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Physiological mechanisms underlying a trade-off between growth rate and tolerance of feed deprivation in the European sea bass (*Dicentrarchus labrax*)

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SUMMARY

The specific growth rate (SGR) of a cohort of 2000 tagged juvenile European sea bass was measured in a common tank, during two sequential cycles comprising three-weeks feed deprivation followed by three-weeks *ad libitum* re-feeding. After correction for initial size at age as fork length, there was a direct correlation between negative SGR (rate of mass loss) during feed deprivation and positive SGR (rate of compensatory growth) during re-feeding (Spearman rank correlation R=0.388, P=0.000002). Following a period of rearing under standard culture conditions, individuals representing 'high growth' phenotypes (GP) and 'high tolerance of feed deprivation' phenotypes (DP) were selected from either end of the SGR spectrum. Static and swimming respirometry could not demonstrate lower routine or standard metabolic rate in DP to account for greater tolerance of feed deprivation. Increased rates of compensatory growth in GP were not linked to greater maximum metabolic rate, aerobic metabolic scope or maximum cardiac performance than DP. When fed a standard ration, however, GP completed the specific dynamic action (SDA) response significantly faster than DP. Therefore, higher growth rate in GP was linked to greater capacity to process food. There was no difference in SDA coefficient, an indicator of energetic efficiency. The results indicate that individual variation in growth rate in sea bass reflects, in part, a trade-off against tolerance of food deprivation. The two phenotypes represented the opposing ends of a spectrum. The GP aims to exploit available resources and grow as rapidly as possible but at a cost of physiological and/or behavioural attributes, which lead to increased energy dissipation when food is not available. An opposing strategy, exemplified by DP, is less 'boom and bust', with a lower physiological capacity to exploit resources but which is less costly to sustain during periods of food deprivation.

Key words: aerobic scope, compensatory growth, specific dynamic action, specific growth rate, standard metabolic rate.

INTRODUCTION

Teleost fish exhibit significant intraspecific variation in their growth rates and intrinsic growth capacity, a fact that has been exploited in selection programmes by the aquaculture industry (Gjedrem, 2005; Dupont-Nivet et al., 2008) and that has also been explored for its ecological and evolutionary significance (Björklund et al., 2003; Carlson et al., 2004; Stamps, 2007). A capacity for rapid growth should provide ecological advantages (Arendt, 1997) but the persistence of slower-growing individuals in populations has stimulated research into potential physiological and ecological costs of growing fast (Arendt, 1997; Arendt and Wilson, 2000; Metcalfe and Monaghan, 2001; Biro et al., 2004; Stamps, 2007).

Many fish grow throughout their lifespan, and growth rate may influence the ability to escape predation, competitiveness and elements of fitness such as age at first maturity (Jobling, 1994; Arendt, 1997). Individual growth rates within fish populations are known also, however, to be highly dependent upon food availability (Persson and De Roos, 2006), and starvation is a seasonal stress for many species (Wang et al., 2006), which can lead to selective mortality (Byström et al., 2006). The fact that food deprivation is a repetitive feature in the lifestyle of many species may explain the phenomenon of 'compensatory growth' whereby fish will exhibit higher feed intake and growth rates after a period of starvation than their rates when fed continuously (Ali et al., 2003).

There is evidence in a number of animal groups, including fishes, that tolerance of food deprivation may trade-off against a capacity for rapid growth (Bochdansky et al., 2005; Stoks et al., 2006; Bang et al., 2007; Scharf et al., 2009). It has been predicted that this trade-off has a physiological basis whereby a capacity for rapid biosynthesis and growth would require the maintenance of physiological and biochemical machinery, which has metabolic costs, so fuel stores would be consumed rapidly during periods of food deprivation. Conversely, animals tolerant of food deprivation would be so because they have low metabolic costs but this implies that they lack the biosynthetic machinery to respond to opportunities for rapid growth. Although there is evidence for such a physiological basis to this trade-off in invertebrates (Stoks et al., 2006; Scharf et al., 2009), this remains to be demonstrated in fishes (Bochdansky et al., 2005; Bang et al., 2007).

This study investigated the hypothesis that a trade-off could be demonstrated between tolerance of feed deprivation and compensatory growth rate during feeding in juvenile life stages (age 0+ to 1+ years) of a temperate marine teleost, the European sea bass *Dicentrarchus labrax* L. The sea bass was chosen because of the

characteristics of its life cycle in the western Mediterranean, where it has a genetically distinct population (Garcia De Leon et al., 1997). Adult sea bass spawn offshore in winter/spring; eggs hatch in a few days and pelagic larvae drift inshore towards warm sheltered waters (Pickett and Pawson, 1994). The western Mediterranean has many coastal lagoons and estuaries, which are essential settlement zones for sea bass larvae (Dufour et al., 2009). The juveniles grow in these habitats over their first summer and then leave them as water temperatures drop in late autumn to overwinter in the open sea. Many sea bass then continue to occupy lagoons seasonally, as they grow to maturity (Quignard, 1984). Lagoons are often highly productive but also 'naturally stressed' environments, with great diversity and variability in abiotic conditions (UNESCO, 1981). The sea bass presumably cannot be sure of the conditions they will encounter, particularly the juveniles in their critical first summer. The stochastic nature of these environments, and the seasonal migration between them and the open sea, might be expected to provide disruptive selection pressures underlying a trade-off between capacity for growth *versus* tolerance of feed deprivation.

Relatively little is, in fact, known about the traits of physiological energetics, which underlie individual variation in growth rate in fishes (McKenzie et al., 2003; Bang et al., 2007; McKenzie et al., 2007; Millidine et al., 2009). Following proposals made for fish larvae (Bochdansky et al., 2005; Bang et al., 2007), we investigated the hypothesis that phenotypes with greater tolerance of feed deprivation would have lower costs of maintenance; hence, lower routine and standard metabolic rates (RMR and SMR, respectively) than phenotypes with a high capacity for growth. We also, however, investigated the hypothesis that a capacity for rapid growth would be related to a greater capacity to process meals (Millidine et al., 2009). Furthermore, it has been suggested that overall aerobic capacity should be linked with a capacity for growth in fishes (Metcalfe et al., 1995; Cutts et al., 2001; McKenzie et al., 2003; Bang et al., 2007). We therefore also investigated the hypothesis that overall cardiorespiratory capacity and performance would differ as a function of growth rate *versus* tolerance of feed deprivation, and would be greater in fish with high rates of compensatory growth.

This study exploited a large-scale aquaculture programme, which evaluated tolerance of feed deprivation and compensatory growth rates as indirect indicators of residual feed efficiency in sea bass (Grima et al., 2010). This provided access to biometrical data of 2000 individually tagged sea bass (selected at random from 328 families derived from wild western Mediterranean broodstock) that had been submitted to two sequential six-week cycles of feed deprivation *versus* re-feeding. We calculated, and compared, their specific growth rates (SGR) during the feed deprivation and re-feeding cycles to reveal a negative correlation between rates of mass loss when starved and rates of mass gain during re-feeding. We then selected individuals with a high compensatory growth rate (high positive SGR when fed) *versus* a high tolerance of feed deprivation (low negative SGR when starved). We used techniques of respirometry to compare their SMR and RMR and their ability to process meals in terms of the speed and the size of their specific dynamic action (SDA) response, which is the transient increase in metabolic rate that accompanies digestion of a meal (Jobling, 1983; Secor, 2009). Finally, individuals were fitted with flow probes on their ventral aorta and submitted to an incremental 'critical speed' (U_{crit}) exercise protocol in a swim-tunnel respirometer to compare their cardiorespiratory performance when fasted and also when digesting a meal (Dupont-Prinet et al., 2009; Jourdan-Pineau et al., 2010). These experiments revealed physiological mechanisms underlying the trade-off, although our hypotheses were not all supported.

MATERIALS AND METHODS

Experimental animals

The initial fish population was produced and maintained at the Ifremer Station Expérimentale d'Aquaculture, Palavas-les-Flots, France. It comprised a group of 328 full and half-sib families derived from a fully factorial mating design combining eight dams and 41 sires, all wild broodstock from the western Mediterranean (Grima et al., 2010). Immediately after fertilisation, eggs from all families were placed into a single 0.5 m^3 incubator, supplied with bio-filtered aerated seawater at 14°C. A standard sea bass rearing protocol was followed (Chatain et al., 1994). After hatching, water temperature was gradually increased from 14°C to 20°C over the first 68 days post-fertilisation, after which fish were transferred into a common 5 m^3 fibreglass tank, supplied with bio-filtered aerated seawater, and maintained until 306 days post-fertilisation while fed *ad libitum* daily, by self-feeder, with a standard commercial diet (Neogrower, Le Gouessant, France) containing 45% protein and 17% lipid.

At 306 days post-fertilisation, 2000 fish were randomly chosen and individually tagged with a Passive Integrated Transponder (AEG-Id, Ulm, Germany). The tagged fish were stocked in a single 5 m^3 tank within a recirculating bio-filtered system, with water at 20°C, a salinity of 37 g l^{-1} and under a photoperiod of 12 h:12 h light:dark. Fish were fed *ad libitum* by self-feeder for a period of four weeks and then anaesthetised (2-phenoxy-ethanol 0.4 ml l^{-1}), they were then individually identified using a PIT-Tag reader, weighed to the nearest 0.1 g and their fork length measured to the nearest 1 mm. They were then submitted to two successive cycles of three-weeks feed deprivation and three-weeks *ad libitum* re-feeding by self-feeder, with their body mass and fork length measured as described above at the end of each of the deprivation *versus* re-feeding periods as described in Grima et al. (Grima et al., 2010). Individual SGR (in % day^{-1}) was calculated as described by McKenzie et al. (McKenzie et al., 2007) for each weighing interval, and the mean SGR was then calculated for each individual for the two periods of feed deprivation and for the two periods of re-feeding.

The sea bass were then stocked in 12 tanks (vol. 3 m^3) supplied with bio-filtered seawater at a photoperiod of 16 h:8 h light:dark, and reared until an age of approximately 750 days post-fertilisation and a mass of approximately 350 g, while fed daily *ad libitum* on the commercial feed. During this interval, the animals were studied for their residual feed efficiency within an entirely independent study that did not report on their SGR (Grima et al., 2010). This period of growth, during which the fish approximately doubled in mean body mass, ensured that the individuals studied for their metabolism (see below) were in a similar nutritional state and their physiology was not directly influenced by any responses to the repeated fasting and re-feeding protocol.

At the conclusion of the feeding period, 48 individuals were made available for the investigation of their physiology. In order to select the most appropriate among these individuals, they were screened to identify nine that had the lowest negative SGR during feed deprivation, which were considered 'deprivation phenotypes' (DP). The nine with the greatest positive SGR during re-feeding were identified and called 'growth phenotypes' (GP). These individuals were transferred by road to the Station Méditerranéenne de l'Environnement Littoral in Sète, a distance of some 25 km. Upon arrival, fish were transferred into a rearing tank supplied with a flow of bio-filtered seawater (35±1 g l^{-1}, 21±1°C) under a natural photoperiod. They were acclimated for three weeks to these conditions and fed by hand once daily, to satiation, with the commercial feed. All fish were fasted for 48 h prior to use in any experiments.

Static respirometry and specific dynamic action

These measurements were made on two fish at a time, comparing a DP with a GP phenotype. Metabolic rate and SDA were measured by respirometry, as rates of oxygen uptake (Steffensen, 1989; Jordan and Steffensen, 2007; Dupont-Prinet et al., 2009). Each fish was submitted sequentially to two treatments, with at least 48 h between them. Firstly, they were lightly anaesthetised in tricaine methane sulphonate (MS-222; 0.1 g l^{-1}, Sigma Chemical Co., St Louis, MO, USA) until righting reflexes were lost, and submitted to a sham-feeding operation, where a pair of plastic forceps was inserted as far as their stomach.

The animals were then transferred to one of two respirometers (vol. 9.56 l each), placed in parallel in a tank provided with a constant flow of aerated bio-filtered seawater at 21°C. Instantaneous oxygen uptake ($\dot{M}_{O_2}$, in mg kg^{-1} h^{-1}) was measured by intermittent stopped-flow respirometry (Steffensen, 1989) once every 30 min as described previously by McKenzie et al. (McKenzie et al., 2007). The tank containing the respirometers was isolated in a constant-temperature chamber, regulated at 21°C and with the appropriate seasonal photoperiod, and disturbance was kept to a minimum during measurements. The water surface was shielded with opaque polystyrene to prevent visually disturbing the fish during any experimental activities. Oxygen uptake was then measured for 48 h, during which the fish recovered from the manipulation, and provided an estimate of SMR. The sham operation allowed correction for the effects of handling on the SDA response.

In order to measure the SDA response, individual sea bass were anaesthetised as described above and then force-fed a piece of fish fillet equivalent to 3% of their body mass, placed into their stomach with plastic forceps (Axelsson et al., 2002; Altimiras et al., 2008). Their $\dot{M}_{O_2}$ was then measured for 48 h while they digested the fish fillet. At the end of each experiment background $\dot{M}_{O_2}$ was measured following removal of the fish from the respirometer and values corrected accordingly. These never exceeded 10% of the $\dot{M}_{O_2}$ of the fish. All $\dot{M}_{O_2}$ values were then corrected to a fish mass of 400 g, using the mass coefficient calculated empirically by Lemarie et al. (Lemarie et al., 1992).

SMR

RMR during fasting was calculated as the overall mean of the $\dot{M}_{O_2}$ values for the 42 h of $\dot{M}_{O_2}$ measurements that followed recovery from sham feeding/handling stress in the fasted sea bass (McKenzie et al., 2007). SMR theoretically corresponds with the minimal metabolic demands required to sustain the fish when fasted and 'resting' (Fry, 1971; Brett and Groves, 1979). This was estimated using two different methods, for the 42 h of $\dot{M}_{O_2}$ measurements that were considered in calculating fasted RMR. Firstly, a method developed by Steffensen et al. (Steffensen et al., 1994) whereby a frequency distribution is fit to the dataset, typically revealing a bimodal distribution. A small peak at high values of $\dot{M}_{O_2}$ can be attributed to initial handling effects or subsequent brief periods of spontaneous activity. A larger and distinct peak of lower $\dot{M}_{O_2}$ values corresponds with the majority of measurements when metabolic rate is relatively constant and stable. Using Table Curve software (Jandel Scientific, San Rafael, CA, USA), a bimodal normal distribution was fit to the dataset, and Steffensen et al. suggested that the mode of the distinct peak of lower values is an estimate of SMR (Steffensen et al., 1994).

Secondly, a custom-designed program in R software was used to calculate SMR with a quantile approach (D. Chabot, G.C., A. P. Farrell, R. Koenker and J. F. Steffensen, unpublished). This assumes that a certain proportion of the observed $\dot{M}_{O_2}$ values are actually below true SMR because of measurement error and biological variability. The quantile splits the dataset into the q smallest and the 1–q largest values, where q is a proportion chosen by the experimenter. In the current study, q was fixed at 0.15, such that 15% of values were considered to fall below SMR.

SDA

Once again, two different analytical approaches were taken to describe the various elements of the SDA response in the fed sea bass. Firstly, an empirical approach was taken (Jordan and Steffensen, 2007). The raw data indicated that the effects of handling were visible for the first 3 h in sham-fed fish. Thus, to correct for any contribution of handling to the metabolic rate during SDA, the $\dot{M}_{O_2}$ following sham feeding was subtracted from $\dot{M}_{O_2}$ following feeding for each fish for the first 3 h of measurements. The difference was then assumed to be equal to the net increase above SMR due to SDA in this initial period. The highest absolute peak $\dot{M}_{O_2}$ was determined during the SDA, referred to as $\dot{M}_{O_{2peak}}$. The data were then normalised to the SMR calculated according to Steffensen et al. (Steffensen et al., 1994) to reveal the net metabolic effects of the SDA. Following this data treatment, the maximum amplitude (the difference between $\dot{M}_{O_{2peak}}$ and SMR) and the time to the $\dot{M}_{O_{2peak}}$ (T_{peak}) were identified for each individual. The duration of the SDA was estimated as the time required to return to within +10% of SMR (Jordan and Steffensen, 2007), and the total area of the SDA was then calculated by integrating under the resulting curve. The resulting total $\dot{M}_{O_2}$ due to the SDA was converted to energy consumption using an oxycalorific coefficient of 14.06 kJ gO^{-1} (Gnaiger, 1983).

Secondly, the same elements of the SDA response were estimated by non-parametric quantile regression (D. Chabot, G.C., A. P. Farrell, R. Koenker and J. F. Steffensen, unpublished). Initially, all data following feeding were corrected for handling effects, as described above and normalised to SMR but in this case to the SMR calculated by the quantile method (see above). Quantile regression finds a line that splits any dataset into a proportion q of the values that fall below the line and a proportion 1–q that are above the line (Koenker, 2005). A function to fit non-parametric regression models, rqsss, exists within the R software package 'quantreg' (Koenker, 2008) (D. Chabot, G.C., A. P. Farrell, R. Koenker and J. F. Steffensen, unpublished). This applies a piece-wise non-linear model, which followed the lower edge of the clouds of data points on a scatterplot of net SDA $\dot{M}_{O_2}$ *versus* time for each fish. The rqss function requires two parameters, τ and λ. τ is analogous to q in quantiles and therefore determined the proportion of the data points that fell below the curve. λ, however, controlled the stiffness of that same curve, and its value depends on the scale of the x variable (D. Chabot, G.C., A. P. Farrell, R. Koenker and J. F. Steffensen, unpublished), i.e. hours in this study. For the current dataset, τ was set to 0.15 (as was q for SMR) and λ was set to 2. This then allowed calculation of values for maximum amplitude, T_{peak}, SDA duration and total area (D. Chabot, G.C., A. P. Farrell, R. Koenker and J. F. Steffensen, unpublished). The resulting total $\dot{M}_{O_2}$ due to the SDA was, once again, converted to energy consumption using an oxycalorific coefficient of 14.06 kJ gO_2^{-1} (Gnaiger, 1983).

Swimming respirometry and cardiorespiratory performance

Individual sea bass were anaesthetised in MS-222 (0.1 g l^{-1}, Sigma Chemical Co.) until breathing movements ceased. They were transferred to an operating table and their gills irrigated with aerated water containing 0.05 g l^{-1} MS-222. An ultrasound flow probe (2S-type Transonic, resolution 0.1 ml min^{-1}; absolute accuracy ± 15%,

EMKA, Paris, France) was placed around the ventral aorta to measure total cardiac output ($\dot{Q}$) as described by Axelsson et al. (Axelsson et al., 2002). After surgery, fish were transferred to opaque PVC chambers supplied with a flow of aerated seawater and allowed 24 h to recover.

Following this recovery period, fish were transferred to a Brett-type swimming respirometer, previously described in detail by McKenzie et al. (McKenzie et al., 2001). They were allowed at least 12 h recovery (overnight) while swimming gently at a current speed of 20 cm s^{-1}. At this low speed, the sea bass rested on the bottom and maintained position by gentle sculling of their pectoral fins and occasional tail flicks. The following day, fish were exposed to progressive increments in swimming speed, to 40, 60, 80, 90, 100 and then 110 cm s^{-1}, every 30 min, until fatigue. Swimming speeds were corrected for the solid blocking effect of the fish as described by Bell and Terhune (Bell and Terhune, 1970). The experiment was terminated when the fish were unable to remove themselves from the posterior screen of the swimming chamber despite gentle encouragement by sudden increases in current velocity (Chatelier et al., 2005). U_{crit} [body lengths per second (BL s^{-1})] was calculated using the equation provided by Brett (Brett, 1964), which adds the velocity of the most recently completed increment to the product of the incremental increase in velocity and the proportion of the final increment completed before fatigue.

The sea bass were then allowed 24 h recovery in the respirometer, swimming gently at a speed of 20 cm s^{-1}. They were then gently removed from the respirometer without air exposure, lightly anaesthetised and force-fed a fish fillet equivalent to 3% of their body mass. They were returned to the swim tunnel and allowed 6 h recovery while swimming gently at 20 cm s^{-1}, while they developed their SDA response, to investigate the effects of the response on exercise performance (Altimiras et al., 2008; Dupont-Prinet et al., 2009; Jourdan-Pineau et al., 2010). They were then given the same U_{crit} protocol as when fasted. The fish were always swum first fasted and then fed, with the protocol always provided in the same order (Altimiras et al., 2008; Dupont-Prinet et al., 2009), to reduce the overall time required to complete the studies on the instrumented fish. Jourdan-Pineau et al. demonstrated, however, that randomising the order of fasted *versus* fed trials did not influence metabolic responses to feeding and exercise, or their relationship with U_{crit} performance (Jourdan-Pineau et al., 2010).

Exercise respirometry

During the U_{crit} protocols, measurements of $\dot{M}_{O_2}$ were made at each swimming speed as described in McKenzie et al. (McKenzie et al., 2007), once every 15 min, i.e. twice for each speed increment, and the mean of the two values taken. The maximum metabolic rate (MMR) was identified during the swimming protocol, and always occurred at speeds approaching U_{crit} (Chatelier et al., 2005; Chatelier et al., 2006). Extrapolation of $\dot{M}_{O_2}$ back to the y-intercept, a notional swimming speed of zero, was then employed to correct for the contribution to $\dot{M}_{O_2}$ of locomotor-muscle activity (Brett, 1964; Fry, 1971). The value thus derived was termed 'immobile metabolic rate' (IMR) (McKenzie et al., 2003; Dupont-Prinet et al., 2009). In fasted animals this is considered to be an estimate of SMR (Brett, 1964; Fry, 1971) whereas in the fed animals this value will be raised by an amount that is presumably equal to the net metabolic cost of the SDA response. Aerobic scope of exercise (AS) was calculated as the difference between MMR and IMR (Fry, 1971; McKenzie et al., 2003) for both fed and fasted animals (Dupont-Prinet et al., 2009; Jourdan-Pineau et al., 2010).

Cardiac performance

Measurement of $\dot{Q}$ (in ml min^{-1} kg^{-1}) was made at each swimming speed during the exercise protocol (Altimiras et al., 2008; Dupont-Prinet et al., 2009). Heart rate (f_H, in beats min^{-1}) was derived from the $\dot{Q}$ flow signal and was used to calculate stroke volume (V_S) as described by Axelsson et al. (Axelsson et al., 2002). Routine $\dot{Q}$ was taken as the value measured with the sea bass swimming gently at 20 cm s^{-1}, and maximum $\dot{Q}$ was identified during exercise, which always coincided closely with MMR (see above). The values of f_H and V_S associated with routine and maximum $\dot{Q}$ during exercise were also derived.

Statistical analysis

Statistics were performed with Sigmastat (Systat Systems, Inc., Point Richmond, CA, USA). In all cases, data were checked for normality and homogeneity of variance prior to application of parametric tests and, when they failed these requirements, non-parametric tests were applied. The correlation between negative SGR during fasting and positive SGR when feeding was assessed for the 2000 individuals by Spearman rank correlation.

For each phenotype, the effects on $\dot{M}_{O_2}$ of either sham or true force-feeding were assessed by two-way analysis of variance (ANOVA) for repeated measures, based upon mean hourly values. One factor was feeding state (sham or true), the repeated factor was time elapsed since feeding (h) and each fish was a subject. To compare net metabolic SDA responses between the two phenotypes over time, a two-way ANOVA for repeated measures was performed based upon mean hourly net SDA values normalised empirically to SMR (see above). One factor was phenotype, the repeated factor was time elapsed since feeding (h) and each fish was a subject. The net effects of the SDA were compared against a control value of zero, because data were normalised to SMR. For derived single variables (SMR, SDA variables, as described above) a Student's t-test was used to compare the two phenotypes.

For the exercise protocol, on fasted and fed sea bass, the analysis was limited to the variables measured or derived for routine and maximal exercise. Single variables measured or derived under routine conditions were compared by two-way ANOVA for repeated measures, where one factor was phenotype and the repeated factor was feeding state (fed *versus* fasted).

In those cases where a significant difference was observed in the two-way ANOVA, Holm–Sidak *post-hoc* tests were undertaken to identify where in the dataset this difference lay. The level of statistical significance was taken as $P<0.05$.

RESULTS

The trade-off between tolerance of feed deprivation and compensatory growth rate

Fig. 1 shows the relationship between negative SGR during fasting and positive SGR when feeding in the cohort of 2000 sea bass. Although there was some individual variation within the overall dataset, there was nonetheless a clear and highly significant negative correlation between fasting and feeding SGR (Spearman rank correlation R=0.467, P=0.000002). When SGR was corrected for initial fork length, to correct for effects of size-at-age in the cohort, the rank correlation was R=0.388, P=0.000002. Fig. 1 also shows where in the dataset the individuals were situated that were used for the comparison of the physiology of the GP *versus* DP. The mean (±s.e.m.) mass and fork length of the two sets of phenotypes was not different, when used for the physiological experimentation, being 376±44 g *versus* 420±42 g, and 292±11 mm *versus* 307±10 mm, in the DP and GP, respectively.

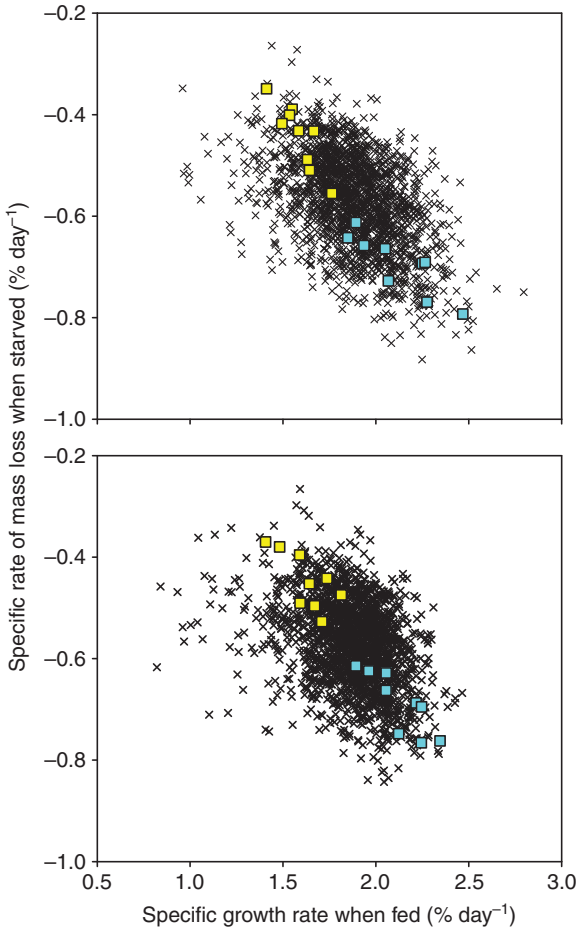

Fig. 1. The relationship between negative specific growth rate (SGR) during feed deprivation and positive SGR during re-feeding in a cohort of 2000 individual sea bass aged 0+ years. The fish were submitted to two sequential six-week cycles comprising three weeks feed deprivation and three weeks re-feeding. Each datapoint represents the mean SGR for an individual for the two periods of deprivation *versus* the two periods of re-feeding. Upper panel shows SGR data, lower panel shows SGR data corrected for initial body length (please see text for details). The coloured squares indicate the individuals that were subsequently studied for their physiology, yellow being 'deprivation phenotypes' and blue being 'growth phenotypes'.

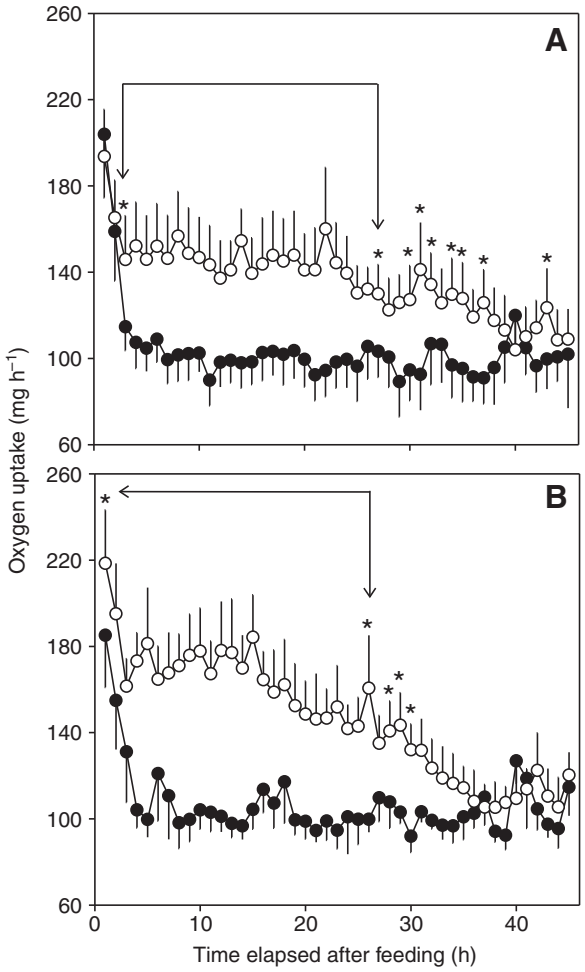

Fig. 2. Mean (±s.e.m.) rates of oxygen uptake in two groups of sea bass over 45 h after either sham feeding (closed symbols) or force-feeding with a ration of fish fillet equivalent to 3% of their body mass (open symbols). The groups represent phenotypes from the opposing ends of the trade-off between tolerance of feed deprivation and compensatory growth rate carried in Fig. 1. (A) Deprivation phenotypes, (B) growth phenotypes. *N*=7 in all cases. Rates are corrected to a mean fish mass of 400 g. An asterisk indicates a significant difference between sham and fed at that time point, all values within the arrows are significant ($P<0.05$ by Holm–Sidak test *post-hoc* to two-way ANOVA for repeated measures, see text for further details).

Metabolic rate and specific dynamic action under static conditions

Fig. 2 shows the effects of sham feeding or force-feeding on $\dot{M}_{O_2}$ in DP (Fig. 2A) or GP (Fig. 2B). Sham feeding was associated with a large initial increase in $\dot{M}_{O_2}$ that was presumably due to handling effects, a response that did not differ between the two phenotypes and which had disappeared by 6 h. The phenotypes then showed a relatively stable rate of fasted $\dot{M}_{O_2}$ that did not differ between them and was used to calculate RMR and SMR. RMR did not differ between the two phenotypes and, regardless of the method used to calculate SMR, this did not differ either (Table 1). Feeding caused a marked increase in $\dot{M}_{O_2}$ relative to the starved state in both phenotypes, which endured for a number of hours (Fig. 2). In the DP, the increase in fed *versus* fasted $\dot{M}_{O_2}$ was not significant until 3 h after force-feeding, and then endured until 37 h post-feeding, aside from at 28 h (Fig. 2A). In the GP, the increase in fed *versus* fasted state was significant from the outset and but then only up to 27 h after feeding (Fig. 2B). There were no significant differences in fed $\dot{M}_{O_2}$ between the phenotypes at any time interval but the differences in timing of the response within each phenotype led to significant differences in the characteristics of their SDA response (Fig. 3).

Fig. 3 shows the mean SDA response in each phenotype, normalised to SMR as calculated according to the method of Steffensen (Steffensen et al., 1994), with the SDA response calculated by the empirical approach of Jordan and Steffensen (Jordan and Steffensen, 2007). The DP showed a significant increase in net SDA $\dot{M}_{O_2}$ between 4 h and 34 h after feeding (Fig. 3A). The GP showed a significant increase in net SDA $\dot{M}_{O_2}$ between 2 h and 29 h after feeding, aside from at 3 h, 21 h and 27 h (Fig. 3B). Furthermore, net SDA $\dot{M}_{O_2}$ was significantly lower in the DP than in the GP at various time intervals at the beginning of the response, namely at 1–2 h, then also at 5 h and

Table 1. Metabolic rates of two groups of European sea bass, representing phenotypes from the opposing ends of the trade-off between tolerance of feed deprivation and compensatory growth rate ['deprivation phenotypes' (DP) *versus* 'growth phenotypes' (GP) see Fig. 1]

	Phenotypes		
	DP	GP	*P*
Routine metabolic rate	108±6	113±7	0.61
SMR*	110±12	106±5	0.74
SMR†	89±4	87±4	0.75

Data for standard metabolic rate (SMR) are reported according to two different methods (*Steffensen et al., 1994; †D. Chabot, G.C., A. P. Farrell, R. Koenker and J. F. Steffensen, unpublished). Please see text for further details. Mean (±s.e.m.), *N*=7. *P* value, significance of Student's *t*-test comparing the two phenotypes for that variable. Metabolism is reported as mg O_2 h^{-1}, standardised to a fish mass of 400 g (see text for details).

then between 10 h and 15 h (Fig. 2B). By contrast, net SDA $\dot{M}_{O_2}$ was significantly higher in the DP than in the GP towards the end of the response, namely at 33 h. These differences in net SDA $\dot{M}_{O_2}$ were linked to significant differences between the phenotypes in their derived SDA variables (Table 2). The $\dot{M}_{O_2peak}$ was almost significantly different between the two phenotypes when calculated by the empirical method (P=0.06) whereas GP had a significantly $\dot{M}_{O_2peak}$ when calculated by the quantile method (Table 2). The peak amplitude of the SDA response was significantly higher in the GP than the DP, as calculated by both the empirical and the quantile methods (Table 2). The overall duration of the SDA was significantly less in the GP than in the DP fish, when calculated by both methods (Table 2). Despite these differences in dynamic, however, the T_{peak}, SDA area and SDA energy were similar in both phenotypes, for both methods of calculation (Table·2).

Metabolic rate and cardiac performance during aerobic exercise

Table 3 shows the metabolic and performance variables measured or derived during exercise, and Table 4 shows the results of the two-way ANOVA comparing phenotypes and feeding state. Table 4 shows that there were no significant differences between the phenotypes for any given variable or any significant interactions between phenotype and feeding state. Feeding state did, however, have significant effects on a number of variables (Table 4).

Thus, there was no significant difference between the two phenotypes for the $\dot{M}_{O_2}$ of fasted fish swimming at 20 cm s^{-1}, nor for IMR derived by backward extrapolation to a notional swimming speed of zero (= SMR in fasted fish) (Table 3). There was also no significant difference in MMR and, therefore, AS did not differ between the phenotypes. Feeding induced significant increases in IMR, $\dot{M}_{O_2}$ at a swimming speed of 20 cm s^{-1} and MMR in both phenotypes. These values did not, however, differ between the phenotypes (Tables 3, 4). That is, although mean MMR and AS are numerically higher in the GP, both for fasted and fed conditions, the range of values in each group overlapped completely (347–719 mg O_2 kg^{-1} h^{-1} for GP compared with 413–758 mg O_2 kg^{-1} h^{-1} for DP). These metabolic data were not mass-corrected, as the static respirometry data were (see above), because it would not be possible then to relate them to the cardiac performance variables (see below) for which no mass exponent is available. If, however, the raw values for each individual (i.e. uncorrected for mass) were plotted against their mass, the residuals of the resultant significant negative linear relationship did not differ between the two

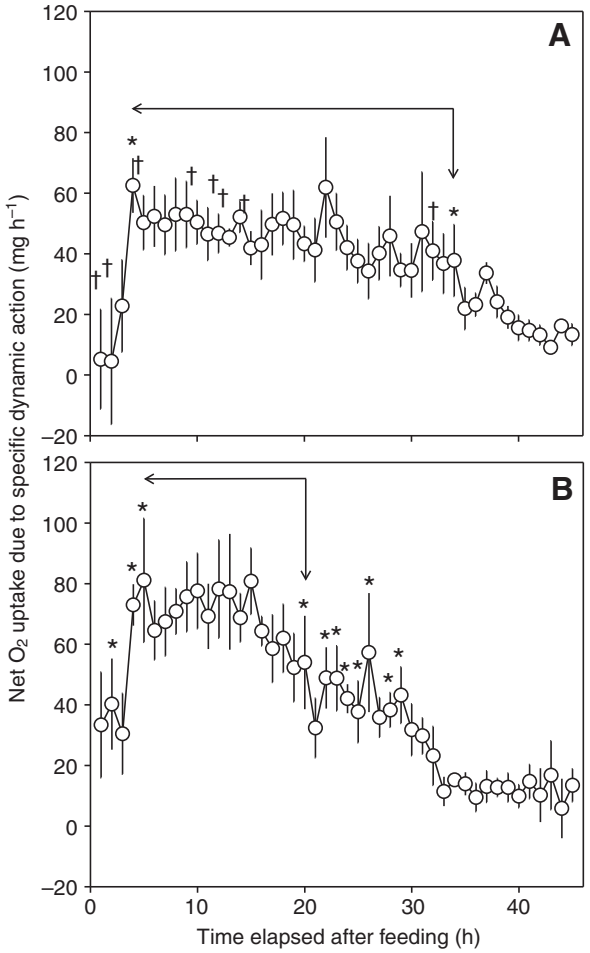

Fig. 3. Mean (±s.e.m.) rates of oxygen uptake due to specific dynamic action (normalised against standard metabolic rate) in two groups of sea bass for 45 h after force-feeding with a ration of fish fillet equivalent to 3% of their body mass. The groups represent phenotypes from the opposing ends of the trade-off between tolerance of feed deprivation and compensatory growth rate carried in Fig. 1. (A) Deprivation phenotypes, (B) growth phenotypes. *N*=7 in all cases. Rates are corrected to a mean fish mass of 400 g. An asterisk indicates a significant difference from zero (standard metabolic rate) at that time interval for that phenotype (all values within the arrows are significant), a dagger indicates a significant difference between phenotypes at that time interval (P<0.05 by Holm–Sidak test *post-hoc* to two-way ANOVA for repeated measures, see text for further details).

phenotypes (data not shown). The U_{crit} swimming performance was not different between the two phenotypes, and was not affected by feeding (Tables 3, 4).

In both phenotypes, $\dot{Q}$ increased significantly during exercise, in both fasted and fed conditions (Table 3). This was almost exclusively a result of increases in f_H, with only a small increase in V_S between routine and maximum $\dot{Q}$. Feeding itself caused slight but significant increases in $\dot{Q}$ and f_H under routine conditions but these cardiac effects of feeding disappeared at maximum $\dot{Q}$ during exercise, because the maximum $\dot{Q}$ and f_H did not differ between fasted and fed conditions (Tables 3, 4). A comparison of the two phenotypes did not reveal any differences in routine or maximum $\dot{Q}$, f_H or V_S, whether under fasted or fed conditions (Tables 3, 4). If the raw values of $\dot{Q}$ and V_S for each individual (i.e. uncorrected for mass) were plotted against the fish mass, the residuals of the resultant negative linear relationship did not differ between the two phenotypes (data not shown).

Table 2. Components of the specific dynamic action (SDA) response in two groups of European sea bass, following force-feeding with a ration of fish fillet equivalent to 3% of their body mass

	Phenotypes		
	DP	GP	*P*
Empirical method*			
$\dot{M}_{O_2peak}$	177±9	220±20	0.06
Amplitude	71±11	110±15	0.04
T_{peak}	6.5±1.3	7.1±1.0	0.71
Duration	39.3±2.8	30.8±2.4	0.03
SDA area	1800±197	1764±214	0.90
SDA energy	25.3±2.8	24.8±3.0	0.90
Quantile method†			
$\dot{M}_{O_2peak}$	146±6	180±8	<0.005
Amplitude	59±9	91±7	0.01
T_{peak}	9.1±3.9	11.7±2.0	0.53
Duration	40.9±1.1	34.9±0.6	<0.005
SDA area	1031±171	1381±183	0.16
SDA energy	14.5±2.4	19.4±2.6	0.16

The groups represent phenotypes from the opposing ends of the trade-off between tolerance of feed deprivation and compensatory growth rate ['deprivation phenotypes' (DP) *versus* 'growth phenotypes' (GP) see Fig. 1]. The SDA variables were derived by two different methods (*Jordan and Steffensen, 2007; †D. Chabot, G.C., A. P. Farrell, R. Koenker and J. F. Steffensen, unpublished); see the text for further details. Means (±s.e.m.), N=7 for each phenotype. P value, significance of Student's t-test comparing the two phenotypes for that variable. All metabolic variables are standardised to a fish mass of 400 g (see text for details). $\dot{M}_{O_2peak}$, the maximum oxygen consumption observed during SDA (mg O_2 h^{-1}); amplitude, the difference between peak oxygen consumption and SMR (mg O_2 h^{-1}); T_{peak}, the time required to reach $\dot{M}_{O_2peak}$ (h); duration, the time required to return to SMR after force-feeding (h); SDA area, total oxygen consumption used during the digesting (mg O_2); SDA energy, total oxygen consumption converted to energy using an oxycaloric coefficient (kJ).

Table 3. Measured and derived variables for responses to incremental exercise (critical swimming speed, U_{crit}, protocol) in two groups of European sea bass, before *versus* after force-feeding with a ration of fish fillet equivalent to 3% of their body mass

	Phenotype and feeding state			
	DP		GP	
	Fasted	Fed	Fasted	Fed
IMR	141±28	203±38*	126±19	185±15*
$\dot{M}_{O_220}$	199±32	257±38*	182±18	248±17*
MMR	523±58	550±61*	545±60	576±55*
AS	383±53	409±55*	419±78	450±71*
U_{crit}	93±7	96±4	96±5	98±4
$\dot{Q}_{20}$	54±8	58±7	44±3	56±6
$\dot{Q}_{max}$	91±9	89±9	80±10	84±12
f_{H20}	70±3	77±6*	61±5	77±5*
f_{Hmax}	104±6	111±5	104±5	109±9
V_{S20}	0.8±0.1	0.7±0.1	0.8±0.1	0.7±0.1
V_{Smax}	0.8±0.1	0.8±0.1	0.8±0.1	0.8±0.1

The groups represent phenotypes from the opposing ends of the trade-off between tolerance of feed deprivation and compensatory growth rate ['deprivation phenotypes' (DP) *versus* 'growth phenotypes' (GP) see Fig. 1]. Means (±s.e.m., N=7 for each phenotype). An asterisk denotes a significant difference from the fasted value for that phenotype (P<0.05, Holm–Sidak test *post-hoc* to two-way ANOVA). IMR, immobile metabolic rate; MMR, maximum metabolic rate; AS, aerobic scope (MMR – fasted IMR); U_{crit}, critical swimming speed (cm s^{-1}); $\dot{Q}$, cardiac output (ml min^{-1} kg^{-1}), f_H, heart rate (beats min^{-1}); V_S ventricular stroke volume (ml kg^{-1}); subscript '20' indicates as measured at the lowest swimming speed (20 cm s^{-1}), subscript 'max' indicates as measured at MMR.

DISCUSSION

The results of the fasting/re-feeding cycles, performed on 2000 offspring from 328 families, demonstrate that individual variation in growth rate reflects, in part, a trade-off against tolerance of feed deprivation in the European sea bass. Phenotypes representing the two contrasting energetic strategies exhibited significant differences in traits of physiological energetics, notably in their ability to process meals but not in standard metabolic rate or maximum cardiorespiratory performance.

The trade-off between growth rate and tolerance of feed deprivation

This trade-off had been hypothesised to exist in the pelagic larval phases of marine fishes, by Bochdansky et al. (Bochdansky et al., 2005) and Bang et al. (Bang et al., 2007). The current data indicate that it can also be demonstrated in later life stages, in an experimental population that suffered no mortality selection. The absence of mortality selection may account for some of the observed variability in the dataset. Food deprivation is a repetitive seasonal feature in the life history of many teleosts, which are remarkable for their ability to tolerate starvation (Wang et al., 2006). Indeed, what is referred to as 'compensatory growth', the phenomenon whereby fish grow more rapidly after a period of food deprivation than they do if fed continuously (Ali et al., 2003) may be a recurring event in their life history (Carlson et al., 2004). In the current study, it seems likely that a longer period of feed deprivation would have raised rates of compensatory growth in all animals, because this will presumably have influenced their motivation to feed. It is not clear therefore to what extent the rates of compensatory growth in each individual depended simply on their actual mass loss during feed deprivation, rather than being indicative of a greater 'scope' for growth. As described in detail below, however, the physiological data clearly indicate that the GP could process food faster and therefore were physiologically different from the DP. Grima et al. investigated heritability of familial rates of mass loss during feed deprivation and mass gain during re-feeding in the sea bass used in the current study, and found that there was a significant heritable component (Grima et al., 2010).

The trade-off is presumably a consequence of the life cycle of the sea bass from the western Mediterranean, where they form a genetically distinct population (Garcia De Leon et al., 1997). In particular, it may be related to their facultative colonisation of a multitude of coastal lagoons and estuaries as nursery habitats, where they metamorphose and grow for their first summer. They presumably cannot be sure of the conditions they will encounter; the persistence in the population of phenotypes tolerant of food deprivation must indicate that an ability to tolerate this stress is sometimes important for survival, even if it trades-off against a capacity to exploit resources rapidly when these are available. Therefore, the two contrasting energetic strategies may represent two alternative approaches to achieving adult size-at-age in a stochastic environment and with seasonal food deprivation.

The trade-off was not related to differences in SMR

The values of SMR in the two phenotypes were similar to previous reports for this species at this temperature (Claireaux and Lagardère, 1999; Claireaux et al., 2006). It was unexpected that SMR did not differ between the two phenotypes, regardless of the method used to estimate it, and that RMR did not differ either. It has often been suggested that a high SMR should be correlated with a high capacity

Table 4. Results (*F* and *P* values) of the two-way analysis of variance with repeated measures, assessing effects of phenotype (deprivation phenotypes *versus* growth phenotypes, see Fig. 1) and feeding state (fasted *versus* fed as the repeated variable, with each individual fish as a subject) on various measured or derived metabolic and performance variables during incremental exercise by sea bass

	F and *P* values for factors and their interaction					
	Phenotype		Feeding state		Phenotype × state	
	F	*P*	*F*	*P*	*F*	*P*
IMR	0.37	0.55	42.1	<0.001	0.03	0.87
$\dot{M}_{O220}$	0.19	0.67	39.9	<0.001	0.26	0.61
MMR	0.15	0.71	27.1	<0.001	0.19	0.67
AS	0.32	0.58	27.0	<0.001	0.20	0.66
U_{crit}	0.31	0.59	1.22	0.29	0.01	0.94
$\dot{Q}_{20}$	1.34	0.27	3.62	0.08	0.79	0.39
$\dot{Q}_{max}$	0.29	0.60	0.11	0.74	0.32	0.58
f_{H20}	0.94	0.35	31.9	<0.001	4.45	0.06
f_{Hmax}	0.03	0.87	2.31	0.15	0.07	0.80
V_{S20}	0.42	0.53	0.79	0.39	1.18	0.30
V_{Smax}	<0.001	0.98	0.52	0.48	0.83	0.38

For each variable, degrees of freedom are phenotype, 1; subjects (phenotype), 12; feeding state, 1; phenotype × state, 1; residual, 12; total, 27.

IMR, immobile metabolic rate; MMR, maximum metabolic rate; AS, aerobic scope (MMR – fasted IMR); U_{crit}, critical swimming speed (cm s^{-1}); $\dot{Q}$, cardiac output (ml min^{-1} kg^{-1}), f_H, heart rate (beats min^{-1}); V_S ventricular stroke volume (ml kg^{-1}); subscript '20' indicates as measured at the lowest swimming speed (20 cm s^{-1}); subscript 'max' indicates as measured at MMR.

for growth in fishes, although this remains to be demonstrated explicitly (Metcalfe et al., 1995; Bang et al., 2007; Millidine et al., 2009). It is possible that differences in SMR existed in the younger fish, when the differences in tolerance of feed deprivation and growth rate had actually been measured. This possibility cannot be discounted, although relative individual variation in SMR is temporally stable and repeatable over a 20-fold increase in mass in salmonids (McCarthy 2000; Cutts et al., 2001). In the current study the sea bass only doubled in mass between the measurements of fasting/re-feeding and of their metabolic rates, and none of the methods used to estimate SMR, whether by static respirometry (Brett and Groves, 1979; Steffensen et al., 1994) (D. Chabot, G.C., A. P. Farrell, R. Koenker and J. F. Steffensen, unpublished) or swimming respirometry (Brett, 1964; Beamish, 1978), provided the slightest indication of a difference between the two phenotypes.

The higher rates of mass loss by the GP during feed deprivation must, nonetheless, have reflected increased rates of energy dissipation. The fasting *versus* re-feeding cycles were performed in a single large rearing tank, where the fish had the opportunity to swim, so the more rapid loss of mass may have reflected higher levels of spontaneous activity in the GP, perhaps reflecting increased foraging behaviours (Stamps, 2007). The higher rates of mass loss may also have reflected dynamic differences in blood flow allocation to the gut (Altimiras et al., 2008; Dupont-Prinet et al., 2009), in particular the continued maintenance of an active gastro-intestinal tract by GP individuals as food deprivation progressed, in anticipation of a possible meal (Wang et al., 2006). Although SMR is, by definition, measured over 48 h in post-absorptive fish (Brett and Groves, 1979), it is possible that had we measured for extended periods of feed deprivation, a significant difference between GP and DP might have emerged. The current dataset cannot, therefore, account for the difference in tolerance of feed deprivation between GP and DP in terms of their post-absorptive SMR.

The trade-off was related to differences in SDA

The SDA results demonstrated significant differences between the two phenotypes, with the response being more pronounced in the beginning in the GP but lasting longer in the DP. The SDA response is thought to reflect in large part the processes of protein turnover and tissue deposition that follow assimilation of amino acids from a meal, so to reflect the energetic costs of growth (McCue, 2006; Fraser and Rogers, 2007; Secor, 2009). The fact that the GP individuals completed their SDA faster than the DP, by achieving a larger peak response, would allow them to process meals more rapidly and so feed more frequently than DP. These data are therefore consistent with a greater capacity for growth in the GP. Furthermore, the fact that the SDA area was the same in both phenotypes indicates that the same amount of the energy from the meal was dissipated to meet the costs of growth. This result differs from Atlantic salmon (*Salmo salar*) juveniles, where individuals with higher SMR could complete their SDA response faster but they also dissipated significantly greater energy in the SDA and hence were less efficient (Millidine et al., 2009).

The current study therefore provides a clear proximal physiological mechanism underlying intra-specific diversity in growth rate in the sea bass. The ability of GP fish to complete the SDA response faster may reflect a larger gastro-intestinal tract and greater capacity for nutrient assimilation but also perhaps a greater capacity for protein turnover and deposition in all body tissues. It has been demonstrated that only a minor proportion of the increase in oxygen uptake that comprises the SDA response can be accounted for by post-prandial rates of blood flow allocation to the gastro-intestinal tract in sea bass (Altimiras et al., 2008; Dupont-Prinet et al., 2009) This response must therefore reflect processes, presumably protein handling, in other body tissues.

The trade-off was not related to differences in cardirespiratory performance

The values for MMR, AS, maximum $\dot{Q}$ and U_{crit} performance were very similar to those obtained in other studies on this species at a similar temperature (Chatelier et al., 2006; Claireaux et al., 2006; Dupont-Prinet et al., 2009; Jourdan-Pineau et al., 2010). As has been described in detail previously (Dupont-Prinet et al., 2009; Jourdan-Pineau et al., 2010), the sea bass were able to achieve a higher MMR after feeding than they achieved when fasted. This allowed them to allocate the same amount of $\dot{M}_{O_2}$ to swimming as when fasted, thereby showing no post-prandial decline in U_{crit}, while also maintaining their SDA response. Speculating on the mechanisms that allow the sea bass to increase their MMR and thereby maintain their post-prandial exercise performance is beyond the scope of the current study, but this ability represents a notable difference from salmonids, which suffer a decline in U_{crit} performance if they are exercised while also performing SDA (Alsop and Wood, 1997; Thorarensen and Farrell, 2006). Dupont-Prinet et al. found that the increased MMR in digesting sea bass was not related to greater post-prandial cardiac performance. The current results confirm this finding, because maximum $\dot{Q}$ during exercise did not differ between fasted and fed states, in either phenotype (Dupont-Prinet et al., 2009).

It has previously been suggested that a relationship may exist between growth capacity and overall aerobic capacity in fishes (Metcalfe et al., 1995). This hypothesis was not supported in the current study on sea bass, as both phenotypes exhibited similar

cardiorespiratory performance during incremental exercise, including when exercised after consumption of a meal. Thus, the ability of the GP individuals to process meals faster did not reflect increased aerobic metabolic capacity and underlying cardiac performance. It might be argued that differences in these traits could have been evident in the younger fish, when the differences in tolerance of feed deprivation *versus* growth rate had actually been measured. Relative individual variation in U_{crit} performance is known, however, to be temporally repeatable over extended periods and a doubling of body mass in the European sea bass (Claireaux et al., 2007), and there is evidence that relative variation in exercise and cardiac performance may be stable individual lifetime traits in teleosts (Claireaux et al., 2005). Although the sea bass were tested for their U_{crit} performance starting at 6 h after feeding, and therefore they completed the test over the period when they had exhibited their maximum SDA amplitude under static conditions, the actual SDA response was lower in the swimming fish and did not differ between the two phenotypes. This was presumably because sustained aerobic exercise, including at low speeds, curtails blood flow to the gastro-intestinal tract in sea bass (Altimiras et al., 2008; Dupont-Prinet et al., 2009), which may have hindered development of the SDA response. Nonetheless, if the GP had greater cardiorespiratory capacity, it might be expected that they would sustain a larger SDA response than in DP but this was not the case.

CONCLUSIONS

The results demonstrate that a trade-off exists between compensatory growth rate and the ability to tolerate feed deprivation in the European sea bass. The study of phenotypes selected from the opposing ends of this trade-off (GP *versus* DP) could not demonstrate a lower SMR that might account for greater relative tolerance of feed deprivation in DP or a greater cardiorespiratory performance that might account for the greater rates of compensatory growth in GP. The increased compensatory growth rate of the GP was, however, directly linked to an ability to complete the SDA response faster than the DP, with no difference in relative energetic efficiency. This would allow this phenotype to feed more frequently and hence grow more rapidly when food was available. The results indicate that individual variation in growth rate in sea bass reflects, in part, a trade-off against tolerance of food deprivation. The two phenotypes represented the opposing ends of a spectrum. The strategy exemplified by GP would involve the rapid exploitation of resources when these were available, to grow (and presumably develop fuel stores) as fast as possible, but at the cost of physiological and/or behavioural attributes which lead to increased energy dissipation when food is not available. The opposing strategy, exemplified by the DP, is a less 'boom and bust' approach, with a lower physiological capacity to exploit resources but which is less costly to sustain during periods of food deprivation. Further research is needed to explore the physiological basis of these two energetic strategies.

LIST OF ABBREVIATIONS

AS	aerobic scope of exercise
DP	deprivation phenotypes
f_H	heart rate
GP	growth phenotypes
IMR	immobile metabolic rate
MMR	maximum metabolic rate
$\dot{M}_{O_2}$	metabolic rate (rate of O_2 consumption)
$\dot{M}_{O_2peak}$	peak $\dot{M}_{O_2}$ during the SDA response
$\dot{Q}$	cardiac output
RMR	routine metabolic rate
SDA	specific dynamic action
SGR	specific growth rate
SMR	standard metabolic rate
T_{peak}	time to $\dot{M}_{O_2peak}$ during the SDA response
U_{crit}	critical swimming speed
V_S	stroke volume

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