Thermal and Temporal Stability of Swimming Performance in the European Sea Bass

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ABSTRACT

Studies of locomotor performance have contributed to the elucidation of how suborganismal traits ultimately relate to fitness. In terrestrial populations, exploring the physiological and environmental contributions to whole-animal performance measures has improved our understanding of phenotypic selection. Conversely, very little is known about the links between phenotypic selection and swimming abilities in fish. Most research on swimming performance in fish has focused on morphological, physiological, and biochemical traits contributing to performance or has used swimming performance as a measure of environmental suitability. Few studies have explored how swimming performance is integrated with life-history traits or contributes to Darwinian fitness. In addition, while there are many studies on how the environment influences the swimming performance of fish, few have been done at the individual level. The objective of this study was to broaden our understanding of the relevance of fish swimming performance studies by testing the hypothesis that swimming performance (endurance and sprint) is ontogenetically and temporally stable across fluctuating environmental conditions. We found that individual sprint performances recorded at 12°C were significantly repeatable after a 4-wk acclimation to 22°C, although relative sprint performance of fish that survived 6 mo of natural conditions in a mesocosm was not significantly repeatable. Endurance swimming performance, as measured by critical swimming speed (U_{crit}) before and after the 6-mo exposure to simulated natural conditions, was significantly re- peatable within survivors. Relative sprint and critical swimming performances were not significantly related to each other. We concluded that within a time frame of up to 6 mo, the swimming performances of individual bass are ontogenetically nearly stable (sprint) to stable (endurance) despite large fluctuations in environmental conditions. Moreover, because they rely on different physiological performance traits, critical swimming and sprinting follow different patterns of change. This observation suggests the absence of a trade-off between these two swimming modes and introduces the possibly of independent selection trajectories.

Introduction

The question of whether natural selection favors individuals with enhanced locomotor capacities remains a critical issue for physiologists and evolutionary biologists. According to Darwinian theory, in order to be a target for natural selection, a trait must be heritable, it must be a determinant of an individual's fitness, and it must possess variation among individuals that is demonstrably repeatable (Falconer and McKay 1996). With the growing interest in microevolutionary studies and because of the close link between an animal's locomotion and its ecology (Garland and Losos 1994; Irschick and Garland 2001), a large number of investigations have focused on intraspecific variation in locomotor performance (Huey and Dunham 1987; Pough 1989; Bennett and Huey 1990; Garland et al. 1990; Boggs and Frappell 2000; Rønning et al. 2006). However, most of these studies examined terrestrial species, and we know very little about individual variation of swimming performance and its contribution to differential fitness in aquatic organisms (Billerbeck et al. 2001; Langerhans et al. 2003; Ghalambor et al. 2004; Walker et al. 2005). Temporal stability/repeatability of between-individual variation in swimming performance has rarely been examined critically (Kolok 1999; Reidy et al. 2000; Plaut 2001; Nelson et al. 2002; Nelson and Claireaux 2005). Yet, repeatability is an essential property of whole-animal performance traits if these are to be considered as potential targets for natural selection (Arnold 1983; Falconer and McKay 1996; Dohm 2002).

It has been proposed that repeatability actually sets the upper limit to the heritability of a given trait (Falconer and McKay 1996). However, heritability considers only genetic differences among individuals, while repeatability includes genetic and environmental sources of variation. As a result, properly inter-

preting repeatability estimates requires an adequate understanding of the interaction between genetics and environment in determining the trait variation (Dohm 2002). In that context, we investigated environmental and life-history influences on the repeatability of relative swimming performance in a population of juvenile European sea bass. Two swimming performances were specifically examined—sprint speed (Nelson et al. 2002; Nelson and Claireaux 2005) and a modified estimate of maximal sustainable or critical swimming speed U_{crit} (Brett 1964). This examination was conducted in three phases.

In the first phase, we explored how thermal acclimation influenced the distribution and individual repeatability of sprint performance in sea bass. Sprint speed has been shown to be repeatable in fish (Reidy et al. 2000; Martínez et al. 2002; Nelson et al. 2002; Nelson and Claireaux 2005). However, whether acclimation to new thermal conditions affects relative individual swimming performance in fish has rarely been tested (Kolok 1992; O'Steen and Bennett 2003), and thermal stability of sprint performance per se has not been examined. Temperature is the most pervasive and important physical factor in the environment of an aquatic ectothermic organism (Reynolds and Casterlin 1979). Typically, the rate of enzymatic biochemical reactions accelerates with increasing temperature, reaches a maximum or plateau, and then declines (Cossins and Bowler 1987). The exact shape of the response function is phenotypically plastic and is modifiable through thermal acclimation (Cossins and Bowler 1987).

During the second phase of our work, we examined the distribution and ontogenetic consistency of swimming performance under naturally fluctuating environmental conditions in a simulated natural environment. Here we addressed the question of whether the temporal stability of sprint and critical swimming speeds is congruent in the timescale during which the mortality component of natural selection takes place (van Berkum et al. 1989). For selection on a trait to be observable, the relative performance must be consistent over a period that is long enough for the trait to influence the fitness and/or survival of the individual. In fish, the first year of life is associated with important mortality. For instance, 30% of a cohort of Mediterranean sparids can be culled each day (McPherson et al. 1997; Planes et al. 1998). Moreover, during early life-history stages, fast-growing juveniles are submitted to a broad phenotypic reshaping that is liable to affect repeatability. On that basis, we considered that 6 mo was an appropriate time interval in which to investigate temporal stability of swimming performance under simulated natural conditions.

The third phase of our study examined the possibility of trade-offs between sprint and critical swimming speed. Burst and prolonged swimming rely on overlapping but distinct morphological and physiological systems and therefore respond differently to environmental cues (O'Steen and Bennett 2003). Moreover, interspecific comparative data and functional studies of locomotion have not been able to establish to what extent

a trade-off between aerobic and anaerobic swimming exists or whether a fish can achieve specialization in one type of performance only by compromising its ability at the other (Reidy et al. 2000).

Material and Methods

Fish Collection and Maintenance

A total of 200 juvenile European sea bass of both sexes, progeny of the same brood stock (16.23 ± 0.05 cm total length and weighing 40.32 ± 0.52 g), were obtained from a local hatchery (Ferme Marine des Baleines, Ile de Ré, France) and brought to the Centre de Recherche sur les Ecosystèmes Marins et Aquacoles (CREMA) in L'Houmeau, France. On arrival at the laboratory, bass were successively anesthetized (2-phenoxyethanol; dilution 0.3 mL L^{-1}), weighed, measured for length, width, and depth, and individually marked with passive integrated transponder tags inserted subcutaneously behind the dorsal fin. Fish were then transferred to three 500-L indoor tanks supplied with recirculated and filtered natural seawater (salinity 28%–32%; water renewal rate = 30%–50% per week). While in the laboratory, fish were kept under natural photoperiod conditions and were fed twice a week on commercial dry pellets (Bar D Perform Natura 4.5, Sica du Gouessant, Lamballe, France). Feeding was discontinued 24 h before any manipulation of the animals and at least 3 d ahead of any swimming performance test. Fish were acclimated to the laboratory conditions for at least 10 wk before experimentation.

Schedule of Operations

Two series of experiments were conducted. The first series was aimed at testing the effect of water temperature on the short-term repeatability of sprint performance. Thirty-two sea bass were subjected to two series of sprint tests. The first sprint test was performed at $12.2° \pm 0.1°C$, and the second was at $21.7° \pm 0.3°C$. Fish were acclimated to the experimental temperature for 3–4 wk before each test by placing them in a temperature-controlled room ($\pm 0.5°C$). The changeover from 12° to 22°C was realized by raising the room temperature at an approximate rate of 2°–3°C per day.

The second series of experiments examined the long-term repeatability of endurance and sprinting performances and the relationship between the two. One hundred and twenty bass were initially examined individually for their sprinting and endurance performances at 15°C. These fish were then transferred to two earthen tidal ponds, where they were maintained for 6 mo under natural environmental and feeding conditions. Only 52 bass survived this period in the ponds. The swimming performances (sprint and endurance) of these survivors were tested a second time following a 4-wk reacclimation period to laboratory conditions and 15°C. A full description of the experimental chronology is given in Figure 1.

Long-term repeatability	2002												2003							
	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8
Acclimation to the laboratory	■	■											■							
Endurance tests			■	■												■	■	■	■	■
Sprint tests					■	■								■	■					
Tidal ponds							■	■	■	■	■	■								
Short-term repeatability																				
Acclimation to 12 °C													■							
Sprint tests														■		■				
Acclimation to 22 °C															■					

Figure 1. Timetable of experiments.

Sprint Performance

Chamber Construction. The sprint performance chamber (2.0 m length × 0.25 m width × 0.3 m height) was modeled after the chamber described by Nelson et al. (2002) and is described in detail by Nelson and Claireaux (2005). Briefly, as a fish traversed the length of the chamber, it intersected curtains of laser light that were continuously monitored by photocells connected to a microcomputer.

Test Protocol. At least 0.5 h before the initiation of a sprint trial, a fish was netted from its holding tank and placed into the sprint chamber with minimal air exposure. The sprint chamber contained filtered seawater maintained at 15°C. The fish voluntarily oriented to an area with a black background immediately before the first detector array. A trial began by observing the fish in proper position, arming the computer, and grasping (or attempting to grasp) the fish's caudal peduncle. The fish then burst down the raceway, triggering the photocell circuits and recording the time elapsed between consecutive beam breakages. A minimum of 5 min was allowed to elapse between subsequent sprint trials. Each fish was sprinted between four and six times consecutively before being returned to the holding tank. For each individual, only the top sprint velocity realized over a distance >16 cm was considered for analysis from each trial.

Endurance

Swim Tunnel. A Brett-type swim tunnel (39 L) was used to assess U_{crit}. The working section of the tunnel was 60 cm long and 11.5 cm in diameter. The upstream section of the swimming chamber was darkened to motivate the fish to occupy an upstream position. Water temperature in the respirometer was controlled to $15° \pm 0.2°C$ with a chiller connected to a titanium heat exchanger situated in the water loop. A variable-speed pump propelled the water at a constant velocity. A plastic honeycomb grid and deflectors placed upstream from the swimming section promoted rectilinear flow and uniform velocity profiles. A flowmeter (Marsh-McBirney 200, Frederick, MD) was used to calibrate water velocity to revolutions of the pump impeller. The relationship between controller settings (Hz) and water velocity (m s^{-1}) was linear ($r^2 = 0.99$). Equations derived from Bell and Terhune (1970) were used to correct swimming speeds for solid blocking effects.

Experimental Protocol. At least 16 h before swimming, a fish was netted from its holding tank and placed into either the swim-tunnel or a 13-cm diameter, 1-m-long supplementary acclimation tube designed to acquaint the animals with a tunnel environment. In an earlier study, we showed that the swimming performance of 85 sea bass did not depend on whether acclimation was in the respirometer or in the acclimation tube (Nelson and Claireaux 2005). During acclimation, the fish were exposed to a 0.10 m s^{-1} current and were trained to avoid resting at the back of the tube by the presence of a light gradient. Fish acclimated in the supplementary tube were gently slid (no exposure to air) into the swim tunnel at least 1 h before initiation of an experiment.

A swimming trial started with a relatively fast increase in water velocity from 0.1 to 0.5 m s^{-1}. During that phase, the speed increment was 0.1 m s^{-1} every minute, and time at each speed was 10 min. Above 0.5 m s^{-1}, however, speed was increased by 0.1 m s^{-1} every 30 min, until exhaustion. Exhaustion was defined as the point where fish were unable to remove themselves from the posterior retaining grid. The U_{crit} was calculated as described by Brett (1964).

Fieldwork

Facilities at CREMA include a field site with 10 identical 200-m², 1-m-deep earthen tidal ponds connected to the Atlantic Ocean via a canal. These ponds are naturally provided with food suitable for juvenile European sea bass on each incoming tide, while sets of standpipes and meshing prevent fish from escaping. Previous research and empirical observations have determined that juvenile sea bass occur naturally in these ponds, which have a trophic carrying capacity of 3 kg of fish per pond. The food items of interest for bass consisted mainly of crustaceans *Palaemonetes varians* (Leach, 1814), *Palaemon serratus* (Pennant, 1777), and *Philocheras triptinosus* (Hailstone, 1835). A complete description of earthen pond fauna

can be found in de Montaudouin and Sauriau (2000). Readers may also consult http://www.ifremer.fr/crema/PGSauriau/indexmarinpertuisdatabase.htm.

European sea bass juveniles of known performance were released into two earthen tidal ponds at densities that ensured vigorous intraspecific competition for food (60 fish per pond, ~2.5 kg total mass). Previous research had established that for fish and ponds of this size, density begins to limit growth at 30 fish per pond. Avian predation was prevented in this experiment by covering the ponds with fine-mesh netting. The animals were in the ponds from July 1, 2002, until December 4, 2002 (24 wk), and were removed to assess survivorship and growth on August 29 and October 17. After the second time interval, all animals had lost mass, so the decision was made to supplement the food in each marsh with equal volumes of natural food seined from an adjacent pond. Retrieving fish from the ponds was accomplished by drawing down the water and netting the occupants. Water temperature and salinity were monitored hourly.

Data Analysis

Fish length, depth, and width were measured to the nearest millimeter and mass to the nearest tenth of a gram. Statistical analyses were performed with Statgraphics 5 Plus (Manugistics). Throughout this article, results are given as mean ± SE. Differences between samples were tested using repeated-measure ANOVA. An ANCOVA model with fish size as a covariate was used to test the relationship of individual performances in different swimming tests. Repeatability of swimming performances was examined using Spearman rank correlation coefficients. In all cases, P values less than 0.05 indicated a statistically significant difference or correlation.

Results

Size

We found no significant relationship between fish mass and sprint speed (premesocosm $F = 2.99$, $P = 0.09$, $r^2 = 0.05$; postmesocosm $F = 0.71$, $P = 0.40$, $r^2 = 0.01$). However, the fish were originally chosen to be of similar size, diminishing the inferential value of this result. Conversely, a significant relationship between fish mass and U_{crit} was found (premesocosm $F = 7.33$, $P = 0.01$, $r^2 = 0.22$; postmesocosm $F = 7.60$, $P = 0.01$, $r^2 = 0.27$).

Effect of Acclimation Temperature on the Short-Term Repeatability of Sprint Performance

Our experiment confirmed that sprint performance is repeatable on a daily basis in sea bass (Fig. 2). This prerequisite being met, we were in a position to test the thermal stability of sprint speed. Mean top sprint performance of sea bass increased sig-

nificantly with temperature ($P < 0.001$, $n = 32$), from 1.70 ± 0.05 m s^{-1} at 12°C to 2.06 ± 0.05 m s^{-1} at 22°C ($Q_{10} = 1.21$). Examination of the frequency distribution of sprint performances revealed that although both data sets were normally distributed, acclimation to higher temperature generated additional variability. The coefficient of variation (CV) increased from 14.28 at 12°C to 16.48 at 22°C (Fig. 3). Skewness of the distribution curve also increased marginally from 1.16 at 12°C to 1.41 at 22°C. Spearman's coefficient of rank correlation showed that individual sprint performances recorded at 12°C were repeatable after a 4-wk acclimation to 22°C ($r_s = 0.43$, $P = 0.021$, $n = 32$; Fig. 4).

Field Repeatability of Sprint Performance

Fifty-two of the 120 fish initially transferred to the earthen ponds were still alive after 6 mo. During that period, the mean weight and length of these fish increased significantly ($P < 0.005$), from 40.38 ± 0.84 g to 71.44 ± 2.10 g and from 16.16 ± 0.09 cm to 19.05 ± 0.17 cm, respectively. A posteriori testing showed that the initial (i.e., before transfer to the earthen ponds) mean sprint performance of the survivors and non-survivors did not differ (1.89 ± 0.05 m s^{-1}, $n = 52$ and 1.84 ± 0.04 m s^{-1}, $n = 68$, respectively) and that they were not different from mean sprint performance of the whole cohort (1.86 ± 0.03 m s^{-1}, $n = 120$). Similarly, the CV was 18.46, 16.32, and 17.28 in survivors, nonsurvivors, and the whole
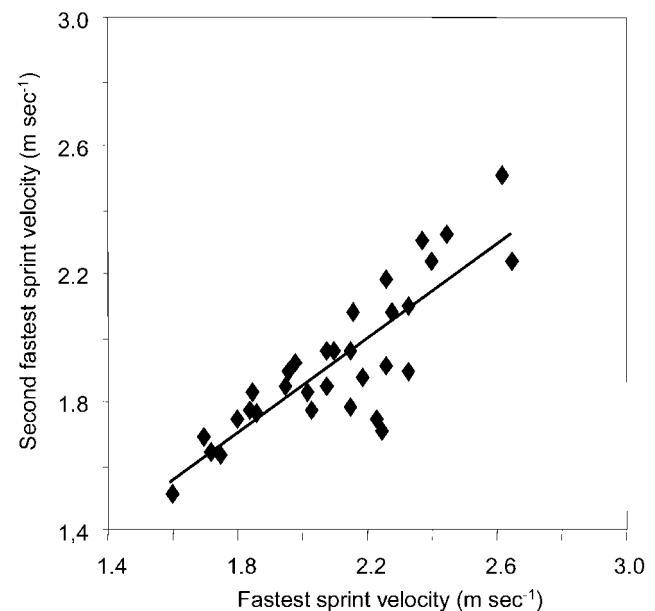

Figure 2. Example of daily repeatability of sprint performance in the European sea bass (22°C). This figure shows the relationship between the highest and second-highest sprint velocity reached by each individual fish ($Y = 0.73X + 0.38$, $r^2 = 0.71$, $n = 32$). See "Material and Methods" for further details.
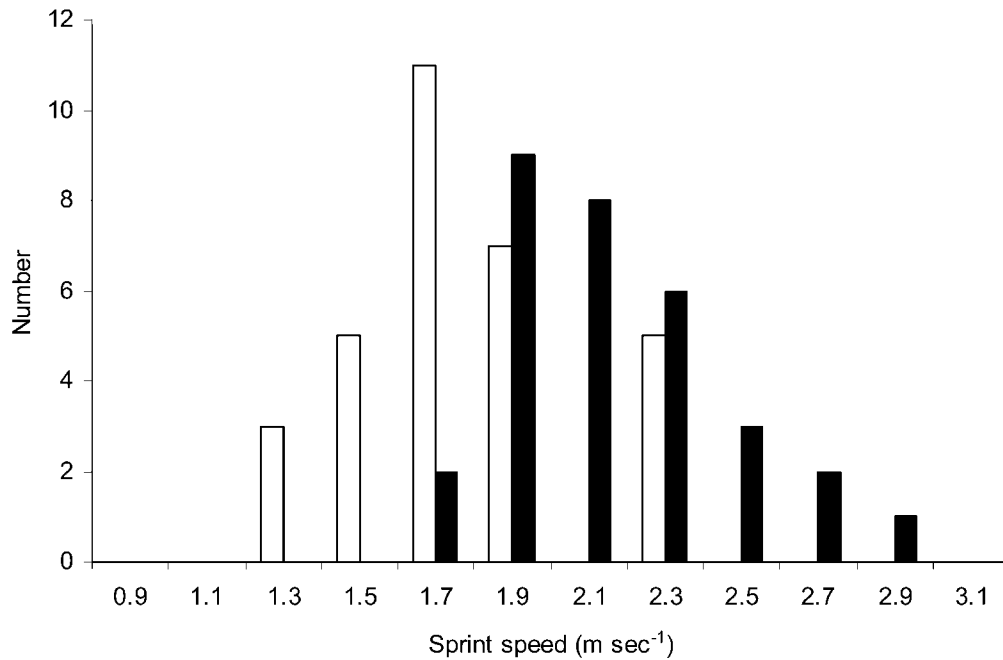
Figure 3. Frequency distribution of sprint performance in sea bass acclimated at 12°C (*white bars*) and then acclimated at 22°C (*black bars*).

cohort, respectively (Fig. 5). The initial (before transfer to the earthen ponds) and final (after 6 mo in the earthen ponds) mean sprint speeds of the survivors were compared, and a significant difference was found (1.89 ± 0.05 m s^{-1} and 2.21 ± 0.05 m s^{-1}, respectively; $P < 0.001$, $n = 52$). This was associated with substantial growth of the animals and a decrease of CV from 18.46 to 14.85 (Fig. 5). Spearman's coefficient of rank correlation showed that relative sprint performance of the 52 survivors tested after 6 mo of simulated natural conditions was not quite repeatable ($r_s = 0.23$, $P = 0.10$, $n = 52$).

Field Repeatability of Critical Swimming Speed

The initial (before transfer to the earthen ponds) mean critical swimming speeds of the survivors and nonsurvivors were not significantly different (0.81 ± 0.01 m s^{-1}, $n = 52$ and 0.79 ± 0.01 m s^{-1}, $n = 68$, respectively) and were not different from that of the whole cohort (0.80 ± 0.01 m s^{-1}, $n = 120$). The corresponding CVs were 9.48, 12.47, and 11.29 for survivors, nonsurvivors, and the whole cohort, respectively (Fig. 6). Of the 52 fish that survived the 6-mo stay in the seminatural ponds, 32 randomly selected individuals were submitted to a second U_{crit} test. The comparison of the means indicated that initial and final U_{crit} values were significantly different (0.91 ± 0.02 m s^{-1} and 1.02 ± 0.04 m s^{-1}, respectively; $P < 0.001$, $n = 32$) and the CV increased from 10.80 to 17.49. Spearman's coefficient of rank correlation showed that U_{crit} measured before and after

the 6-mo sojourn in the seminatural earthen ponds was significantly repeatable ($r_s = 0.44$, $P = 0.025$, $n = 32$; Fig. 7).

Relationship between Critical Swimming Speed and Sprint Performance

The existence of a possible trade-off between aerobic and anaerobic swimming was specifically examined. However, we found no significant relationship between U_{crit} and sprint speed (ANOVA: $P > 0.05$). This lack of correlation persisted whichever combination was examined between whole cohort, survivors, nonsurvivors, and before or after the fish's stay in the seminatural ponds.

Discussion

Effect of Acclimation Temperature on the Short-Term Repeatability of Sprint Performance

Our results (Fig. 2) confirmed an earlier study that established the daily repeatability of sprint performance in the European sea bass (Nelson and Claireaux 2005). Moreover, a comparison of the frequency distributions of sprint performance at 12° and 22°C showed that raising acclimation temperature resulted in a 21% increase in mean sprint speed (Fig. 3). A change in the shape of the sprint velocity frequency distribution was also observed, which was manifested in a 15% increase in the coefficient of variation and a marginal increase in skewness.

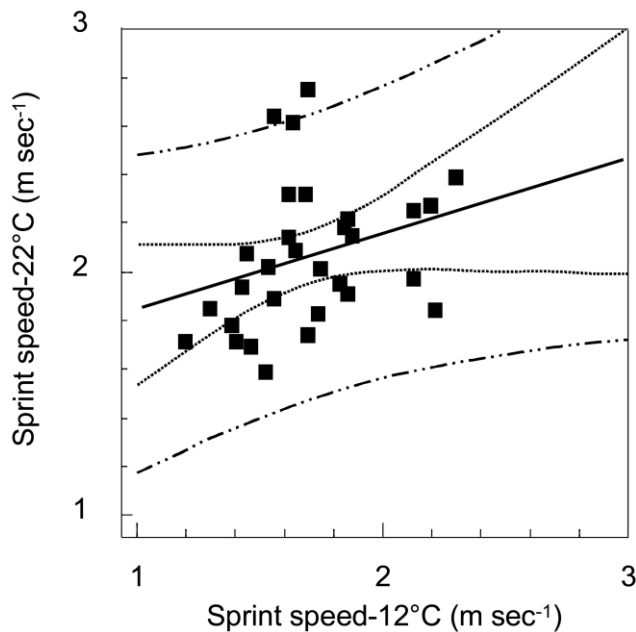Existing information about the effect of temperature on un-

Figure 4. Relationship between individual sea bass sprint speed at 12° and 22°C. Solid line: $Y = 0.34X + 1.47$ ($r_s = 0.43$); dotted lines: 95% confidence interval; dashed lines: 90% confidence interval.

steady swimming relates primarily to fast starts (e.g., Webb 1978; Johnson and Bennett 1995; Johnson et al. 1996; O'Steen and Bennett 2003) and therefore is limited to the first tail-beat cycle. Fast-start and sprint swimming are morphologically and kinematically different. A fast start consists of a stereotypical, asymmetrical movement of the fish body (Zottoli 1977), while a sprint involves a series (>2) of rapid tail beats that are kinematically similar to those observed during sustained swimming (Domenici and Blake 1997). Moreover, fast starts are associated with a simple reflex arrangement of specific neurons (Mauthner cells) that innervate the fish's lateral musculature (Eaton and Farley 1975; Hackett and Faber 1983). In contrast, sprint swimming combines the performance of a number of anatomical and physiological systems that are also mobilized during routine swimming. Although information on the subject is scarce, it is generally held that temperature exerts little influence on burst speed (Beamish 1978). Low temperatures have been shown to cause a reduction in the power-generating capabilities of fish muscles, but thermal acclimation partly compensates for this loss in muscle power output (Rome and Swank 2001). Consequently, Q_{10} for fast starts is generally between 1 and 1.5 (Beddow et al. 1995; Johnson and Bennett 1995; Johnson et al. 1996; Temple and Johnston 1998; O'Steen and Bennett 2003). As shown in Figure 3, a 10°C increase in acclimation temperature was associated with a 1.2-fold increase in sprint performance. The fact that sprinting and fast starts display similar Q_{10} is noteworthy if one considers that sprint swimming integrates a larger number of biological processes than fast

starts. Moreover, a Q_{10} of 1.2 is in the range of what is expected from a simple physical process change between 12° and 20°C (Withers 1992).

The cause for the increased CV and right skew of the distribution curve at 22°C is uncertain, but we suggest that it may be due to an interaction between swimming ability and thermal tolerance. The thermal optimum of sea bass is 22°–24°C, and it has been shown that metabolic performance drops sharply on both side of this optimum (Claireaux and Lagardère 1999). Like any other physiological traits, thermal optima are likely to display interindividual differences. Because it affects swimming abilities, we speculate that variability in thermal tolerance acted as a source of supplementary variation, affecting the within-population distribution in sprint performance at 22°C.

Field Repeatability of Sprint Swimming Speed

The repeatability of locomotor performance over various timescales and environmental conditions has been documented in a variety of species, primarily reptiles (Huey and Hertz 1984; Garland and Else 1987; Huey and Dunham 1987; van Berkum et al. 1989). In fish, only two studies have examined the long-term repeatability of sprinting performance (Reidy et al. 2000; Martínez et al. 2002). These laboratory studies showed that sprint performance of Atlantic cod (*Gadus morhua*) was stable over a 1.5- to 3-mo period. Comparison of sprint speed in sea bass that survived the 6-mo stay in the seminatural earthen ponds revealed that sprint speed was marginally stable over such a long timescale ($P = 0.10$). If one considers the level of "noise" associated with such field experiments, an even marginal stability is surprising. During their stay in the ponds, fish were submitted to a broad range of biotic and abiotic conditions, and it is quite certain that individual fish responded differently to these conditions, generating an additional source of variation (Dohm 2002). For instance, fish experienced a wide range of dietary conditions. They began on a diet of commercial food under controlled laboratory conditions and were abruptly moved to tidal earthen ponds where they had to learn to feed on natural prey items such as shrimp and small fish. Initially, food was abundant in the ponds, but the high density of juvenile sea bass generated intraspecific trophic competition for resources. Feeding conditions gradually changed to a situation where natural food was scarce, with fewer intraspecific competitors as animals gradually died off. Finally, the natural food supply was supplemented with natural food from adjacent ponds, and abundant feeding conditions were restored. O'Connor et al. (2000) reported that contrary to what was observed in individuals fed ad lib. (see also McCarthy 2000), the basal metabolic rate of food-deprived Atlantic salmon was not repeatable. Conversely, Martínez et al. (2002) showed that the sprint performance of Atlantic cod subjected to alternating periods of starvation and feeding was repeatable under laboratory conditions. Thus, differential ability to capture or rec-
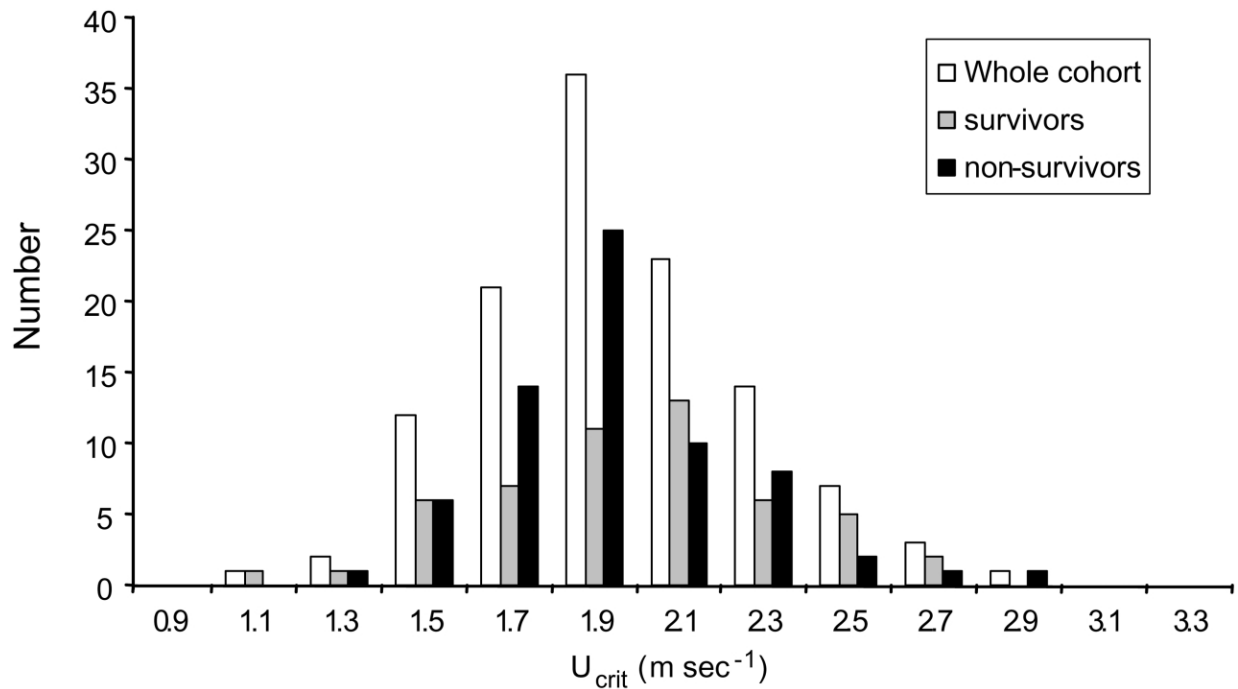
Figure 5. Frequency distribution of sprint speeds of sea bass before and after a 6-mo rearing period in seminatural tidal ponds. See text for further details.

ognize prey in the mesocosms may have introduced enough physiological variability to marginalize the repeatability of sprint performance in juvenile sea bass.

Food quality as well as food quantity can have profound effects on fish physiological performance. Dietary fatty acids, for instance, have been shown to influence fish swimming performance (McKenzie et al. 1998; Chatelier et al. 2006) and repeatability (Wagner et al. 2004). Dietary effects on exercise performance are well documented in the human performance literature (Coyle et al. 2001). Since the initial sprint performance trials were performed on animals fed an identical diet, the natural diet may have introduced an additional interaction. Thus, if animals were specializing on particular dietary items in the mesocosms, it may have contributed to additional variability in sprinting capacity.

Photoperiod has also been found to influence swimming performance of largemouth bass *Micropterus salmoides* (Kolok 1991). Since premesocosm sprint performance was measured in late spring–early summer and postmesocosm performance in winter, an interaction between individual swimming ability and photoperiod may have also contributed to the low field repeatability estimate.

Marginal field repeatability may also have resulted from the fact that fast-growing juveniles are subjected to a broad phenotypic reshaping that is liable to shuffle the between-individual hierarchy. Similar to metamorphosis in amphibians (Watkins 1997), ontogenetic thresholds may exist in fish, across which

locomotor performance is not repeatable. In that case, an early assessment of a trait loses its predictive power (McCarthy 2000).

Field Repeatability of Critical Swimming Speed

After comparing the U_{crit} data of the subpopulation of bass that survived the 6-mo period in the tidal earthen ponds, we found that U_{crit} was temporally stable. The U_{crit} procedure has generally been found to be repeatable under laboratory conditions. Kolok and Farrell (1994) showed that the surgical and recovery procedures associated with the implantation of an ultrasonic flow probe around the ventral aorta of northern squawfish (*Ptychocheilus oregonensis*) did not significantly change the ranking on U_{crit} established before surgery. Gregory and Wood (1998) demonstrated short-term (days) repeatability of U_{crit} and stamina in rainbow trout (*Oncorhynchus mykiss*). Nelson et al. (1996) showed 3-mo repeatability of U_{crit} in Atlantic cod (*G. morhua*), which had been shown by Butler et al. (1989) to have repeatable U_{crit} after surgery. Kolok (1992) demonstrated significant repeatable U_{crit} in largemouth bass (*M. salmoides*), and Nelson et al. (2002) showed that modified U_{crit} values of blacknose dace (*Rhinichthys atratulus*) were repeatable 1 mo apart. The 6-mo stability of the U_{crit} test, even under the fluctuating conditions of the mesocosm, bodes well for its future use as a fitness parameter in European sea bass.

Few studies in fish have investigated physiological diversity at the individual level, but the general observation is that in-
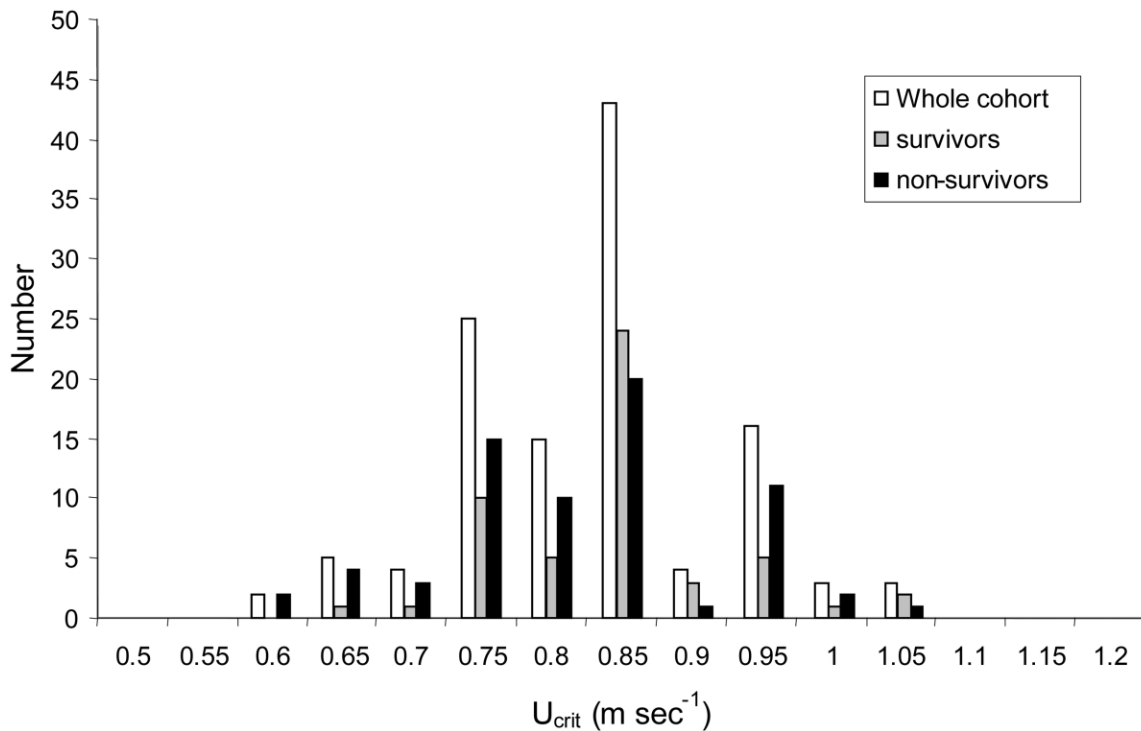
Figure 6. Frequency distribution of critical swimming speed (U_{crit}) of sea bass before and after a 6-mo rearing period in seminatural tidal ponds. See text for further details.

terindividual variability is larger than intraindividual variability for most tests (e.g., Reidy et al. 2000). One important contribution of our study is to show that interindividual difference in U_{crit} is large (0.67–1.22 m s^{-1}) and relatively stable in growing European sea bass. These observations suggest that U_{crit} is a potential target for natural selection, provided that the link between repeatability and heritability can be established (Dohm 2002). The ecological relevance of U_{crit} has been discussed at length and, to some extent, questioned (Plaut 2001; Nelson et al. 2002). The U_{crit} protocol was originally designed to investigate the swimming performance of upstream-migrating salmon (Brett 1964, 1967), and reservations concerning its actual relevance for assessing the adaptive value of swimming ability in less active species have been expressed (Nelson 2002). However, the value of the U_{crit} protocol essentially lies in the fact that it allows an integrated diagnosis of the physiological conditions of an individual fish (Claireaux et al. 2005, 2006). Suborganismal mechanisms and processes are not directly submitted to natural selection. Natural selection operates at the organismal level, sorting phenotypes on the basis of their integrated performance (Garland et al. 1990). Critical swimming speed is a whole-animal performance that quantifies the combined action of a cluster of traits (e.g., cardiorespiration, muscle contraction, neuroendocrine regulation, and metabolism) that are involved not only in swimming but more generally in broad-

sense environmental adaptation. We therefore believe that U_{crit} represents a piece of information worth considering when analyzing differential fitness.

Relationship between Critical Swimming Speed and Sprint Performance

We found no significant correlation between sprint and critical swimming velocity in sea bass at any point in the study. Chappell and Odell (2004) reported similar findings for the guppy (*Poecilia reticulata*). There might be several reasons for this lack of correlation. The most obvious one is that it may not exist at all. Burst and prolonged swimming rely on overlapping but distinct morphological and physiological systems. For instance, U_{crit} is heavily dependent on cardiorespiratory traits and may be limited by delivery of fuel or oxygen to the exercising musculature. In contrast, burst swimming is anerobically fueled and therefore largely disconnected from the processes involved in oxygen uptake and transport and most likely to be limited by neuromuscular factors or intrinsic muscular ATP production. This disconnection may account for the fact that U_{crit} and sprint speeds respond differently to environmental constraints, and it introduces the possibility of independent selection trajectories for the two performances.

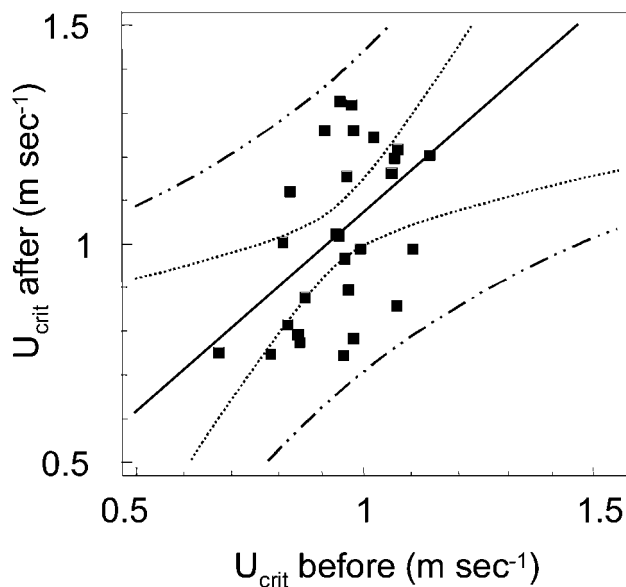The lack of relationship between burst and maximum swim-

Figure 7. Relationship between individual sea bass critical swimming speed (U_{crit}) before and after a 6-mo rearing period in seminatural tidal ponds. Solid line: $Y = 0.20X + 0.73$ ($r_s = 0.44$); dotted lines: 95% confidence interval; dot-dashed lines: 90% confidence interval.

ming speed may also result from the complexity of the environmental covariation with these two traits. During the cohort's tenure in the lab and in seminatural mesocosms, fish were exposed to a wide range of environmental variations, and these stresses may have affected sprinting and maximum swimming abilities differently, blurring any potential relationship between them. Accordingly, O'Steen and Bennett (2003) showed that voluntary, maximum, and critical swimming velocities of cyprinids were influenced differently by thermal acclimation conditions. Similarly, Jain and Farrell (2003) showed in rainbow trout (*O. mykiss*) that U_{crit} was repeatable after a 40-min recovery period in 5°C-acclimated fish but was not repeatable in 15°C-acclimated fish. Thus, interactions with environmental factors such as temperature and diet may have overridden any correlation or trade-off between these two performance measures.

Conclusion

Our study highlighted a relatively large distribution in swimming performances. This could be due to the fact that our experimental fish were obtained from a fish farm. However, a companion study demonstrates that the distributions of sprint performance in farmed and wild sea bass populations of the same size range are not significantly different (C. Handelsman, J. A. Nelson, and G. Claireaux, unpublished manuscript). We have found a reasonable level of field repeatability of critical swimming speed over a 6-mo period and a marginally insig-

nificant lack of repeatability of sprint performance over the same interval. Hence, one of the prerequisites is met for natural selection to act on these traits. It remains to be demonstrated that these traits are heritable and have a consequence for fitness. This latter point was the focus of a companion study, which directly investigated the links between interindividual differences in swimming abilities and differential fitness in the field (C. Handelsman, J. A. Nelson, and G. Claireaux, unpublished manuscript). Our results also suggest that, although repeatable, swimming performances are relatively plastic and context dependent. This caveat is important to consider for future full-scale quantitative genetic studies (Dohm 2002).

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