Individual variation and repeatability in aerobic and anaerobic swimming performance of European sea bass, *Dicentrarchus labrax*

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SUMMARY

Studies of inter-individual variation in fish swimming performance may provide insight into how selection has influenced diversity in phenotypic traits. We investigated individual variation and short-term repeatability of individual swimming performance by wild European sea bass in a constant acceleration test (CAT). Fish were challenged with four consecutive CATs with 5 min rest between trials. We measured maximum anaerobic speed at exhaustion (U_{CAT}), gait transition speed from steady aerobic to unsteady anaerobic swimming (U_{gt}), routine metabolic rate (RMR), post-CAT maximum metabolic rate (MMR), aerobic scope and recovery time from the CATs. Fish achieved significantly higher speeds during the first CAT ($U_{CAT}=170\,cm\,s^{-1}$), and had much more inter-individual variation in performance (coefficient of variation, CV=18.43%) than in the subsequent three tests ($U_{CAT}=134\,cm\,s^{-1}$; CV=7.3%), which were very repeatable among individuals. The individual variation in U_{CAT} in the first trial could be accounted for almost exclusively by variation in anaerobic burst-and-coast performance beyond U_{gt}. The U_{gt} itself varied substantially between individuals (CV=11.4%), but was significantly repeatable across all four trials. Individual RMR and MMR varied considerably, but the rank order of post-CAT MMR was highly repeatable. Recovery rate from the four CATs was highly variable and correlated positively with the first U_{CAT} (longer recovery for higher speeds) but negatively with RMR and aerobic scope (shorter recovery for higher RMR and aerobic scope). This large variation in individual performance coupled with the strong correlations between some of the studied variables may reflect divergent selection favouring alternative strategies for foraging and avoiding predation.

Key words: individual variation, repeatability, sea bass, fish, swimming, aerobic performance, anaerobic performance, constant acceleration, gait transition, metabolic rate, recovery time.

INTRODUCTION

Locomotor ability is a key organismal performance trait in the chain of interactions that link biochemical, morphological and physiological traits to fitness (Arnold, 1983). For many species, essential ecological functions such as predator–prey interactions, reproductive activities or foraging, are dependent upon an animal's capacity for movement. The intuitive recognition of this relationship has led to a consistent interest in fish locomotion among scientists, but the nature of the relationship between locomotion and fitness remains largely unknown for most fish species.

The study of fish locomotion began in earnest around 60 years ago (e.g. Black, 1955; Bainbridge, 1958a; Bainbridge, 1958b; Brett, 1964; Fry, 1971; Beamish, 1978) but there are still large gaps in our understanding of the elements that determine swimming performance. For instance, the nature of maximal swimming performance as well as the factors which contribute to the transition between aerobic and anaerobic swimming modes, and to exhaustion, are still poorly understood. Furthermore, we know almost nothing about the ecological and evolutionary relevance of aerobic or anaerobic swimming abilities (e.g. Lankford et al., 2001) and whether natural selection operates on them. For instance, it is unknown whether aerobic and anaerobic performance are linked or whether they follow independent evolutionary trajectories. Quite clearly, investigating how individual fish from wild populations

respond to locomotor challenges is one way to explore the link between swimming performance and fitness (Kolok, 1999; Plaut, 2001; Nelson and Claireaux, 2005).

To investigate whether swimming performance responds to natural selection, three different issues must be considered: (1) the performance trait must show variation amongst individuals that is relatively stable over time – i.e. their performance should be repeatable; (2) it must be shown to contribute to differential fitness among individuals; and (3) it must be heritable (Endler, 1986). Unfortunately, there are very few fish studies that have addressed any of these issues. Only within the past two decades have investigators begun to look at the most tractable among them, the repeatability of individual variation in performance (e.g. Randall et al., 1987; Butler et al., 1989; Kolok, 1992; Nelson et al., 1994; Gregory and Wood, 1998) and only very recently have investigators broached the topics of fitness and heritability, using small fishes with short generation times (e.g. Lankford et al., 2001; O'Steen et al., 2002; Walker et al., 2005).

When it has been studied, individual repeatability of locomotor performance has been primarily examined in incremental velocity tests patterned after the critical swimming speed (U_{crit}) test designed by Brett (Brett, 1964) (e.g. Randall et al., 1987; Butler et al., 1989; Kolok, 1992; Kolok and Farrell, 1994; Nelson et al., 1994; Gregory and Wood, 1998; Nelson et al., 2002). The U_{crit} test has generally

proven to be repeatable, even across thermal regimes, surgical treatments and 6 months of mesocosm residence (Kolok, 1992; Butler et al., 1989; Kolok and Farrell, 1994; Claireaux et al., 2007). Sprint swimming, which is used to capture prey or avoid predatory pursuit, also exhibits much intraspecific variation that is relatively stable, being repeatable over time periods spanning from hours to months (Reidy et al., 2000; Nelson et al., 2002; Nelson and Claireaux, 2005; Nelson et al., 2008) and across different thermal and nutritional conditions (Martinez et al., 2002; Claireaux et al., 2007). There is also evidence that fast-start performance, which is a critical component of some 'sit and wait' predator–prey encounters, is stable and repeatable over hours and weeks (Fuiman and Cowan, 2003) (S.M., unpublished observations). Constant acceleration tests (CATs), the focus of the present study, have been shown to be repeatable in the Atlantic cod (Reidy et al., 2000). This type of test evaluates a swimming performance that fish may employ when manoeuvring through strong currents, being pursued by strong swimming predators, or trying to escape a fishing trawl.

The European sea bass *Dicentrarchus labrax* L. is a temperate perciform species that is economically important in the Mediterranean and western Atlantic. They are active predators, which catch their prey by pursuit, and adults are known to swim over 1000 km to forage and reach spawning grounds (Pickett and Pawson, 1994). The species has a complex life cycle; spawning occurs offshore in late winter and the pelagic larvae hatch in the open sea. They drift inshore and colonize sheltered transitional coastal habitats in the spring, in particular lagoons and estuaries, where they metamorphose to juveniles and grow for their first summer (Pickett and Pawson, 1994; Dufour et al., 2009). Predation pressure by other fish and birds may cause a significant number of mortalities during this phase (Quignard et al., 1984; Dufour et al., 2009). The sea bass leave the lagoons and estuaries as temperatures drop in autumn, but they continue facultative seasonal migrations between the open sea and the transitional habitats as they grow to maturity. Thus, European sea bass have a life cycle that intimates an important role for locomotion, in which both anaerobic burst swimming and sustained aerobic swimming performance could potentially influence an individual's ability to survive, grow to maturity and reproduce.

In the present study, individual variation in a CAT, and its repeatability over the short term (minutes), was investigated in European sea bass. The CAT can be completed much more rapidly than the more widely used U_{crit} protocol [minutes *vs* hours (Nelson et al., 2002; Farrell, 2008)] and can provide a measure of both aerobic and anaerobic performance. Sea bass performance was measured consecutively four times with a 5 min interval between each CAT. The fish were filmed to analyse changes in swimming gait: aerobic performance was measured as the speed at which the fish transitioned from steady aerobic to a 'burst-and-coast' swimming gait where thrust production was supplemented with anaerobic muscle contractions; anaerobic performance was then taken as the difference between the gait transition speed (U_{gt}) and the maximum speed achieved in the CAT (U_{CAT}). Oxygen consumption was measured to assess routine metabolic rate (RMR) (Fry, 1971) prior to the CATs, to estimate maximum metabolic rate (MMR) as excess post-exercise oxygen consumption (EPOC) (Gaesser and Brooks, 1984), and to analyse the time required to recover from the four successive CATs.

MATERIALS AND METHODS
Fish collection and maintenance
Experimental animals (wild European sea bass; total length 29.3±0.5 cm, mass 190.1±11.6 g, N=16) were initially caught from a local lagoon (Palavas les Flots, France) and kept at the Station Méditerranéenne de l'Environnement Littoral in indoor tanks supplied with natural seawater (salinity 29–31‰) pumped from the adjacent lagoon (Etang de Thau, Sète). Fish were maintained for 2 years under natural temperature and photoperiod and fed twice a week with commercial pellets (Aphytec, Mèze, France). Experiments were conducted in August 2007 after fish had been acclimated for at least 3 weeks to the experimental temperature (23°C). Feeding was discontinued 48 h before moving the fish to the experimental set-up, by isolating the fish without air exposure in a transfer tube that also served to acclimatize the fish to an enclosed environment (Nelson and Claireaux, 2005). All animal handling procedures complied with French national law.

Experimental set-up
Fish oxygen uptake ($\dot{M}_{O_2}$) and swimming performance were measured in a 49 l modified Brett-type swim-tunnel respirometer (for details, see McKenzie et al., 2001) thermoregulated at 23±0.5°C. Briefly, the working section of the tunnel was 60 cm in length, 16 cm in width and 16 cm in height. The upstream swimming section was darkened to motivate the fish to occupy an upstream position. A plastic honeycomb grid and deflectors were inserted into the recirculation loop to promote rectilinear flow and uniform velocity profiles. Water flow was generated by a variable-speed electrical motor and propeller. Flow characteristics were assessed visually by observing dye flow patterns. The water speed to motor voltage output relationship was established by measuring flow (Hontzsch HFA, Waiblingen, Germany) at 33 separate voltage settings at a single point in the middle of the swimming section and calculating the best-fit line by the method of least squares. Swimming speeds were corrected for maximum solid blocking effects (Bell and Terhune, 1970; Claireaux et al., 2006).

A flow-through, fibre-optic trace oxygen sensor (PreSens GmbH, Regensburg, Germany) was used to measure oxygen concentration in the water pumped from the respirometer with an Ismatec MV-GE peristaltic pump (Ismatec SA, Glattbrugg-Zurich, Switzerland). The oxygen sensor was calibrated daily at air temperature and pressure. Fish $\dot{M}_{O_2}$ was calculated as described in Claireaux et al. (Claireaux et al., 2006).

A Sony Mini DV camera (25 frames s^{-1}) placed over the respirometer chamber recorded fish swimming patterns during the test. Videos were then converted from mini-dv tape to avi format and were analysed using video analysis software (Redlake Imaging MotionScope, San Diego, CA, USA). These recordings allowed identification of the U_{gt} between steady (aerobic) swimming and burst-and-coast swimming (the animal presumably supplementing performance by recruiting anaerobic fast-twitch glycolytic muscle fibres). Two variables were considered to determine U_{gt}: (1) tail beat frequency (TBF), as the number of tail beats per second (with one beat being one complete oscillation of the caudal fin); (2) tail beat amplitude (TBA), as the ratio between fish total length and the distance in centimetres between the lateral-most excursion of the tip of the tail calculated perpendicular to the axis of the direction of swimming. These variables were analysed from 30 cm s^{-1} until fish exhaustion. One block of 5 s was analysed every 30 s of a 5 cm s^{-1} increase in water current speed. The first statistical difference in variables between two consecutive blocks was used to assess U_{gt}. Video analyses were calibrated with the total length of the fish.

Experimental protocol
Individual fish were transferred to the swim tunnel without air exposure or human contact at an initial current velocity of 30 cm s^{-1}. Following a 15 h overnight acclimation period, RMR was assessed

over 2 h (measuring period: 10 min; flushing period: 10 min). After at least five of these $\dot{M}_{O2}$ routine measurements, a CAT was performed as described previously (Reidy et al., 2000). Briefly, water velocity was increased steadily by 10 cm s^{-1} min^{-1} until exhaustion. Exhaustion was defined as the fish falling back against the retaining grid at the posterior end of the swim tunnel and being unable to resume swimming. Water velocity at exhaustion was considered to be the maximum speed attainable by the fish using its highest power output, assuming that ground speed was essentially zero, and was recorded as U_{CAT}. At U_{CAT}, water velocity was immediately decreased to the initial velocity of 30 cm s^{-1} and oxygen uptake monitored for the following 5 min, after which the whole procedure was repeated three more times. At the end of the final trial, water velocity was returned to 30 cm s^{-1} and $\dot{M}_{O2}$ measured for at least 4 h (measuring time: 12 min; flushing time: 12 min). The highest $\dot{M}_{O2}$, measured throughout the 5 min of rest immediately following each CAT, was designated maximum $\dot{M}_{O2}$ (MMR). MMR was then used to calculate an available aerobic scope for each fish by subtracting the RMR. Individual recovery rate was assessed as the time required for oxygen uptake to return from the maximal post-exercise $\dot{M}_{O2}$ to 50% of RMR. Fish were then removed from the swim tunnel, anaesthetized (2-phenoxyethanol; 0.3 ml l^{-1}) and measured for length, width, depth and mass. Finally, background oxygen consumption was assessed by monitoring oxygen consumption of the respirometer without any fish, at a current speed of 30 cm s^{-1} for 1 h.

Data analysis and statistics

Values are means ± s.e.m. and significance was accepted at the $P<0.05$ level. Statistical analyses were performed using SigmaStat 3.1 (Systat software; www.systat.com) and Statistica 5.0 (Statsoft; www.statsoft.com). A statistical comparison between the four swim trials was carried out using a parametric analysis of variance for repeated measures (rm ANOVA) and a *post hoc* Tukey test was used to identify differences between trials. Repeatability was tested by two different procedures. The first procedure used the Spearman rank order test to investigate repeatability of the swimming performance for individual fish in successive trials, and a Kendall concordance coefficient (KCC) was calculated to assess repeatability across multiple trials. The second procedure used the intraclass correlation coefficient (ICC). This coefficient is the ratio of variance among individuals to the total variance (among+within) and is calculated from the mean square terms of the ANOVA (Becker, 1984; Lessells and Boag, 1987). The ICC ranges from 0 to 1. It is 0 when all individuals have the same mean, while it is 1 when all individuals have a different mean and all measurements on the same individual are identical (i.e. perfect repeatability). Pearson correlation was used to detect any relationship between recovery time and other variables. A probability of less than 5% ($P<0.05$) was taken as the limit for statistical significance.

RESULTS
Constant acceleration performance

Although fish ranged from 124 g to 297 g in mass, and from 22.7 cm to 31 cm in fork length, size did not significantly influence CAT swimming performance ($U_{CAT,mass}$, $P=0.40$; $U_{gt,mass}$, $P=0.71$; $U_{CAT,length}$, $P=0.62$; $U_{gt,length}$, $P=0.75$). The U_{CAT} achieved by the fish at the end of the first test was significantly higher than U_{CAT} in the subsequent three trials (169.6±7.9 cm s^{-1} *vs* 136.6±1.6, 134.5±2.9 and 131.5±2.9 cm s^{-1}, respectively; ANOVA $P<0.01$; Fig. 1A). The variation in U_{CAT} (coefficient of variation, CV) decreased from 18.43% in the first trial to 4.57, 8.53 and 8.77% in
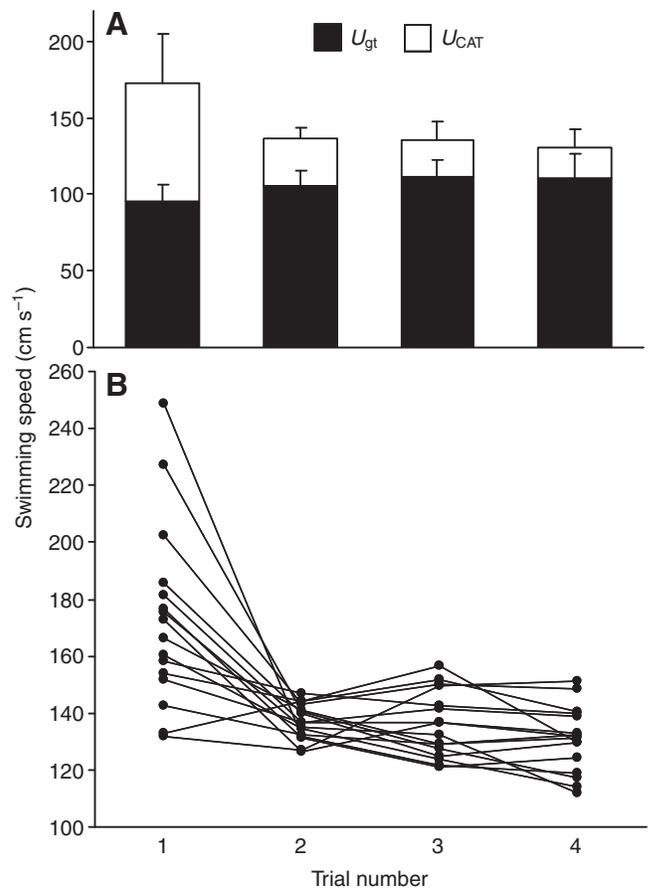

Fig. 1. (A) Maximum speed (mean + s.e.m.) in the European sea bass achieved with a constant acceleration test (CAT) in four successive trials (5 min rest between trials). Open rectangles: final water velocity at which exhaustion occurred (U_{CAT}). Filled rectangles: point at which fish transitioned between steady swimming and 'burst-and-coast' swimming (U_{gt}). See text for the statistical analysis of U_{CAT} and U_{gt} among trials. (B) Maximum speed achieved by individual sea bass (U_{CAT}) during the four consecutive CATs (N=16).

trials 2, 3 and 4, respectively. We also found that U_{gt} was significantly lower in the first trial (95.8±10.9 cm s^{-1}) than in the subsequent trials 105.6±10.3, 111.2±10.8 and 110.3±16.3 cm s^{-1} for trials 2, 3 and 4, respectively (ANOVA, $P<0.01$; Fig. 1A). The CV for U_{gt} were, however, relatively uniform among trials (11.35, 9.74, 9.76 and 14.78%, respectively). Individual repeatability of U_{CAT} was not significant across all four trials (KCC=0.31, $P=0.22$, ICC=0.06) but was significant across the final three trials (KCC=0.65, $P<0.01$, ICC=0.40; Fig. 1B). The U_{gt} was significantly repeatable among individuals across all four trials (KCC=0.33, $P<0.05$, ICC=0.21) and highly so among the last three trials (KCC=0.93, $P<0.01$, ICC=0.38). The relative contribution to the final U_{CAT} performance of the period of unsteady burst-and-coast swimming gait was calculated by subtracting the U_{gt} for each fish from its U_{CAT} for the first test (Fig. 2). This showed that the variation in U_{CAT} could be accounted for almost exclusively by the variation in performance beyond U_{gt}, hence the burst-and-coast, presumably anaerobic, component.

Fish showed a linear increase in TBF as water velocity increased up to their U_{gt}, i.e. until they initiated burst-and-coast swimming. Beyond U_{gt}, however, TBF reached a plateau and remained almost unvaried at its highest frequency thereafter. TBA was constant
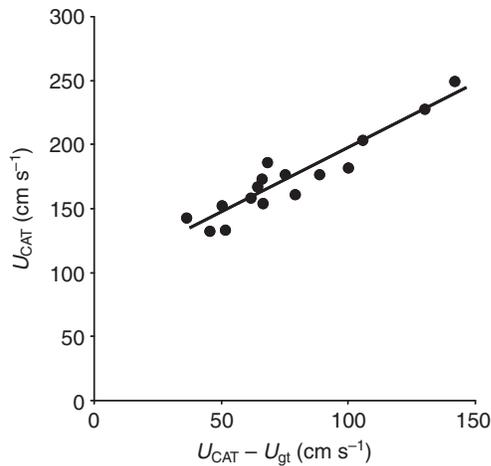
Fig. 2. The relationship between final U_{CAT} and U_{CAT} minus U_{gt}, in the first CAT test, revealing the relative contribution to the final U_{CAT} of the anaerobic burst-and-coast swimming component beyond U_{gt}. (Linear regression: $y=1.0071x+95.238$; $R^2=0.8838$, $P<0.01$.)
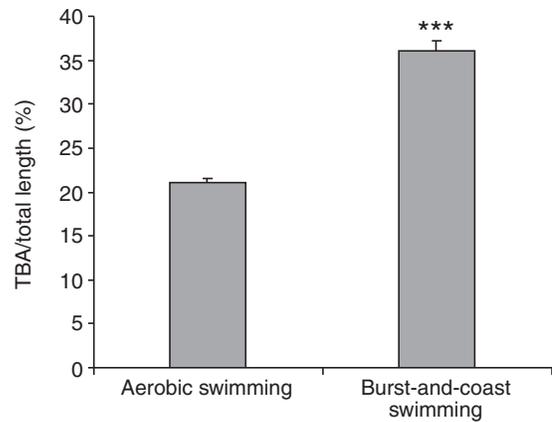

Fig. 3. Tail beat amplitude (TBA) divided by fish total length during steady swimming and during the burst propulsive phase of burst-and-coast swimming. Means + s.e.m. are presented. ***$P<0.01$.

throughout the test up to U_{gt}. Beyond gait transition, during the bursts of propulsive thrust, TBA was significantly wider than during the aerobic swimming (ANOVA, $P<0.01$; Fig. 3). Once initiated, the mean number of burst thrusts increased steadily as water velocity increased (Fig. 4).

Post-exercise metabolism and recovery from exhaustive swimming

Inter-individual variation in metabolic rate exceeded intra-individual variation in replicate measurements for all periods of the experiment. For the period prior to the CAT (swimming at $30\,cm\,s^{-1}$), the RMR varied among individuals from 7.56 to $30.28\,\mu mol\,O_2\,min^{-1}$, but the KCC for each individual's three lowest measurements was 0.79 and the ICC was 0.48. Similarly, measurements of immediate post-exercise $\dot{M}_{O_2}$ varied significantly among individuals in the four trials, ranging from 22.91 to $99.16\,\mu mol\,O_2\,min^{-1}$ (ANOVA, $P=0.04$). However, they were remarkably repeatable for each individual across the four trials (KCC=0.71, $P<0.01$, ICC=0.51). Oxygen uptake declined rapidly during recovery from the CAT trials, but the rank order of fish across the first 11 $\dot{M}_{O_2}$ measuring cycles (3.5 h) was again very reproducible (KCC=0.84, $P<0.01$, ICC=0.63). Generally, it took more than 3.5 h for post-exercise $\dot{M}_{O_2}$ to fully return to the RMR level. Thus, time to 50% recovery was taken as an index of recovery and total EPOC was not estimated. The most robust fit to the post-exercise $\dot{M}_{O_2}$ data was a sigmoid curve that was then used to calculate a mean time for 50% recovery back to RMR. However, the frequency distribution of time-to-50% recovery highlighted a bimodal pattern with two groups having significantly different recovery rates, being either about 40 min or about 180 min (t-test, $P<0.01$; Fig. 5). The extent of the post-exercise recovery period was significantly positively related to the U_{CAT} achieved in the first trial ($P<0.05$; Fig. 6A), but unrelated to performance in the following three trials and unrelated to any of the U_{gt} measurements. However, recovery period was significantly negatively related to RMR ($P<0.01$; Fig. 6B) and aerobic scope ($P<0.05$; Fig. 6C).

DISCUSSION

The key results of this study are that both aerobic metabolic rate and swimming speed at the transition from aerobic to anaerobic swimming modes are significantly repeatable within individuals, although varying substantially between individuals. We also identified a discontinuous distribution with respect to rate of recovery from exhaustive exercise, routine metabolic rate and recruitment of anaerobic metabolism to support exhaustive exercise that may be indicative of disruptive selection in nature.

Constant acceleration performance

Previous studies have shown that U_{CAT} is significantly higher than U_{crit}. This difference was 30% in largemouth bass, 20–60% in rainbow trout and 77% in Atlantic cod (Farlinger and Beamish, 1977; Farrell, 2008; Reidy et al., 2000). The U_{CAT} in the present study was approximately 60% higher than U_{crit} measured in similar-sized sea bass at similar temperatures (Claireaux et al., 2006). The observed U_{CAT} (~$150\,cm\,s^{-1}$) is still appreciably lower than the velocity of $200\,cm\,s^{-1}$ achieved during a single startle response (Lefrançois and Domenici, 2006) or of $205\,cm\,s^{-1}$ in an aquatic 'drag strip' (Claireaux et al., 2007). Performance in the CAT was independent of size across a fairly broad range, mirroring the previously determined size independence of sprint performance (Nelson and Claireaux, 2005; Claireaux et al., 2007). Thus, a picture is emerging for sea bass where individual differences in physiology overwhelm scaling effects when the size range is modest.
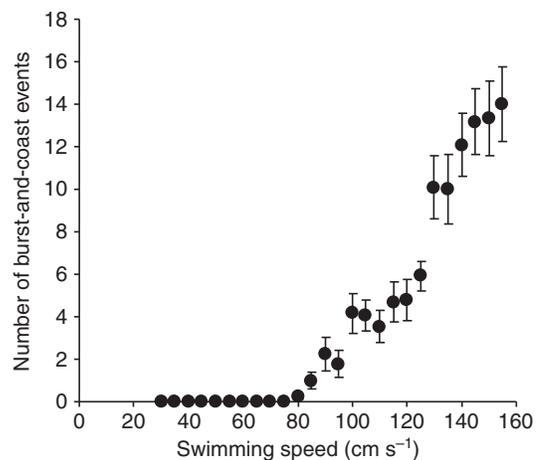

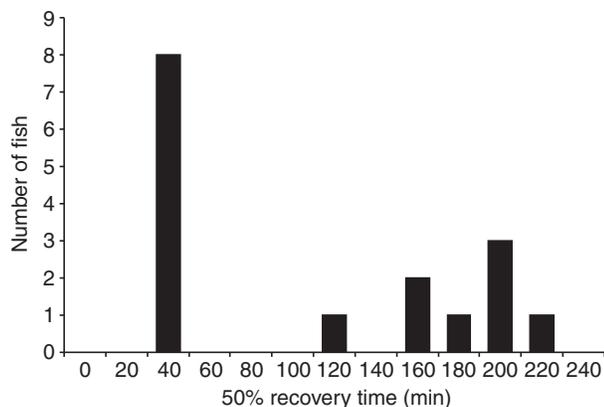Fig. 4. Mean number of burst-and-coast events ±s.e.m., measured as a function of swimming speed.

Fig. 5. Frequency distribution of the time it took individual fish to recover to 50% of the peak post-exercise oxygen consumption ($\dot{M}_{O_2}$) back to RMR. See text for further details.

Overall, sea bass performed significantly better in the first CAT, because all but two of the 16 individuals had their best performance during the first test. Subsequent tests were remarkably homogeneous both when analysed as group mean and when analysed as individuals. Pedersen and Malte (Pedersen and Malte, 2004) subjected brown trout (*Salmo trutta*) to multiple CATs over a short time period (30 s recovery time between consecutive trials) but did not report the actual individual U_{CAT} in these sequential trials. The analysis of U_{gt} allowed us to divide CAT performance into a presumably entirely aerobic component of steady swimming supported by aerobic 'red muscle' fibres, and a component at the top end of the performance range, where the burst-and-coast swimming gait indicated the recruitment of the large anaerobic 'white muscle' mass (Peake, 2008). It is apparent from this analysis that the greater U_{CAT} in the first test was attributable to a larger anaerobic component at the top end of performance. During the first CAT, fish either had greater access to fuels to support anaerobic white muscle metabolism or were better able to process end-products of anaerobic metabolic activity.

During anaerobic swimming, fish muscle primarily uses three endogenous fuel sources: adenosine triphosphate (ATP), phosphocreatine (PCr) and glycogen. In the very first stages of white muscle work, energy is supplied from the breakdown of ATP whose intracellular concentration is buffered by the rapid hydrolysis of PCr [less so in fish than in mammals; ATP levels can drop more than 50% in exhausted fish (Nelson, 1990)]. These two energy sources are quickly mobilized but are also very rapidly exhausted (Dobson and Hochachka, 1987). After intracellular PCr stores are exhausted, glycogenolysis provides the majority of ATP anaerobically (Wood, 1991; Milligan, 1996), causing the depletion of muscle glycogen and the accumulation of the organic electron acceptor lactic acid. Metabolic protons accumulate from both depletion of the ATP stores and the production of lactic acid (Nelson, 1990). Following exercise, ATP and PCr stores are replenished within 1 h post-exercise in some fish (Milligan and Wood, 1986; Booth et al., 1995; Wang et al., 1994) while recovery from lactate accumulation and the re-synthesis of glycogen can require 12 h or more (Milligan and Wood, 1986; Nelson, 1990; Booth et al., 1995; Wilkie et al., 1996; McDonald et al., 1998). Because we provided fish with only 5 min of recovery time between trials, it is most likely that the reduction in swimming performance between the first trial and the three subsequent trials resulted from the incomplete replenishment of intramuscular energy
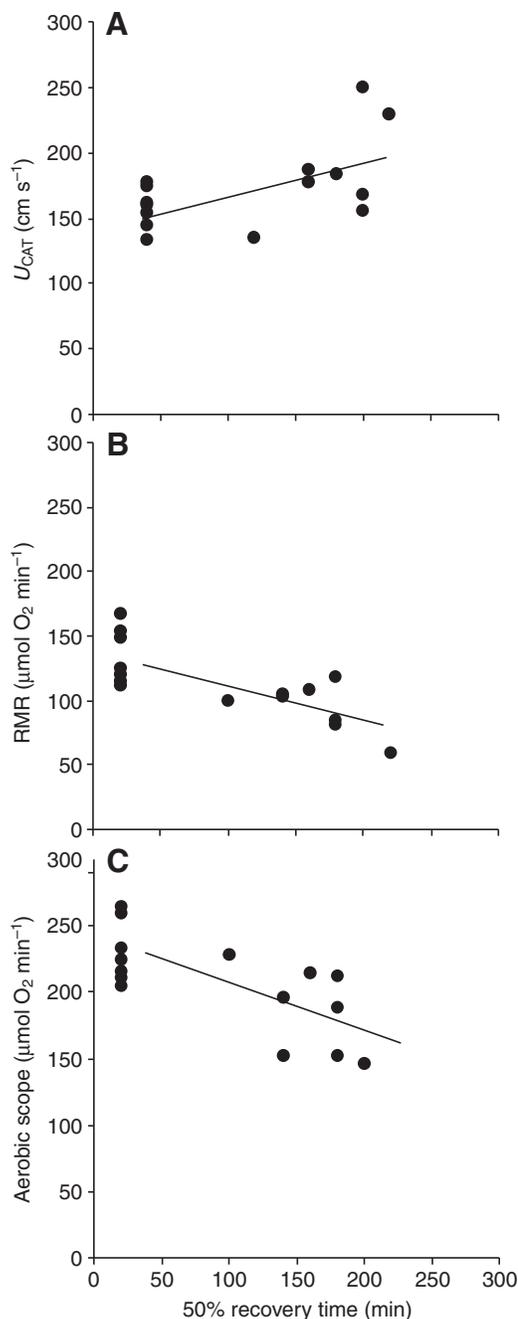

Fig. 6. Relationship between 50% recovery time from exhaustive exercise and (A) maximum swimming speed attained in the animal's first trial ($U_{CAT,1}$: $y=0.281x+144.7$, $R^2=0.503$), (B) routine metabolic rate (RMR: $y=-0.2843x+145.6$, $R^2=0.589$) and (C) aerobic scope ($\dot{M}_{O_2,max}$–RMR: $y=-0.3331x+244.7$, $R^2=0.502$), $N=16$.

stores and/or the accumulation of end-products which further compromised white muscle function.

As stated above, individual variation in U_{CAT} in the first trial is largely accounted for by variation in anaerobic burst-and-coast performance beyond U_{gt}. Therefore, because the coefficient of variation of U_{CAT} diminished between the first trial and the following three, it is likely that the same physiological factors responsible for better performance in the initial CAT (e.g. endogenous fuels stores) were also responsible for most of the inter-individual variation in anaerobic performance observed during that first CAT.

In contrast to the inferred anaerobic support of performance, the presumed limit of aerobic-only exercise (U_{gt}) was much less variable across all four tests, although performance improved significantly from CAT 1 to 4. The increase in U_{gt} may be a consequence of several phenomena associated with exhaustion induced by CAT 1, among which is the release of catecholamines into the bloodstream (Tang et al., 1989). Such a release has been shown to improve oxygen transport (Claireaux et al., 1988), to support oxygen delivery to the tissues (Tang et al., 1989) and to facilitate the mobilization of energy stores (Gamperl et al., 1994). The potential physiological and/or behavioural mechanisms underlying this improvement in aerobic performance after the first CAT will require further study. Nonetheless, the intra-individual repeatability of aerobic metabolism and U_{gt} coupled with relatively small inter-individual variation in these variables signals the importance of preserving maximal aerobic function at all times in this species and may indicate that these traits are subject to stabilizing selection.

Post-exercise metabolism and recovery from exhaustive swimming

As has been reported previously, metabolic rate was highly variable among individual sea bass (Claireaux and Lagardere, 1999; Nelson and Claireaux, 2005; Claireaux et al., 2007), a finding in common with those in other fish species (Farmer and Beamish, 1969; Febry and Lutz, 1987; Tang et al., 1994). Some authors have attributed this high degree of variation to confinement or handling stress, and to measurement errors (Febry and Lutz, 1987; Steffensen, 1989). However, the individual repeatability of metabolic rate while swimming has received very little attention. In the present study, the rank order of oxygen consumption among 16 sea bass was significantly repeatable across all phases of the experiment, i.e. under routine conditions (swimming at $30\,cm\,s^{-1}$), immediately following exhaustion and over the final 3.5 h recovery period after the four consecutive CAT tests. While this unprecedented level of repeatability in ranking indicates that variation in metabolic rate may be of ecological significance and a potential determinant of fitness in sea bass, future research should confirm whether the variation is stable over longer time periods.

The measurement of $\dot{M}_{O_2}$ after the four consecutive CATs revealed two groups of animals that differed in their pattern of recovery. Animals that recovered relatively quickly, within about 40 min, tended to have higher metabolic rates during routine swimming ($30\,cm\,s^{-1}$) and a higher aerobic scope, but were unable to reach as high a U_{CAT} as the other group of animals that relied more upon anaerobic support for swimming. Those animals that achieved the highest U_{CAT}, with the most extensive use of the burst-and-coast swimming mode, did so at the expense of an approximately fivefold increase in their recovery period compared with the animals that used less anaerobic support. This indicates the possibility of a trade-off between speed of recovery and maximal swimming performance. Moreover, the fact that the rate of recovery was significantly related to RMR and aerobic scope suggests that expensive morphological traits that facilitate high rates of aerobic metabolism, such as a high density of mitochondria, large hearts and higher capillary densities (etc.), may be the outcome of natural selection for fast recovery from exercise and not for exercise performance *per se*. Although the physiological basis of this apparent trade-off remains to be determined, the presence of two groups of fish, one composed of cruising specialists (higher aerobic performance, quick recovery from strenuous swimming, but low maximum burst speeds) and a second group of sprinting specialists (higher maximum burst speeds, but lower aerobic performance and slow recovery from strenuous swimming), may be the result of disruptive (or diversifying) selection. There may be advantages for cruising specialists in long-distance foraging and seasonal migration whereas sprinting specialists may be favoured in predator avoidance and prey capture.

LIST OF SYMBOLS AND ABBREVIATIONS

CAT	constant acceleration test
CV	coefficient of variation
EPOC	excess post-exercise oxygen consumption
ICC	intraclass correlation coefficient
KCC	Kendall concordance coefficient
MMR	maximum metabolic rate
$\dot{M}_{O_2}$	oxygen consumption
PCr	phosphocreatine
RMR	routine metabolic rate
TBA	tail beat amplitude
TBF	tail beat frequency
U_{CAT}	final water velocity attained in the constant acceleration test
U_{crit}	critical swimming speed
U_{gt}	gait transition speed

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