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Comparative effects of long-term hypoxia on growth, feeding and oxygen consumption in juvenile turbot and European sea bass

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Abstract: When juvenile turbot *Scophthalmus maximus* and sea bass *Dicentrarchus labrax* were fed to satiation, growth and food intake were depressed under hypoxia (3·2±0·3 and 4·5±0·2 mg O_2 l^{-1}). However, no significant difference in growth was observed between fishes maintained in hypoxia and fed to satiation and fishes reared in normoxia (7·4±0·3 mg O_2 l^{-1}) and fed restricted rations (same food intake of fishes at 3·2 mg O_2 l^{-1}). Routine oxygen consumption of fishes fed to satiation was higher in normoxia than in hypoxia due to the decrease in food intake in the latter. Of the physiological parameters measured, no significant changes were observed in the two species maintained in hypoxia. This study confirms the significant interaction between environmental oxygen concentrations, feeding and growth in fishes. Decrease in food intake could be an indirect mechanism by which prolonged hypoxia reduces growth in turbot and sea bass, and may be a way to reduce energy and thus oxygen demand.

Keywords: turbot; sea bass; hypoxia; growth; oxygen consumption

INTRODUCTION

Acute decreases in water oxygen (O_2) concentrations may occur in intensive fish farming, especially when fishes are reared at high densities. Considerable attention has been paid to oxygen, as low ambient O_2 concentrations are known to affect growth, food consumption and physiological state of fishes (Jobling, 1994). O_2 levels at which the decrease in growth is observed vary according to the species. In coho, *Oncorhynchus kisutch* (Walbaum) and sockeye salmon *O. nerka* (Walbaum), largemouth bass *Micropterus salmoides* (Lacépède) and carp *Cyprinus carpio* (L.), growth is afffected by O_2 concentrations < 4-5 mg l^{-1} (Brett, 1979; Brett & Blackburn, 1981). In rainbow trout, *O. mykiss* (Walbaum), the O_2 concentration threshold for growth is much higher, 7 mg l^{-1} (Pedersen, 1987).

Most of the studies on the relationship between O_2 and growth have been conducted on freshwater fish species. The present study was undertaken to examine the interactions between oxygen availability and growth in two, economically important, marine fishes, turbot *Scophthalmus maximus* (L.) and sea bass *Dicentrarchus labrax* (L.). In a previous study (Pichavant *et al*., 2000), it was shown that in juvenile turbot growth was reduced when these fishes were maintained in hypoxic water (5.0 mg O_2 l^{-1}). It was hypothesized that one of the mechanisms by which long-term hypoxia reduced growth in juvenile turbot was a decrease in food intake. This hypothesis is tested in the present study.

MATERIALS AND METHODS

FISH AND EXPERIMENTAL DESIGN

Experiments were carried out with 6 to 8 month old hatchery-reared juvenile turbot and sea bass over 42 days in 1 m^2 tanks, with a water volume of 450 l. The tanks were supplied with a continuous water flow, with an exchange rate of 10 l min^{-1}. Before the experiments, the fishes were maintained at 34 ‰ salinity, 16L:8D photoperiod, 2 W m^{-2} light intensity at the water's surface and within the optimal temperature range for growth, 17.0 ± 0.5° C for turbot (Burel *et al*., 1996) and 22.0 ± 0.5° C for sea bass (J. Person-Le-Ruyet, pers. obs.).

The fishes [initial mass: 66.3 ± 0.5 g (S. E.) for turbot and 60.8 ± 0.6 g (S. E.) for sea bass] were divided into eight groups of 80 turbot and eight groups of 65 sea bass and randomly assigned to the experimental tanks. They were then allowed to acclimate to the environmental and feeding conditions for 4 weeks in normoxic seawater (7.4 mg O_2 l^{-1}). The fishes were manually fed twice a day at 0800 hours (morning meal) and 1600 hours (evening meal) to apparent satiation. A commercial dry pellet adapted to each species was used [Le Gouessant®, 4.5 mm diameter, total protein (54 % of dry matter) and crude fat (12 % of dry matter) for turbot and Biomar®, 3 mm diameter, total protein (45 % of dry matter) and crude fat (21.5 % of dry matter) for sea bass]. Food intake was measured after each meal.

After acclimatization, the following experiments were performed in duplicate on both species for 42 days: Reared in 3.2 mg O_2 l^{-1} water and fed to apparent satiation (food intake was assumed to be equal to that provided); reared in 4.5 mg O_2 l^{-1}water and fed to apparent satiation; reared in normoxic condition (7.4 mg O_2 l^{-1}) and fed to apparent satiation; reared in normoxic condition (7.4 mg O_2 l^{-1}) and fed restricted

rations. These rations were equal to the mass of food ingested per fish reared in 3.2 mg O_2 l^{-1} water.

At the beginning of the experiments, the hypoxic tanks were supplied with O_2 deprived water. The hypoxic levels were achieved within 4 h and were maintained throughout the experiments. Hypoxic water was obtained using an oxygen depletion system described by Pichavant *et al.* (2000). Oxygen depletion was controlled by nitrogen flow, and total gas pressure was measured with a tensionometer (300C Novatech®). Normoxia was obtained by adding oxygen instead of nitrogen. Surface gas exchange in the tanks was limited by directing the inflow under water. The O_2 concentration in each tank was monitored continuously according to the method described by Gaumet *et al.* (1995). During the 42 day period, the O_2 concentrations were 3.2 ± 0.3, 4.5 ± 0.2 and 7.4 ± 0.3 mg l^{-1}.

GROWTH AND FEEDING

Every 2 weeks, the fish from each tank were fasted for 18 h and individually weighed to the nearest 0.1 g. No anaesthesia was used for turbot. Sea bass were anaesthetized in a solution of ethylene-glycol-monophenyl-ether (0.5 ‰) before weighing. Apparent food conversion efficiency (E_c) was calculated as $(W_2 - W_1)\ C^{-1}$ where W_2 and W_1 are wet masses (g) at days t_2 and t_1 respectively and C is food intake (dry mass in g) in the period. Daily feeding (F) was calculated from $F = 100\ C_T\ W^{-1}$ where C_T is the mean daily mass (g) of dry food ingested and W is the mean wet fish biomass (g).

OXYGEN CONSUMPTION

Oxygen consumption (MO_2, µmol O_2 g^{-1} h^{-1}) was determined according to the method described by Gaumet *et al.* (1995). Every hour during a 24 h period, the O_2 concentration (µmol l^{-1}) in inflowing (X_i) and outflowing (X_o) water was measured. $MO_2 = Q_w\ (X_i - X_o)\ W^{-1}$ where Q_w (l h^{-1}) is the water flow through the tank, and W (g) is the body mass. Only the mean hourly MO_2 values obtained from three consecutive 24 h periods from day 36 to day 39 are given, as they are representative for the two species throughout the experiments.

BLOOD PARAMETERS

At day 1, 7, 14, 28 and 42, samples of blood (obtained by cardiac puncture) and liver (immediately frozen in nitrogen) were taken from 12 fish per experiment (6 fish per tank) which had been fasted for 18 h. Haematocrit and blood pH (Metrohm® pHmeter fitted with a Fermprobe® microflow pH sensor) were determined immediately after blood sampling. Plasma total CO_2 concentration was measured within 15 min using a Sigma Diagnostics enzymatic kit (132-UV). All other blood parameters were measured on frozen plasma samples: osmolarity using an Advanced Instrument Osmometer®; chloride by argentimetric titration using a Radiometer CMT 10® as described by Gaumet *et al.* (1995); glucose and lactate concentrations using enzymatic kits (16-UV Sigma Diagnostics and 256773 Boehringer-Mannheim, respectively). Plasma concentration of tri-iodothyronine (T_3) in turbot and sea bass and thyroxine (T_4) in turbot was measured using specific radio-immunoassay methods (Boeuf *et al.*, 1989). Liver glycogen was determined according to the method of Carr & Neff (1984). At the end of the experiments, 12 other fish per experiment (6 per tank) were sacrified in a lethal solution of ethylene-glycol-monophenyl-ether (2.5 ‰) and blood was sampled for plasma cortisol analysis by the radio-immunoassay method (Lamers, 1992).

DATA ANALYSIS

Statistical analysis were conducted using STATISTICA for Windows. ANOVA tests were used as the homogeneity of variances and normality of distribution were verified. The effects of O_2 concentrations on growth, physiological parameters and O_2 consumption were estimated using two-way ANOVA taking the tank effect into account. One-way ANOVA was used for food intake and food conversion efficiency analysis. Significant ANOVA were followed by a multiple comparison test (Newman-Keuls test). All the results are expressed as mean ± S. E. Level of significance was taken as $P < 0.05$.

RESULTS

GROWTH PERFORMANCE AND FEEDING

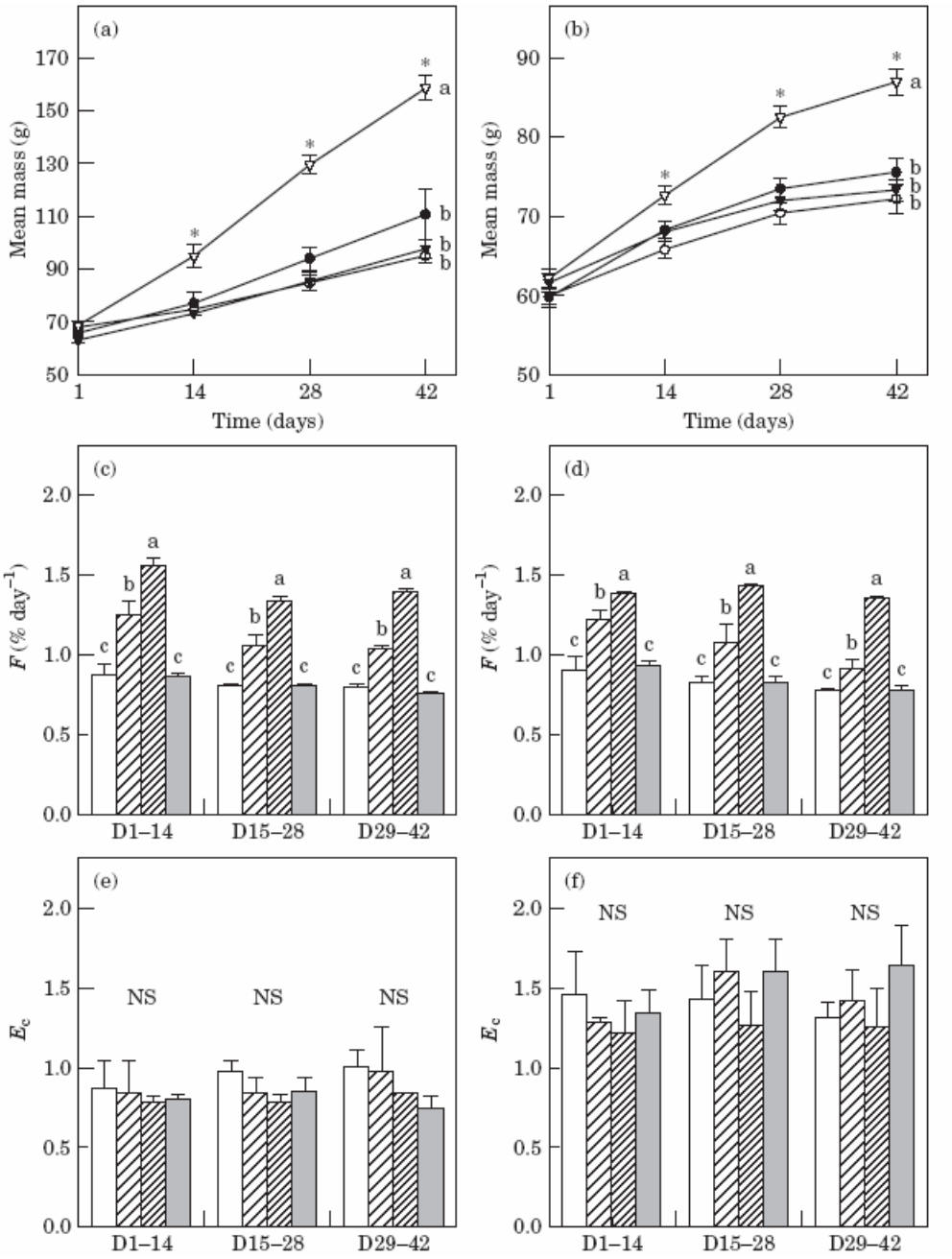
Mass increases in turbot and sea bass kept in hypoxia and fed to satiation were significantly less than in normoxic fishes fed to satiation [Fig. 1 (a), (b)]. In turbot and sea bass, mass gains throughout the 42 day period were similar in fishes at 3.2 mg O_2 l^{-1} and fed to satiation and those at 7.4 mg O_2 l^{-1} and fed restricted rations.

In turbot and sea bass fed to satiation, a significant decrease in the food intake (F) was observed when O_2 decreased [Fig. 1 (c), (d)]. F was × 1.7 to 1.8 lower in turbot and × 1.5 to 1.7 lower in sea bass maintained at 3.2 mg O_2 l^{-1} than in fishes maintained at 7.4 mg O_2 l^{-1}.

Food conversion efficiency (E_c) was always higher in sea bass [1.2-1.6, Fig. 1(f)] than in turbot [0.7-1.0, Fig. 1 (e)]. In both species, E_c were unaffected by oxygen concentration or feeding procedure.

Fig. 1. Mean weight versus time in turbot (1A) and sea bass (1B) in relation to O2-concentration and feeding procedure: 3.2 ( ), 4.5 (•) and 7.4 ( ) mg O2 l-1 and fed to satiety, 7.4 ( ) mg O2 l-1 and fed-restricted. Mean ± SE (n = 2 replicates of 80 turbot each and 65 sea bass each). For every sample time, * indicates a statistical difference (p 0.05). a and b indicate intergroup statistical differences at day 42.

Feed intake (FI) and feed conversion ratio (FCR) versus time in turbot (1C and 1E) and sea bass (1D and 1F) in relation to O2-concentration and feeding procedure: 3.2 ( ), 4.5 ( ) and 7.4 ( ) mg O2 l-1 and fed to satiety , 7.4 ( ) mg O2 l-1 and fed-restricted. Mean ± SE (n = 2 replicates of 80 turbot each and 65 sea bass each). a, b and c indicate intergroup statistical differences (p 0.05); NS = no significant difference between the experimental groups.

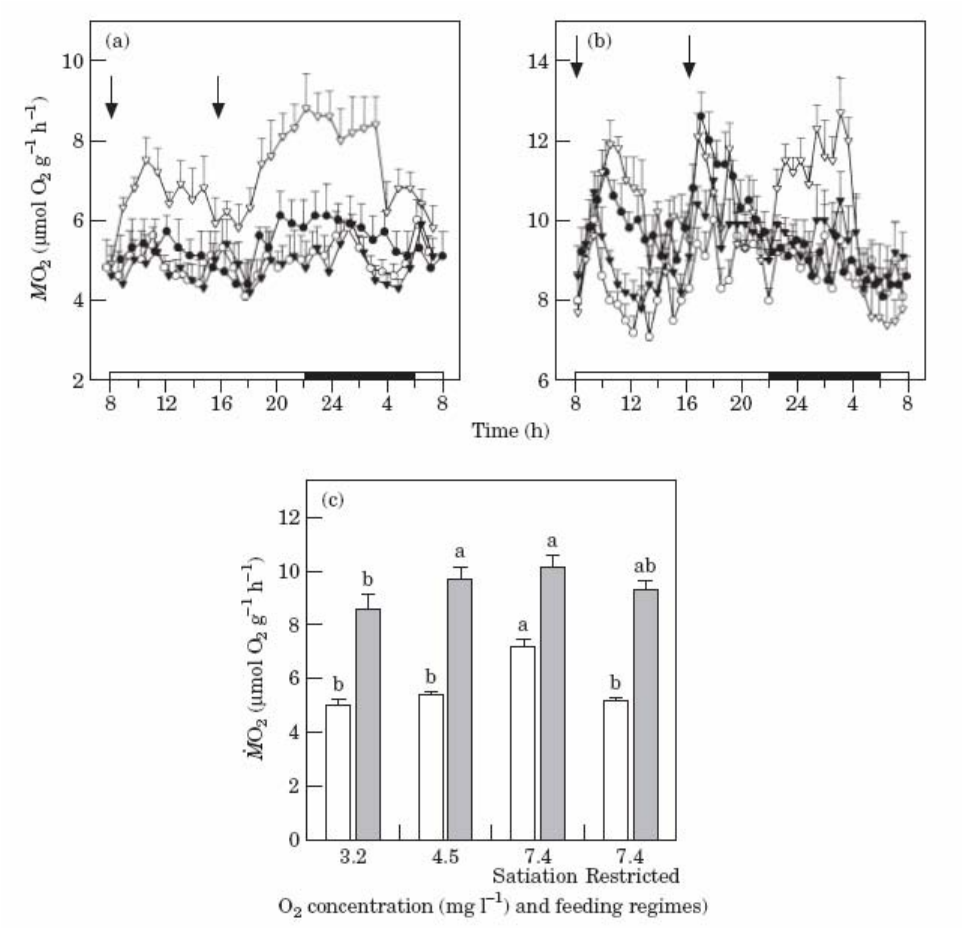


OXYGEN CONSUMPTION

In normoxic fed to satiation turbot, routine O_2 consumption started to increase 2 h after each meal, and reached a maximum 3 h after the morning meal and 7-8 h after the evening meal [Fig. 2(a)]. Mean routine O_2 consumption was significantly higher in normoxic fed to satiation than in hypoxic fed to satiation turbot [Fig. 2(c)].

In normoxic fed to satiation sea bass, a significant increase in routine O_2 consumption was observed after the morning meal whereas a significant decrease occurred 1 h after the evening meal [Fig. 2(b)]. Mean routine O_2 consumption was similar in fed to satiation sea bass reared at 7.4 and 4.5 mg O_2 l^{-1}, and was significantly lower in fed to satiation sea bass maintained at 3.2 mg O_2 l^{-1} [Fig. 2(c)]. Mean O_2 consumption was significantly higher in sea bass than in turbot whatever the experimental condition [Fig. 2(c)].

Fig. 2. Daily patterns of routine O2-consumption (MO2) in turbot (2A) and sea bass (2B) in relation to O2-concentration and feeding procedure from day 36 to 39: 3.2 ( ), 4.5 (•) and 7.4 ( ) mg O2 l-1 and fed to satiety, 7.4 ( ) mg O2 l-1 and fed-restricted. Mean MO2 rate of turbot ( ) and sea bass ( ) from day 36 to 39 (2C) in relation to O2-concentration and feeding procedure. Mean ± SE (n = 2 replicates of 80 turbot each and 65 sea bass each). a and b indicate intergroup statistical differences (p 0.05); NS = no significant difference between the experimental groups.
The horizontal bar on the x-axis indicates the alternative periods of light and dark, and indicates feeding time.



EFFECTS OF HYPOXIA ON PHYSIOLOGICAL PARAMETERS

All the measured physiological parameters, except for osmolarity in turbot, were unaffected by the experimental conditions (Tables I and II).

Table I. Blood parameters in turbot at day 42 in relation to O_2 concentration and feeding procedure.

Mean ± S.E. (n = 2 replicates of 80 turbot). a and b significant differences ($P < 0.05$); NS = non significant.

Oxygen concentration (mg l^{-1})	3.2	4.5	7.4	7.4	
Feeding procedure	Fed to satiation	Fed to satiation	Fed to satiation	Restricted rations	
Osmolarity (mosm l^{-1})	318 ± 1 ^{ab}	329 ± 1 ^{a}	325 ± 1 ^{ab}	314 ± 1 ^{b}	
Cl^- (mmol l^{-1})	143 ± 3	148 ± 2	143 ± 1	143 ± 1	NS
pH	7.62 ± 0.05	7.52 ± 0.01	7.60 ± 0.09	7.60 ± 0.05	NS
Total CO_2 (mmol l^{-1})	6.9 ± 0.3	7.1 ± 0.2	6.8 ± 0.4	6.7 ± 0.5	NS
Lactate (mmol l^{-1})	0.33 ± 0.04	0.35 ± 0.02	0.31 ± 0.01	0.24 ± 0.03	NS
Glucose (mmol l^{-1})	2.5 ± 0.1	2.6 ± 0.1	2.7 ± 0.1	2.5 ± 0.3	NS
Liver glycogen (µmol g fw $^{-1}$)	106 ± 17	148 ± 55	236 ± 89	87 ± 28	NS
Haematocrit (%)	21 ± 1	25 ± 2	24 ± 1	21 ± 4	NS
T_3 (ng ml^{-1})	1.5 ± 0.1	1.7 ± 0.1	2.1 ± 0.2	1.6 ± 0.3	NS
T_4 (ng ml^{-1})	2.6 ± 0.3	3.4 ± 0.4	3.8 ± 0.6	3.5 ± 1	NS
Cortisol (ng ml^{-1})	2.6 ± 1.4	0.8 ± 0.3	2.5 ± 1.2	1.8 ± 1.2	NS

Table II. Blood parameters in sea bass at day 42 in relation to O_2 concentration and feeding procedure

Mean ± S.E. (n = 2 replicates of 65 sea bass). NS = non significant.

Oxygen concentration (mg l^{-1})	3.2	4.5	7.4	7.4	
Feeding procedure	Fed to satiation	Fed to satiation	Fed to satiation	Restricted rations	
Osmolarity (mosm l^{-1})	346 ± 4	335 ± 12	345 ± 9	342 ± 1	NS
Cl^- (mmol l^{-1})	150 ± 1	147 ± 4	145 ± 2	145 ± 2	NS
PH	7.64 ± 0.14	7.66 ± 0.04	7.72 ± 0.05	7.78 ± 0.02	NS
Total CO_2 (mmol l^{-1})	7.2 ± 0.5	6.7 ± 0.4	7.1 ± 0.2	7.0 ± 0.3	NS
Lactate (mmol l^{-1})	2.8 ± 1.5	3.0 ± 1.8	1.6 ± 0.8	2.2 ± 0.5	NS
Glucose (mmol l^{-1})	5.7 ± 1.3	5.9 ± 0.8	5.7 ± 1.9	6.6 ± 0.2	NS
Liver glycogen (µmol g fw $^{-1}$)	283 ± 3	340 ± 14	314 ± 30	339 ± 6	NS
Haematocrit (%)	38 ± 2	38 ± 2	32 ± 2	34 ± 1	NS
T_3 (ng ml^{-1})	7.1 ± 0.2	7.1 ± 0.2	7.9 ± 0.5	7.5 ± 0.2	NS
Cortisol (ng ml^{-1})	0.6 ± 0.2	0.7 ± 0.2	1.0 ± 0.8	0.9 ± 0.6	NS

DISCUSSION

Exposure of juvenile turbot and sea bass to hypoxia induced a marked decrease in growth. This response is in agreement with previous data obtained by Thetmeyer *et al.* (1999) and Pichavant *et al*. (2000) in juvenile sea bass and turbot respectively. Two hypotheses have been made to explain the decrease in growth when fishes are exposed to long-term hypoxia: (1) an increase in energetic cost of ventilation which decreases the amount of energy available for growth (Kramer, 1987); (2) a decrease in food intake which allows fish to save energy (Brett, 1979; Kramer, 1987; Jobling, 1994). Only the latter was tested in the present study.

The search for food, digestion and assimilation are major components of the energy budget of fishes (Brett & Groves, 1979). They can represent up to 60 % of the total energetic expenditure of the animal (Van Dam & Pauly, 1995). As in most fish species (Stewart *et al*., 1967; Adelman & Smith, 1970; Carlson *et al.*, 1980; Brett & Blackburn, 1981; Pedersen, 1987; Thetmeyer *et al*., 1999), the food intake was strongly reduced when turbot and sea bass were exposed to hypoxia. In the present study, no significant difference in growth was observed between fishes reared in hypoxia and fed to satiation and those reared in normoxia and fed restricted rations. Thus, the decrease in food intake could be an indirect mechanism by which chronic hypoxia reduces growth in turbot and sea bass. The decrease in food intake probably reduces energy demand and therefore oxygen requirements.

Hypoxia apparently induces different effects on E_c in fishes. A negative effect of hypoxia on E_c was reported in juvenile largemouth bass (Stewart *et al*., 1967), rainbow trout (Pedersen, 1987) and Atlantic cod, *Gadus morhua* L. (Chabot & Dutil, 1999). Thetmeyer *et al*. (1999) reported that E_c was not affected by exposure of juvenile sea bass to hypoxia. Similarly, no significant difference in E_c was reported in sea bass and turbot in the present study. The discrepancy between these studies could suggest that E_c is more affected by the feeding procedure than by exposure to hypoxia.

The measurement of O_2 consumption is an indirect way to estimate metabolism. The mean O_2 consumption measured in routine metabolic conditions in turbot and sea bass maintained in normoxia was close to values previously reported in the two species (Waller, 1992; Burel *et al.*, 1996; Claireaux & Lagardère, 1999). In fishes maintained in normoxia and fed to satiation, mean routine O_2 consumption was higher in sea bass than in turbot. This result could be explained by the difference in swimming activity between turbot, a benthic fish, and sea bass, a pelagic fish.

The routine O_2 consumption was not constant during a 24 h period in turbot and sea bass. In turbot maintained in normoxia and fed to satiation, the ingestion of food was followed by an increase in O_2 consumption i.e. an increase in the metabolic rate. This mechanism is known as specific dynamic action (SDA), and accounts for all the metabolic expenditures associated with digestion, absorption and storage of nutrients, deamination of amino acids, synthesis of excretory products and biosynthesis, turnover and deposition of tissue components (Jobling, 1981). In the present study, SDA was reduced when turbot were maintained in hypoxia due to the decrease in food intake.

In the sea bass maintained in normoxia and fed to satiation, feeding alone could not explain the fluctuations of routine O_2 consumption. An increase in the routine O_2 consumption was observed after the morning meal. This increase, as in turbot, may be attributed to SDA. The peak in O_2 consumption observed in sea bass during the evening meal could be linked to the concomitant increased swimming activity (Brett & Zala, 1975; Jobling, 1994). In the sea bass maintained in normoxia and fed to satiation, an

increase in routine O_2 consumption was observed during the night. As in the spotted grunter *Pomadasys commersonnii* Bloch (Du Preez, 1986), this increase could be due to a rise in the spontaneous swimming activity occuring during the night. When sea bass were maintained in hypoxia or fed restricted rations, such an increase was not observed. This result could suggest a decrease in swimming activity in hypoxia. Similar responses have been previously reported in white sturgeon, *Acipenser transmontanus* Richardson (Crocker & Cech, 1997), dogfish *Scyliorhinus canicula* L. (Metcalfe & Butler, 1984), rainbow trout (Buschnel *et al*., 1984), and sole *Solea solea* L. (Dalla Via *et al*., 1998).

When turbot and sea bass were maintained in hypoxia, no significant change in most of the physiological parameters measured was observed. Thus, when subjected to chronic hypoxia as low as 3.2 mg O_2 l^{-1}, turbot and sea bass were able to successfully adjust their energy demand so as to avoid resorting to anaerobic metabolism (lactate production).

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