr>
<tr>
<td>SW Crustaceans</td>
<td>1000 (4 days)</td>
<td>4.5*</td>
<td>0.30</td>
<td>8</td>
</tr>
</tbody>
</table>

DWF: deep-water fish; SWF: shallow-water fish; DW: deep-water; SW: shallow-water. The DW species whose M.O₂ is measured at surface were collected at approximately 1000 m (101 ATA). The values are drawn from: (1) Smith and Hessler (1974); (2) Torres and Somero (1988); (3) Belman and Gordon (1979); (4) Sébert and Barthélémy (1985); (5) Simon et al. (1989); (6) Thuesen and Childress (1994); (7) Seibet et al. (1997); (8) Sébert et al. (1997).

* Habitat or corrected using Q₁₀ = 2.

metabolic rates and enzyme activities of deep-sea fish (Childress, 1995), the environment at depth is much more complex than just high pressure and low temperature, the effects of which can be balanced with the effects of other environmental factors. However, physico-chemical studies employing pressure and descriptive information from studies of deep-sea fish have proved useful in identifying some enzyme aspects and various metabolic processes leading to the homeoviscous adaptation hypothesis. Results from long-term pressure experiments on shallow water fish show that pressure has really specific effects. Moreover, except for some experiments measuring oxygen consumption at depth, most measurements on deep species have been performed after decompression (occasionally with recompression at habitat pressure) and corrected for temperature using a Q₁₀ of 2, a value which does not take into account eventual adaptation to low temperatures. The comparison of shallow and deep fish using this correction does not show great differences (see Table 1) as already noted by Roer et al. (1984). Sébert et al. (1995b) have shown that when pressure and temperature are modified simultaneously, the Q₁₀ could be below 1. Consequently, using 2 as the Q₁₀ value to correct the temperature effects in deep fish studies could considerably underestimate oxygen consumption because the thermal sensitivity of metabolism appears to decrease under pressure not only at the fish but also at the mitochondrial level (Sébert et al., 1995b; Theron et al., 2001a).

Using shallow water fish exposed to high hydrostatic pressure has several drawbacks as well. Firstly, most of the results have been obtained from the eel which, during its life cycle, is naturally submitted to high pressure. Eels can thus be considered as pre-adapted to pressure although recent studies on eel tracking (A. japonica and A. anguilla) do not report of any depths greater than 300 m (Fricke and Kaese, 1995; Aoyama et al., 1999; McCleave and Arnold, 1999). However, many of the results observed in the eel are also witnessed in Eriocheir sinensis, a crab living at very low depth (Sébert et al., 1997, 2000): the comparison is not justified from a phylogenetic point of view but it does highlight the specific effects of pressure. Several attempts to acclimate real shallow water fish (trout, goldfish) to high pressure have been made: they have been generally unsuccessful (Sébert, 1997) but it is difficult to totally rule the ability of such species to acclimate to hydrostatic pressure, bearing in mind that these specimens were not wild fish, thus considerably decreasing their capacities (for example, their muscle quality). The second main problem using shallow water fishes at high pressure is the same as for deep fish: muscle samples are available only after decompression. However, in contrast with trawled fish, we have observed (unpublished data) that: (1) eels or goldfish exposed to high pressure
can easily survive several months after decompression; and (2) pressure acclimated eels, which after having been firstly decompressed then exposed again to high pressure some days later, acclimate very rapidly (within 1.5 h). This shows that the changes induced during acclimatization persist after decompression, thus validating the results obtained from muscle samples removed immediately after decompression. The preceding observations show that the two technical approaches rather complement each other and help us to understand how some fish can survive at high pressure. By using deep-sea fish it is possible to study adaptation to a deep environment, whereas using shallow water fish exposed to high pressure relates to the mechanisms involved in pressure acclimatization. Both approaches have pointed out the general decrease in metabolism (oxygen consumption, enzyme activities), the relative temperature effects and their interaction with pressure. Cell membranes are altered by pressure and a variety of behavioral evidence suggests that the pressure tolerance limits of organisms are determined by the effects on membrane functions. These conclusions are largely based on the similar counteracting effects of temperature and pressure on behavioral, cellular and membrane phenomena (Gibbs, 1997).

5. Conclusions and perspectives

A comparison of the reviews by Brauer (1972), Sébert and Macdonald (1993) and Smith and Baldwin (1997) shows the evolution of the available techniques (see also 8.6 in Kinne, 1970). The developed techniques will provide a better description of in situ behavior and animal collection for in situ respirometry and/or studies at atmospheric pressure. The best solution is obviously to use a hyperbaric/trap aquarium, which can maintain fish at their deep habitat temperature and pressure. Although maintaining in situ temperature is routinely achieved, the pressure problem has not yet been resolved. A few attempts have been made with bathypelagic fish but for only about two days due mainly to a drop in pressure (Wilson and Smith, 1985). As the technical problem is considerable, a solution may be found by performing in situ measurements using ingestible baited transmitters (Priede et al., 1990, 1994) with acoustic telemetry. Such a system allows tagging and tracking, monitoring of parameters such as blood flow, heart beat, and gill ventilation which are involved in energy production (see Smith and Baldwin, 1997). Unfortunately biochemical studies of the muscle metabolism cannot be done using such systems! The technical and financial problems raised by using deep-sea fish are partly offset by using shallow water fish. The eel is a good model because it is able to acclimate to high pressure. Most measurements can be performed only after decompression, which constitutes a bias. Another bias is that the eel is submitted to pressure during its migration. However, as reviewed by Sébert (1997), it appears that non-migrating yellow eels acclimated to high pressure (101 ATA) in freshwater exhibit the biochemical, structural and physiological characteristics of seawater fish and probably have the capabilities to migrate. A recent paper by Van Ginneken and Van den Thillart (2000) seems to confirm this view. The environmental differences between the non-migrating yellow eel and the migrating silver eel concern salinity, temperature, light and pressure; these are conditions which are relatively easy to mimic in a laboratory equipped with a hyperbaric chamber. Recent tracking experiments seem to show that the eel apparently migrates in water which is not as deep and not as cold as previously thought (Fricke and Kaese, 1995; Aoyama et al., 1999; McCleave and Arnold, 1999). Thus, a good combination of environmental factors helped by a hormonal treatment (Aoyama et al., 1999; Huang et al., 1999) could lead to a completely artificial maturation (until now, breeding is possible, but not reproduction) although unsuccessful attempts have been performed (Nilsson et al., 1981). The commercial importance of the eel, together with the recognized decline in eel stocks, probably due to a decrease in fitness, could render such experiments interesting for professional fisheries and may facilitate the procurement of funds. Likewise, according to several reports from the aquaculture domain, it seems that the success of fish breeding (and also invertebrates) is inversely proportional to the normal habitat depth of the considered species. This remark is also true for cell cultures. Fundamental experiments in this area, as well as in the artificial maturation of the eels, are likely to attract funds in the future: such projects are already under way in our team.
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