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Fast growers sprint slower: effects of food deprivation and re-feeding on sprint swimming performance in individual juvenile European sea bass

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ABSTRACT

While many ectothermic species can withstand prolonged fasting without mortality, food deprivation may have sublethal effects of ecological importance, including reductions in locomotor ability. Little is known about how such changes in performance in individual animals are related to either mass loss during food deprivation or growth rate during re-feeding. This study followed changes in the maximum sprint swimming performance of individual European sea bass, *Dicentrarchus labrax*, throughout 45 days of food deprivation and 30 days of re-feeding. Maximum sprint speed did not show a significant decline until 45 days of food deprivation. Among individuals, the reduction in sprinting speed at this time was not related to mass loss. After 30 days of re-feeding, mean sprinting speed had recovered to match that of control fish. Among individuals, however, maximum sprinting speed was negatively correlated with growth rate after the resumption of feeding. This suggests that the rapid compensatory growth that occurs during re-feeding after a prolonged fast carries a physiological cost in terms of reduced sprinting capacity, the extent of which shows continuous variation among individuals in relation to growth rate. The long-term repeatability of maximum sprint speed was low when fish were fasted or fed a maintenance ration, but was high among control fish fed to satiation. Fish that had been previously food deprived continued to show low repeatability in sprinting ability even after the initiation of *ad libitum* feeding, probably stemming from variation in compensatory growth among individuals and its associated negative effects on sprinting ability. Together, these results suggest that food limitation can disrupt hierarchies of maximum sprint performance within populations. In the wild, the cumulative effects on locomotor capacity of fasting and re-feeding could lead to variable survival among individuals with different growth trajectories following a period of food deprivation.

KEY WORDS: Foraging, Trade-offs, Ecophysiology, Teleost fish, Food deprivation, Locomotion, Compensatory growth

INTRODUCTION

Extended periods of food deprivation are common for many animal species (McCue, 2010; Wang et al., 2006). There are numerous abiotic factors that can affect food availability, including acute or seasonal fluctuations in temperature or light levels, and in aquatic environments, salinity, turbidity or oxygenation (Post and Parkinson, 2001). Characteristics of individual animals, such as reproductive state, social status and life stage, also affect the willingness or ability to feed (Patton et al., 1970; Robin et al., 1988; Watts, 1990). High predator abundance can also reduce feeding opportunities, possibly leading to diminished growth or condition (Killen and Brown, 2006; Pérez-Tris et al., 2004). Many ectotherms can withstand weeks, months or even years of food deprivation without mortality (Biro et al., 2004; Hervant et al., 2001; Merkle and Hanke, 1988; van Ginneken and Maes, 2005), but food deprivation can have important sublethal effects on behaviour and physiology. Long periods without feeding can lead to the degradation of skeletal muscle as structural proteins are catabolised for fuel (Bugeon et al., 2004; Johnston, 1981; Wang et al., 2006). Food deprivation can also reduce the activity of enzymes involved in aerobic and anaerobic metabolism (Martínez et al., 2004; Martínez et al., 2002), and decrease anaerobic fuel stores (Hervant et al., 2001; Kieffer and Tufts, 1998; Merkle and Hanke, 1988). Together or independently, these factors can reduce the capacity for aerobic and anaerobic exercise and locomotor ability (Gingerich et al., 2010; Kolok, 1992; Martínez et al., 2004).

While pursuing prey or evading predators, many ectotherms are capable of achieving extremely fast sprints over relatively short distances, using muscular contractions powered by anaerobic metabolism (Bauwens et al., 1995; Husak, 2006; Nelson and Claireaux, 2005; Nelson et al., 2002; Vandamm et al., 2012; Vanhooydonck et al., 2001). In fishes, speeds achieved during sprints can exceed those attained during all other types of swimming (including the C-start escape response) and may therefore represent the maximal level of anaerobic locomotor performance (Marras et al., 2013). Previous work on cold-climate fish has shown that maximum sprint speed can be reduced after several months of food deprivation [Atlantic cod *Gadus morhua* (Martínez et al., 2002)], but the effects of food deprivation on sprint performance of other species are unknown. Shorter durations may be important for other species, especially those that live in warmer climates and may consume endogenous fuels more rapidly. Furthermore, there is still little known about how anaerobic performance may recover during a period of re-feeding and how this may relate to individual growth trajectories.

Upon re-feeding after a prolonged fast, many species exhibit a period of rapid compensatory growth, greatly exceeding the growth rates displayed by routinely feeding individuals (Ali et al., 2003; Metcalfe and Monaghan, 2001). This implies that under normal circumstances, individuals are growing at a submaximal rate. Considering the potential benefits of large body size within a cohort, for competitive ability and reproductive success, this presumably indicates that extremely rapid growth carries some physiological costs. Indeed, rapid growth can have a negative effect on locomotory ability

in various taxa (Álvarez and Metcalfe, 2007; Arendt, 2003; Klukowski et al., 1998; Royle et al., 2006). However, changes in the performance of individual animals in relation to the amount of compensatory growth experienced after a period of food deprivation have not been investigated. In addition, while several studies have documented an apparent trade-off between routine growth and aerobic locomotion in fishes (Arnott et al., 2006; Gregory and Wood, 1998; Kolok and Oris, 1995; Sogard and Olla, 2002), few studies have examined the effects of growth on anaerobic locomotion. Among the few studies examining this issue, Handelsman et al. (Handelsman et al., 2010) observed that individual sea bass that displayed higher growth rates in high-food, low-density mesocosms tended to have the lowest maximum sprint speeds. The relationship of such effects to prior mass loss during a period of food deprivation and any additional effects of compensatory growth remain unknown. Following food deprivation, detrimental effects of compensatory growth on swimming performance could impair the ability to avoid predation or capture prey even after food becomes available. Inter-individual variation in the degree to which animals can recover locomotor ability after food deprivation could therefore lead to variability in foraging ability, predator susceptibility and, ultimately, reproductive success (Plaut, 2001).

Sprinting ability has been shown to be repeatable over the short term [e.g. days (Nelson and Claireaux, 2005)] and long term [e.g. months (Reidy et al., 2000; Martınez et al., 2002)], thus making this trait a potential target for natural selection (Dohm, 2002; Endler, 1996). However, changes in food availability could affect the repeatability of performance traits if some individuals are more sensitive to the effects of food deprivation or re-feeding than others (Dupont-Prinet et al., 2010; Killen et al., 2011). If the rank-order of performance traits among individuals within a population changes in response to factors such as food deprivation or rapid growth, different individuals may be more or less prone to selective pressures under different circumstances. Locomotor performance in fishes has been shown to be related to components of fitness (Billerbeck et al., 2001; Ghalambor et al., 2004; Walker et al., 2005), and sprinting ability in particular may enhance the probability of survival in the face of predation risk (Handelsman et al., 2010). Environmental effects on the repeatability of swim performance have received little attention, though Claireaux et al. (Claireaux et al., 2007) observed that sprinting ability when tested after acclimation to two different temperatures (12 and 22°C) was significantly repeatable. Martínez et al. (Martínez et al., 2002) found that sprinting ability in Atlantic cod was largely repeatable with fasting and re-feeding, but did not examine how variation in growth rate may contribute to changes in sprint performance with feeding regime among individuals.

This study followed changes in the maximum sprint swimming performance of individual juvenile European sea bass, *Dicenctrarchus labrax*, during 45 days of food deprivation and 30 days of re-feeding. Juveniles of this species colonise coastal marine environments such as lagoons and estuaries on a seasonal basis (Pickett and Pawson, 1994). Like many fish species, periods of reduced food intake are a common feature in the life cycle of European sea bass (Dupont-Prinet et al., 2010; Killen et al., 2011). Juveniles feed on benthic invertebrates, populations of which exhibit wide fluctuations in abundance and community structure in lagoon environments, both seasonally and inter-annually (Marchini et al., 2004). European sea bass in temperate latitudes undergo prolonged periods of reduced food consumption while overwintering, while populations inhabiting lagoons proximate to the Mediterranean Sea can experience stochastic reductions in prey abundance as a result of warming and eutrophication during the summer months (Marchini et al., 2004). As juvenile European sea bass are frequently targeted as prey by larger fishes and diving birds, sprint swimming ability would be useful in avoiding capture by these predators, as well as for capturing prey. It was hypothesised that: (1) food deprivation would negatively affect the sprint swimming performance of juvenile sea bass; (2) individuals experiencing the highest rates of growth would experience the lowest recovery of swimming ability after re-feeding; and (3) variability in sensitivity to food deprivation and re-feeding would reduce repeatability in sprint ability among individuals during food deprivation and re-feeding.

RESULTS

Mass loss and growth

During the fasting phase, the control treatment maintained body mass essentially unchanged and, although they appeared to show a slight increase in fork length compared to food-deprived fish, this was not significant (Fig. 1, Table 1). Fish in the food-deprived group maintained a constant fork length but lost markedly more mass throughout the fasting phase [general linear model (GLM), $F=105.29$, $P<0.0001$; Fig. 1] compared with the control group.

Throughout the growth phase, mean mass-specific growth rate (G_M) was higher in the food-deprived group as compared with the control group, whether comparisons were made between days 45 and 60 (GLM, $F=8.726$, $P=0.007$), days 60 and 75 (GLM, $F=33.275$, $P=<0.0001$) or over the entire growth phase (days 45 to 75; GLM, $F=105.189$; $P=<0.0001$). Mean length-specific growth rate (G_L) between treatments was not significantly different between days 45 and 60 (GLM, $F=0.528$; $P>0.05$), but was higher in the food-deprived group between days 60 and 75 (GLM, $F=4.609$; $P=0.043$), and over the growth phase as a whole (GLM, $F=8.332$; $P<0.009$). G_L in the food-deprived group was more than twice as high during the last half of the growth phase as compared with the first half [linear mixed model (LMM), $F=13.113$, $P=0.002$], while G_M remained relatively constant in the food-deprived group over the entire growth phase (LMM, $F=0.617$, $P=0.440$). For the control group, G_L was also higher during the second half of the growth phase (as compared with the first; LMM, $F=7.086$, $P=0.015$), while G_M was relatively consistent (linear mixed model, $F=1.985$, $P=0.175$).

Sprint performance

By the end of the fasting phase at day 45, there was a significant effect of treatment on maximum sprint speed (GLM, $F=5.140$, $P=0.034$; Fig. 1). There was no significant difference in maximum sprint speed between treatments at any measurement period during the growth phase (i.e. on days 60 and 75; GLMs, $P>0.05$). There were no significant differences in maximum sprint speed between treatments at any point throughout the growth phase (GLMs, $P>0.05$). There was no effect of body length on maximum sprint speed in either treatment during any measurement period throughout the study.

The short-term repeatability (among trials on a given day) of sprint performance was high within treatments, with strong correlations between the best and second best trial per individual during each measurement period (Pearson correlations, $r=0.74$–0.91, $P<0.0001$). There was low repeatability in maximum sprint speed in both treatments throughout the fasting phase [control: intraclass correlation coefficient (ICC)=0.206; food-deprived: ICC=0.191]. During the growth phase, control fish showed a higher degree of repeatability (ICC=0.514) as compared with those that had previously been food deprived (ICC=0.313), and in both treatments over the study as a whole (control: ICC=0.179; food-deprived: ICC=0.208).
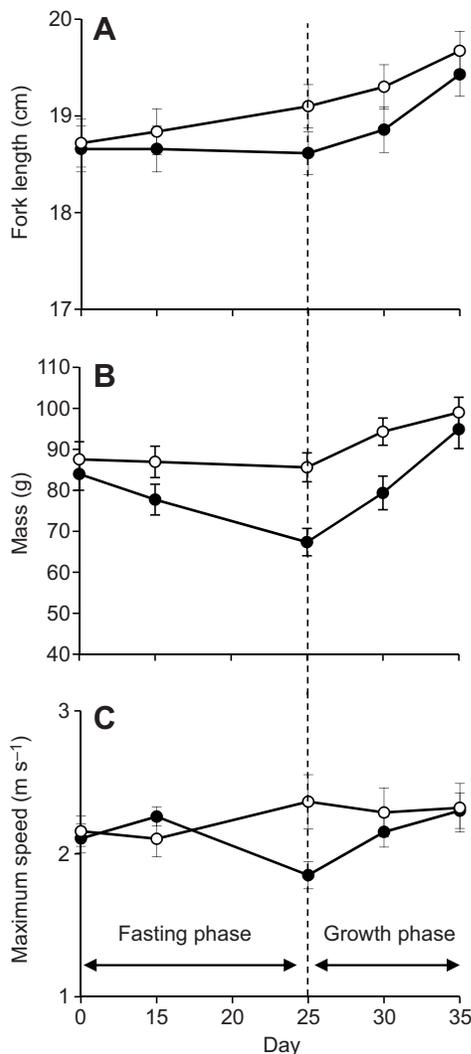
Fig. 1. Growth rates and sprinting ability throughout periods of fasting and re-feeding in juvenile European sea bass. (A) Fork length, (B) body mass and (C) maximum sprint swimming speed in juvenile European sea bass during the study. Filled circles, food-deprived group; open circles, control group. The vertical dashed line indicates the division between the fasting phase from day 0 to 45 of the study, and the growth phase during days 45–75 of the study.

Maximum sprint speed was not related to G_M at any point throughout the fasting phase in either treatment, nor was the change in maximum sprint speed between any two measurement periods during the fasting phase. At day 60 during the growth phase, maximum sprint speed in both treatments had no relation to G_M or G_L measured over days 45–60. At day 75, however, fish in the food-deprived group with the highest G_L between days 60 and 75 tended to have lowest maximum sprint speeds (GLM, $F=18.506$, $P=0.002$; Fig. 2A) and also showed the largest decrease in maximum sprint speed over this same time period (GLM, $F=11.132$, $P=0.008$; Fig. 2B). For control fish, there were no significant relationships between G_M or G_L and either maximum sprint speed or the change in sprint speed at any point throughout the growth phase.

DISCUSSION

While maximum sprint speed was relatively robust to the effects of short-term food deprivation (15 days) in juvenile sea bass, longer-

term fasting (45 days) did cause a significant decline in sprinting ability. An analysis of individual fish revealed that the magnitude of this decline in maximum sprint was not related to the rate of mass loss during food deprivation. During re-feeding, food-deprived fish rapidly recovered sprinting ability. Among individual animals that had been food deprived, however, those with the fastest growth during the re-feeding phase showed lower maximum sprint speeds, and this decrease in sprinting ability occurred during the interval when their structural growth (in length) was most rapid. This analysis of individual animals revealed trends that were not apparent when comparing mean values, and indicates that the rate of compensatory growth by an individual following a period of food deprivation can directly and negatively impinge on their swim performance. Recent work has demonstrated that swim speeds during sprints are the fastest attainable by juvenile sea bass, exceeding those attained during a C-start response (Marras et al., 2013). This suggests that the effects of food deprivation and growth during re-feeding observed in the present study may limit the maximal achievable level of anaerobic performance in individual fish.

Effects of food deprivation on sprint performance
There was no effect of food deprivation on sprint speed after 15 days, suggesting that sprinting ability is somewhat resistant to fasting. However, it can take several weeks or even months of food deprivation in fish before the extensive use of structural proteins as a metabolic fuel source leads to a breakdown of skeletal muscle (Bugeon et al., 2004; Johnston, 1981), and this may have played a role in the reduced sprinting ability observed after 45 days of food deprivation. The large myotomal blocks of glycolytic white muscle, the contraction of which powers anaerobic sprint swimming, are especially vulnerable to degradation during food deprivation, with food-deprived fishes previously being observed to display large reductions in myofibril diameter and Z-disc degradation (Johnston, 1981). There can also be decreases in glycolytic enzyme activity in white muscle following food deprivation (Martínez et al., 2002), and a reduction in white muscle glycogen stores (Kieffer and Tufts, 1998), which is the primary substrate for anaerobic ATP production during burst-type swimming (Kieffer, 2000). Interestingly, however, cytosolic ATP and phosphocreatine are the most likely fuels to be utilised during the short-term bursts that comprise sprinting (Kieffer, 2000), and these are conserved during long-term food deprivation (Kieffer and Tufts, 1998; Gingerich et al., 2010). It is therefore likely that the decreased maximum sprint speed observed after 45 days of food deprivation was due to diminished muscle mass and/or muscle fibre condition, decreased glycolytic enzyme activity or a combination of these factors. Differences in behavioural tendencies among individuals could also influence swimming performance, especially if behaviour is affected by food deprivation (Killen et al., 2011). For instance, some individuals may reduce routine swimming activity during food deprivation in an attempt to conserve energy stores (Méndez and Wieser, 1993), and so may have been less motivated to sprint during trials.

Among individuals, sprint performance after food deprivation was not related to the rate of mass loss during the fasting phase. This is similar to previous findings in Atlantic cod, where the sprint performance of individuals after 6 weeks of food deprivation was not linked to individual condition (Martínez et al., 2002). These results indicate that change in individual body mass alone is not an effective predictor of sprint performance after a period of food deprivation. Individuals are likely to have variable amounts of stored lipids before a period of food deprivation, and therefore experience

Table 1. Mass- and length-specific growth rates (G_M and G_L, respectively) for control and food-deprived European sea bass

Treatment	Period (days)	G_M (% day^{-1})	G_L (% day^{-1})
Control	0–15	−0.029±0.084	0.043±0.015
	15–45	−0.016±0.053	0.047±0.015
	45–60	0.575±0.132	0.069±0.015
	60–75	0.321±0.121	0.129±0.018
	Fasting phase (0–45)	−0.013±0.053	0.045±0.009
	Growth phase (45–75)	0.447±0.041	0.099±0.011
Food-deprived	0–15	−0.518±0.031	−5.31×10^{-5}±0.004
	15–45	−0.479±0.017	−0.0072±0.005
	45–60	1.084±0.116	0.085±0.016
	60–75	1.201±0.092	0.200±0.027
	Fasting phase (0–45)	−0.492±0.014	−0.004±0.003
	Growth phase (45–75)	1.142±0.058	0.143±0.011

Control fish were fed a maintenance ration for the first 45 days of the study while food-deprived fish were not fed. After this point (days 45–75), fish in both treatments were fed *ad libitum*.

different degrees of endogenous protein catabolism. Furthermore, changes in morphology, especially the ratio of caudal fin area to body mass, could change to varying degrees among individuals during food deprivation, thus affecting the ability of an individual to propel itself at a given tail beat frequency.

During the fasting phase, fish in the control group experienced no mean decrease in maximum sprinting speed, suggesting that the maintenance ration was sufficient to preserve sprinting ability. However, the results of this study indicate that long periods without food in the wild, such as while over-wintering in temperate latitudes (Post and Parkinson, 2001) or during summer months in warmer latitudes due to eutrophication (Marchini et al., 2004), could cause a decrease in the maximum sprint speed of individuals. Although mass loss would be slower at cold temperatures, the duration of food deprivation while overwintering is generally much longer (lasting months), and the degree of mass loss observed in the present study was similar to that observed among fish in natural and simulated overwintering conditions (e.g. Martínez et al., 2002; Eckmann, 2004; Sogard and Olla, 2002). An interesting avenue for future research would be to examine how fasting and re-feeding may interact with temperature to affect swim performance. Temperature can have a profound effect on mass loss and growth rates in ectotherms (e.g. Killen and Brown, 2006), possibly leading to differing effects of feeding history and growth trajectories on swim performance among populations of the same species.

An additional consequence of food deprivation in many fish species is an increased willingness to forage under the threat of predation (Gotceitas and Godin, 1991; Killen et al., 2011; Krause et al., 1998). At the same time, however, reduced sprint performance resulting from food deprivation could make individuals even more vulnerable to being killed by a predator during risky foraging behaviour. Food-deprived individuals may also be less able to feed when food does become available (Jonas and Wahl, 1998), especially if required to pursue fast-moving prey. Nutritional deficiencies could also affect the sensory ability of fish (Bell et al., 1995), thus impairing the ability to detect both predators and prey.

Relationship between growth and sprint performance

During the growth phase, there was an increase in G_L in the food-deprived group relative to the control group, suggesting compensatory growth in the synthesis of structural elements upon re-feeding (Nicieza and Álvarez, 2009), and not simply in the accumulation of energy stores that would cause an increase in body mass (Nicieza and Álvarez, 2009). This agrees with previous studies reporting rapid growth during re-feeding after food deprivation in a number of taxa (Ali et al., 2003; Metcalfe and Monaghan, 2001).

The analysis of individual growth rate and sprinting ability revealed links among individual traits that were not apparent when examining mean values between treatments. For example, maximum sprint speed increased among food-deprived individuals during the growth phase, to match that of the control group by day 60 of the study (i.e. after 15 days of re-feeding). Further, at day 75 (the end of the study), the mean maximum sprinting speed in both treatments was also approximately equal. This suggests that, with the resumption of regular feeding, fish are able to quickly recover losses in sprint ability caused by food deprivation. An examination of the data for individual fish suggests, however, this may not entirely be the case. Fish that showed the greatest compensatory growth had the slowest sprint speeds by the end of the growth phase. In agreement with previous studies, this suggests that compensatory growth causes a reduction in swimming performance (Álvarez and Metcalfe, 2005; Álvarez and Metcalfe, 2007; Royle et al., 2006; Sogard and Olla, 2002). Handelsman et al. (Handelsman et al., 2010) noted an apparent trade-off between routine growth and sprint speed in regularly feeding sea bass held in outdoor mesocosms with high access to food and low conspecific density. Interestingly, we did not observe such a negative correlation between growth and maximum sprint speeds among control fish, suggesting that the negative effects of growth on sprinting ability may be exaggerated by compensatory growth as compared with routine growth. It is noteworthy that this negative correlation between compensatory growth rate and sprint performance was only observed between days 60 and 75 of the study, and not during the first portion of the growth phase (days 45–60). This could indicate that the locomotory costs of compensatory growth may be somewhat delayed, perhaps via an initial gain in length before later acquiring bulk that could slow movement. The present study, however, found a nearly opposite trend: G_L in the food-deprived group was much higher during the last half of the growth phase, while G_M remained relatively constant. This is in agreement with previous work showing that starved animals tend to regain energy stores upon the resumption of feeding before devoting resources to structural elements (Jobling and Johansen, 1999; Nicieza and Álvarez, 2009), and suggests that the delayed reduction in sprint performance was probably due to the increased structural growth occurring later in the growth phase. The mechanisms underlying the locomotory costs of compensatory growth have not been investigated directly, although there are differences in the cellular structure and composition of muscle fibres among fish that have undergone rapid growth (Johnston et al., 2002).

The negative effects of compensatory growth could make previously food-deprived animals somewhat prone to predation or less able to capture prey even after they resume feeding following a
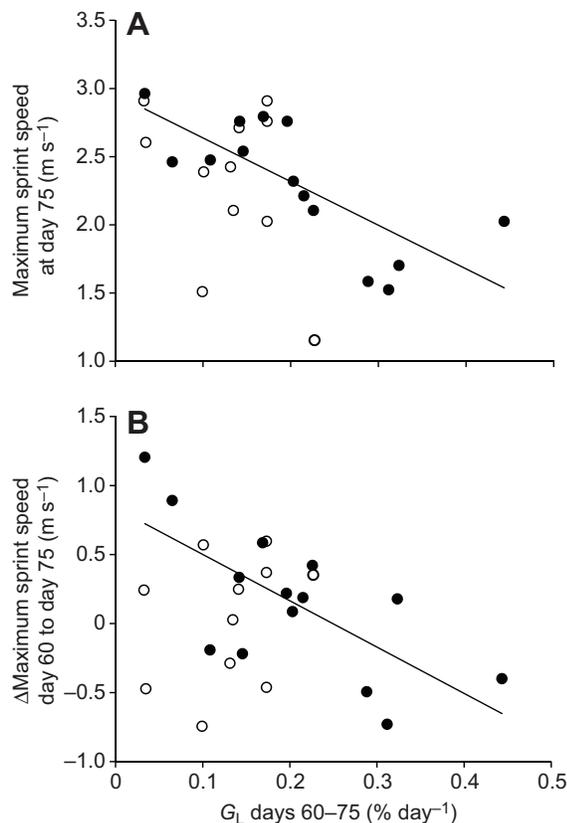
Fig. 2. Relationships between sprinting ability and growth rate in juvenile European sea bass. Relationship between length-specific growth rate (G_L) from days 60 to 75 and: (A) maximum sprint speed and (B) the change in maximum sprint speed between days 60 and 75. Filled circles, food-deprived group; open circles, control group. There were no significant relationships for the control group. Significant regressions for the food-deprived group are as follows: (A) maximum sprint speed=$-3.815G_L$+3.07, r^2=0.649, P=0.0005; (B) Δmaximum speed=$-3.87G_L$+0.925, r^2=0.507, P=0.004.

prolonged period of fasting. One question is why any animal would undergo compensatory growth considering its apparently detrimental effects on locomotor ability. There are, however, many potential benefits associated with rapid growth and large body size in fishes, such as protection from predators (Nilsson and Brönmark, 2000), increased dietary breadth (Werner and Gilliam, 1984), and increased fecundity and reproductive success (Kraak et al., 1999). In some species, larger individuals may also be able to obtain higher quality feeding territories by dominating conspecifics (Cutts et al., 1999), thus ensuring access to food regardless of a reduction in swimming ability. Some individuals appear more willing to accept some cost in terms of reduced locomotion to receive the benefits of increased body size in these other areas. Indeed, the results of this study indicate that the cost resulting from compensatory growth is not an 'all or nothing' response, but that reduction in sprinting performance shows continuous variation in relation to the growth rate experienced by individual animals.

Repeatability of sprint performance

In agreement with previous studies (Claireaux et al., 2007; Handelsman et al., 2010, Marras et al., 2013), repeatability of maximum sprint speeds within a measurement day was high in both treatments. Throughout the fasting phase, however, repeatability in both treatments was low, suggesting that conditions of limited food availability may disrupt performance hierarchies at the population

level. Although control fish were fed a maintenance ration during the growth phase, some individuals gained a small amount of mass during this period while others lost a small amount of mass. Variation in the relative food intake among individuals may therefore be sufficient to alter the relative performance of sprinting ability among individuals. This is supported by the observation that during *ad libitum* feeding throughout the growth phase, the control group displayed strong repeatability across measurement periods until the end of the study. In contrast, fish that had previously been food deprived continued to show low repeatability during this time. This lack of repeatability was likely driven by the apparently negative effects of compensatory growth on sprinting ability among individuals. Overall, these results contrast with those of Martínez et al. (Martínez et al., 2002), who observed that repeatability of Atlantic cod sprint speeds remain stable even during food deprivation and re-feeding. Therefore, it is possible that the effects of food deprivation and re-feeding vary among species, especially if some species experience a higher degree of compensatory growth than others (Sogard and Olla, 2002).

Although sprint performance in fishes has previously been shown to be repeatable over the course of several months (Martínez et al., 2002; Reidy et al., 2000), any changes in repeatability may alter its importance as a target of natural selection. If the repeatability of sprint performance is so sensitive that it is continually disrupted by environmental factors, then its evolutionary significance will be diminished. However, if repeatability changes across situations but then becomes stable under a new set of conditions, then some individuals may become more or less fit in different contexts, especially in scenarios where sprint speed is important for evading predators or capturing food (Handelsman et al., 2010). The results of the present study suggest that the repeatability of maximum sprint speed in juvenile sea bass is labile when food availability is limited and strengthens when food is abundant in animals not undergoing compensatory growth.

Conclusions

This study demonstrates that prolonged food deprivation can cause a reduction in the maximum sprinting speed of juvenile European sea bass. Mean values for sprinting ability appeared to recover quickly, matching that of control fish after only 15 days of re-feeding. An examination of individual fish, however, revealed that the magnitude of the change in sprinting ability was not uniform among fish and was lowest in the fastest-growing individuals. It is possible that these effects of food deprivation and compensatory growth on sprinting capacity could reduce the ability of fish to capture prey or evade predators after long periods of food deprivation. Future studies are needed to examine the extent to which this occurs in the laboratory and in the field, and how these effects may be modulated by additional environmental factors such as temperature.

MATERIALS AND METHODS
Animals

Juvenile European sea bass *Dicentrarchus labrax* (*n*=25) were obtained from a local fish farm (Salses le Chateau, France; 42°49′N, 2°57′E), and stocked under a natural photoperiod (12 h:12 h light:dark) in a large rectangular tank (350×150×100 cm, length × width × height) supplied with re-circulating, filtered natural seawater at a constant temperature (20±0.5°C) and salinity (35.1±0.2‰), for at least 4 weeks prior to use in experiments. The experimental fish were first-generation aquaculture fish from eggs laid and reared in captivity but obtained from wild broodstock captured in the western Mediterranean. Three weeks prior to the start of experiments, all individuals were tagged for identification using VI Alpha tags (Northwest Marine Technology, Inc.). At the beginning of experiments, fish had a mean (±s.e.m.) wet mass of 85.6±2.8 g and 187±17 mm fork length. The

procedures in the study were performed in accordance with the laws governing animal experimentation in France, under a licence (Expérimentation Animale Niv 1) held by D.J.M.

Feeding regimes

Fish were randomly placed into one of two treatments: (1) a 'food-deprived' group that was starved for the first 45 days of the study (n=14); or (2) a 'control' group that received a maintenance ration for the first 45 days of the study (n=11). Throughout the experiment, both treatments were kept in the same large rectangular holding tank divided into three sections using mesh partitions, with each section measuring 117×150×100 cm (length × width × height). Treatments were kept separate in the sections at opposite ends of the tank, with the section in between acting as a buffer to ensure that no feed pellets drifted between the two treatments. For the first 45 days of the experiment (the 'fasting phase'), the control group received a maintenance ration of feed pellets (Aphytec, Mèze, France) equal to 1% of their total body mass per day, while the food-deprived group was not fed. This duration of food deprivation resulted in a degree of mass loss among individuals (19.84±0.49%) nearly identical to that observed in previous studies examining food deprivation in fishes (e.g. Martínez et al., 2002). Animals were inspected daily and did not show visible signs of poor welfare resulting from food deprivation. The control group was not fed a growth ration during this initial phase to avoid large differences in body size between treatments that could confound measurements of sprint swimming speed later in the study. To stimulate growth during the re-feeding phase, all fish were fed *ad libitum*, using rations that exceeded feeding rates reported from studies with self-feeders at the same temperature (Grima et al., 2010; Rubio et al., 2010). Thus, 2% of total body mass per day for the control group and 3% of total body mass per day in the food-deprived group. The difference in ration was owing to differences in hunger level between treatments – individuals in the food-deprived group consuming more food during compensatory growth, characteristic of the hyperphagia often observed among animals undergoing compensatory growth (Ali et al., 2003; Grima et al., 2010; Rubio et al., 2010). The duration of the 'growth phase' lasted 30 days, meaning the duration of the study was 75 days in total.

Measurement of sprint performance

Sprint performance was measured in a raceway chamber as described in Nelson et al. (Nelson and Claireaux, 2005). Dimensions of the raceway were 200×25×30 cm (length × width × height). Light-emitting laser diodes (OnPoint Lasers, Inc., Eden Prairie, Minnesota, and Selectronic, Lille, France) with a power output of 5 mW, a wavelength of 645–670 nm and a beam width of 1.1 mm were placed at intervals of 0.02, 0.04, 0.08, 0.16, 0.25 and 0.50 m from the point at which a fish would begin its sprint. The lasers were placed in front of clear glass windows on one side of the raceway. The laser beam was detected on the opposite side of the chamber by eight arrays of Photodarlington detectors (Honeywell International, Inc., Morristown, NJ, USA). When activated by light, the Photodarlington detector array puts out a 5 V signal to one of eight inputs on a Biopac MP150 data acquisition board (Biopac Systems Inc., Goleta, CA, USA). Data were assimilated with Acqknowledge V.3.7 software (Biopac Systems Inc.), while velocity was calculated from the times of breakage of subsequent laser beams and the distance between detectors utilizing Labview software (National Instruments Corporation, Austin, TX, USA).

The sprint performance of each fish was measured immediately prior to the beginning of the feeding treatments (day 0), after 15 and 45 days of the fasting phase, and then on days 60 and 75 of the experiment, during the growth phase. Before measurement of sprint performance, fish receiving food were fasted for 36 h. Fish were individually transferred to the sprint chamber, without air exposure, and left undisturbed for 1 h. During this period, fish would invariably stay within a darkened area located at the end of the raceway – the point from which the fish would begin their sprint. A trial began by observing that the fish was in proper position, arming the computer, and gently pinching the fish's caudal peduncle (Nelson and Claireaux, 2005). This would cause the fish to burst down the raceway, triggering the photocell circuits and recording the time elapsed between consecutive beam breakages. In many pelagic and benthopelagic fishes, including European sea bass, this behaviour consists of rapid contractions of the body and caudal peduncle (a C- or S-start), followed by one or more vigorous undulations of the caudal fin that propel the fish over short distances at extremely fast speeds (Marras et al., 2013). This was repeated five times for each fish during each measurement period, with 5 min of recovery time between trials. Maximum sprint speed was taken as the fastest speed measured between any two lasers among those located between 0.08 and 0.5 m from the start position in the five sprint trials (Nelson and Claireaux, 2005; Marras et al., 2013).

Data and statistical analyses

Statistics were performed with SPSS statistics v17.0 (SPSS Inc. and IBM). The level of significance for all tests was α=0.05. The normality, linearity and homogeneity of residuals were verified by inspection of residual-fit plots.

Rates of mass loss or growth were estimated in terms of body mass (G_M) and fork length (G_L), and were calculated between measurement periods according to the equation:

$$G = [\ln(s_2) - \ln(s_1)] / t \times 100 , \qquad (1)$$

where s_x is the body mass or standard length at time x, and t is the time elapsed (in days) between time 1 and time 2 (Hopkins, 1992). Differences in growth rate (G_M and G_L) between treatments were examined using general linear models. Separate models were applied to rates of mass loss and growth occurring during the fasting and growth phases, with treatment as a categorical factor. Because growth rate is size dependent (Nicieza and Álvarez, 2009), the initial fork length during each measurement period was also included in models as a covariate. General linear models were also used at each measurement day to examine the effects of treatment (categorical variable), G_M, G_L (continuous variable, calculated since the previous measurement day) and fork length (continuous variable) on maximum sprint speed, and also the magnitude of the change in maximum sprint speed since the previous measurement period.

Short-term repeatability of individual sprint speed was evaluated within each period using Pearson correlations to examine the relationship between the maximum and second-highest sprint speed for each fish measured among trials (Claireaux et al., 2007; Marras et al., 2013). Consistency in maximal sprint speed throughout the course of the study was assessed by calculating the intraclass correlation coefficient within each treatment during each measurement phase (i.e. separately within the fasting phase and growth phase; and across the entire duration of the study).

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