

Swimming Ability and Ecological Performance of Cultured and Wild European Sea Bass (*Dicentrarchus labrax*) in Coastal Tidal Ponds

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ABSTRACT

Locomotor performance is commonly used to predict ecological performance of animals and is often considered a proxy for Darwinian fitness. In fish, swimming performance is often measured in the laboratory, but its contribution to individual success in the field is rarely evaluated. We assessed maximal swimming velocity of wild and cultured juvenile *Dicentrarchus labrax* (European sea bass) in a sprint performance chamber and found substantial variation among individuals within a cohort and differences between wild and cultured fish. Moreover, individual sprint swimming performance was found to be repeatable on a daily basis, making this test potentially useful for studies of individual fitness. Some animals were also tested for endurance performance with a modified critical swimming speed (U_{crit}) test that we had previously reported to be variable among individuals and significantly repeatable over 6 mo. To test whether these different swimming abilities might contribute to differential ecological success in sea bass, cultured juveniles of known sprint and endurance performance were released into experimental estuaries, where they foraged on natural prey under high densities without predation. A second experiment exposed both cultured and wild juveniles of known sprinting ability to natural forage but this time with reduced densities and natural avian predation. Ecological performance was assessed as survival and growth rate. Neither swimming performance was a direct predictor of ecological performance for

cultured fish at high densities. Survival under these conditions was significantly predicted by prior growth rate and condition factor. When exposed to natural avian predators, the better-sprinting wild fish outperformed cultured fish (35% vs. 0% survival), and there was some evidence for sprinting ability contributing to survival within wild fish. Measuring sprint performance in mesocosm survivors revealed a significant inverse relationship between rapid growth and sprinting ability of cultured juvenile sea bass.

Introduction

Locomotor performance measured in the laboratory has frequently been used as a surrogate for fitness in animals (Bennett and Huey 1990). The articulation of research programs delineating animal performance as a component of Darwinian fitness (Arnold 1983) and the development of mathematical tools for analyzing selection on performance characters (Lande and Arnold 1983) have increased our knowledge of the role of performance in natural selection (Bennett and Huey 1990; Garland and Carter 1994; Feder et al. 2000; Irschick and Garland 2001; Kingsolver and Huey 2003) and selection on phenotypic characters in general (Kingsolver et al. 2001).

Although fish locomotor performance has been advanced as an ecologically useful measurement in fishes (Nelson 1989), estimating fitness in animals of known performance has largely been restricted to terrestrial vertebrates (Feder et al. 2000). The few studies that have effectively related performance differences to fitness differences in natural populations of fishes (Billerbeck et al. 2001; Lankford et al. 2001; Ghalambor et al. 2003; Langerhans et al. 2004; Walker et al. 2005) have used short-generation-time species of negligible economic import but have returned important results. Numerous other studies have reported declines in swimming performance when fish have been exposed to rapid environmental change, toxicants, or disease, with the assumption that these reductions in performance would have fitness consequences, but this assumption is usually untested. Selection on swimming performance can be inferred from the numerous adaptations for speed among the most athletic fish species and convergent evolution (e.g., cf. Thunniform fishes with Lamnid sharks) and, intraspecifically, from population-level differences in swimming performance (Billerbeck et al. 2001). Expanding the use of the “morphology-performance-fitness” paradigm (Arnold 1983) to examine selection on performance variability of economically important fishes could help identify physiological or morphological characters to select or to avoid in either remedial stocking programs

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or artificial selection applications and lead to improved ability to predict the effects of environmental change on wild populations.

One reason for the paucity of selection studies on economically important fishes is the necessity of recapturing surviving animals. Quantitative recovery of marked animals from aquatic settings is notoriously difficult and can prove problematic even within ecosystems that are relatively closed, such as small lakes or obstructed streams. The following study employed artificial estuaries that exposed the experimental animals to natural prey, predators, and environmental conditions but allowed recapture of surviving fish.

The European sea bass, *Dicentrarchus labrax*, occupies the eastern Atlantic Ocean from 30° to 60°N latitude and is a popular commercial and sport species. As juveniles, *D. labrax* occupy inshore shallow tidal lagoons and estuaries, where they feed on crustaceans and smaller fish, pursuing their prey by chase (Pickett and Pawson 1994). Juveniles also shuttle between the estuaries and deeper water, as dictated by episodic temperature extremes and hypoxia, often against substantial tidal currents (Pickett and Pawson 1994). Juvenile *D. labrax* have also been observed holding station in strong tidal currents. Finally, juveniles are subject to predation by pelagic fishes and several types of piscivorous birds (Pickett and Pawson 1994). Thus, competence in “sprint,” or “burst type,” locomotion may be essential for juvenile *D. labrax* survival. Laboratory sprint performance of similar-sized juvenile sea bass has been shown to be repeatable on a daily basis and to vary from under 1 m s⁻¹ to more than 3 m s⁻¹ (Nelson and Claireaux 2005; Claireaux et al. 2007). Thus, the first criterion for demonstrating natural selection on sprint locomotion exists in sea bass, namely, repeatable, measurable variation in the trait (Endler 1986). In addition, since sprint swimming is ecologically relevant for this species at this life stage, it is a trait that may be under demonstrable selection (Endler 1986). A primary objective of the following study was to ascertain whether sprint performance measured in the lab contributes to survival or growth in a realistic mesocosm environment.

Piscine aquaculture is expanding worldwide. When the purpose of the aquaculture is, in part, to enhance natural populations of a species, the use is often controversial (Brannon et al. 2004). Although there are no current release programs with cultured *D. labrax* to enhance natural stocks, aquaculture of this species is extensive throughout southern Europe, and escape from farming operations is routine. Thus, mixing farmed stocks with wild stocks is an inevitable consequence of this industry. Much of the controversy concerning cultured fish comes from the potential for diluting the genome of natural populations with genes that have come under selection in culture but are selectively disadvantageous in the wild (Brannon et al. 2004). A second objective of this study was to improve the knowledge base surrounding the debate on release of cultured fish into the wild by comparing the sprint performance, survival, and growth of wild and cultured juvenile sea bass under identical conditions.

Two null hypotheses were evaluated in this study: (1) lab-

oratory measurements of swimming performance in *D. labrax* are unrelated to survival and growth in a simulated natural ecosystem; and (2) survival and growth in simulated natural ecosystems are unrelated to whether an animal was cultured or captured from the wild.

Material and Methods

Fish Collection and Maintenance

Juvenile *Dicentrarchus labrax* of both sexes, progeny of the same brood stock, were obtained from a local hatchery during April 2002 and April 2004 (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. The brood stock was four generations removed from the wild, with a 10% annual renewal rate with wild stock. One hundred and twenty cultured fish were selected for experiments conducted in 2002 (initial mass 40.3 ± 5.7 SD g; initial length 16.2 ± 0.6 SD cm), and 120 cultured fish also began the experiments in 2004. Of the 120 cultured fish in the 2004 experiment, only 40 were eventually released to the estuaries (initial mass 64.6 ± 14.2 SD g; initial length 18.8 ± 1.4 SD cm). The 2004 experiments also employed 40 wild juvenile *D. labrax*. These fish were caught with a beach seine along the northeastern shore of Ile de Ré, France (initial mass 33.1 ± 17.7 SD g; initial length 15.6 ± 2.7 SD cm). Fish size among the cultured fish was deliberately restricted to a narrow range to minimize scaling effects and trade-offs between previous growth rates and swimming performance (Billerbeck et al. 2001). Fish size among the wild fish was constrained by what we were able to catch. In the laboratory, fish were held in three 500-L indoor tanks supplied with recirculated and filtered natural seawater (28‰–32‰ at 20°C; water renewal rate = 30%–50% per week). Fish were kept under natural photoperiod conditions and were fed thrice weekly with commercial dry pellets to satiation (Bar D Perform Natura 4.5; Sica du Gouessant, ZI, BP228, 22402, Lamballe, France). Feeding was discontinued 24 h before any manipulation of the animals and at least 3 d before a sprint performance test. Approximately 1 wk after entering the laboratory, animals were successively anesthetized (2-phenoxyethanol; dilution 0.3 mL L⁻¹); weighed; measured for total length, width, and depth (first experiment only, for calculating solid blocking effects in the endurance swimming trials); photographed; and tagged by inserting a passive integrated transponder tag subcutaneously behind the dorsal fin for purposes of individual identification. Fish were allowed a minimum of 1-wk recovery from tagging before being used in any test. The fish handling protocol was approved by Towson University’s Institutional Animal Care and Use Committee (F9900RR.08) and conformed to French government standards and regulations.

Sprint Performance

The sprint performance chamber (SPC) was modeled after that described by Nelson et al. (2002) but was modified for the

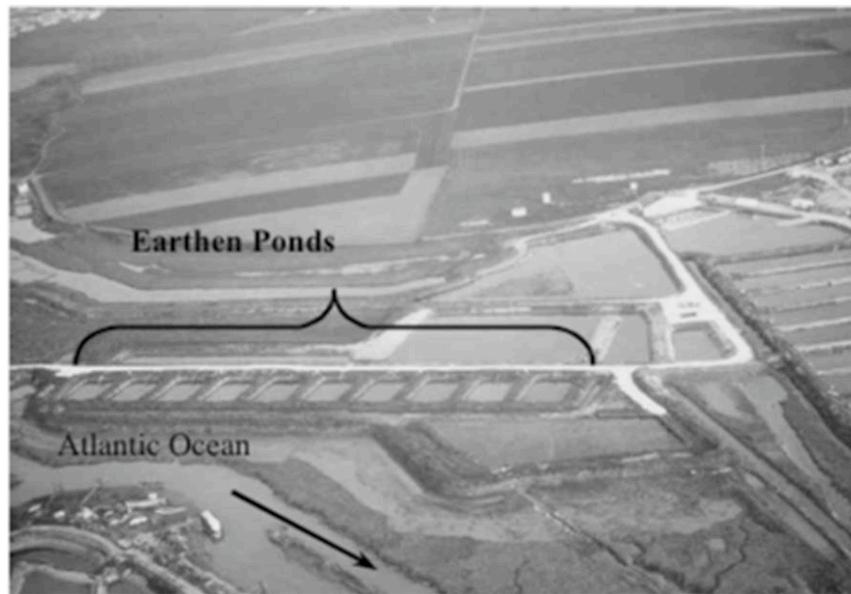


Figure 1. Aerial view of the field site at the CREMA laboratory, L'Houmeau, France, with the experimental earthen estuaries and tidal canal leading to the Atlantic Ocean (Bay of Biscay) highlighted.

dimensions of juvenile *D. labrax* and employed numerous advances in electronic technology as described in Nelson and Claireaux (2005). Briefly, the 2-m-long raceway had light-emitting laser diodes placed at intervals from the point at which a fish began a sprint. A 5-mm glass rod was attached to the front of the laser lens, projecting a vertical plane or “curtain of light” across the raceway. Laser light was detected by arrays of photo Darlington detectors (Honeywell SDP). A computer scanned the first detector array at a rate of 19.2 kHz and began collecting data after the first light beam was broken by a fish; velocity was calculated from the time subsequent laser beams were broken and the distance between detector arrays (Nelson and Claireaux 2005). Fish were sprinted a minimum of four times, but only the top three trials were analyzed. Fish were given at least 0.5-h acclimation to the sprint chamber before the first sprint and a 5-min interval of no human contact between subsequent sprint trials. The fastest recorded velocity in a 25-cm interval was used to represent maximum sprint capacity of that individual for that trial. All fish had their sprint performance measured before entering the artificial estuaries, and the 52 cultured fish that survived 24 wk in the estuaries without predation in 2002 had their sprint capacity reassessed after 5 wk in the laboratory to recover from the stress of capture and to reacclimate to the lab environment.

Endurance Performance

Endurance performance was measured as described in Claireaux et al. (2007). Briefly, a Brett-type swim tunnel (39 L) was used to exhaust the fish in an incremental velocity test (modified critical swimming speed [U_{crit}] protocol). At least 16 h before swimming, a fish was netted from its holding tank and placed either into the swim tunnel or into a 13-cm-

diameter, 1-m-long supplementary acclimation tube designed to acquaint the animals with a tunnel environment. During acclimation, the fish were exposed to a 0.1 m s^{-1} current and were trained to avoid resting at the back of the tube by the presence of a light gradient. A trial began by increasing water velocity from 0.1 to 0.5 m s^{-1} at a rate of 0.03 m s^{-1} each minute. Above 0.5 m s^{-1} , however, water velocity was incremented by 0.1 m s^{-1} every 30 min, until the fish was exhausted. Exhaustion was defined as the point at which fish were unable to remove themselves from the posterior retaining grid. U_{crit} was calculated as described by Brett (1964).

Field Site

CREMA-L'Houmeau's tidal earthen ponds (200 m^2 by $\sim 1 \text{ m}$ deep) facilities were used to test the ecological performance of juvenile *D. labrax*. Here we define “ecological performance” as survival, growth, and fish condition in the mesocosms and not locomotor performance in the field (Irschick 2003). These ponds connect to the Atlantic Ocean (Bay of Biscay) through a tidal canal (Fig. 1), allowing a natural forage base to arrive with each incoming tide, while standpipes and meshing prevent the experimental fish from escaping. Fish were able to forage, compete, and evade predators in an environment similar to what they would be exploiting at this life-history stage in nature (Pickett and Pawson 1994). These ponds also permitted recovery of fish for assessment of mortality and growth rate.

Two separate experiments were performed. In 2002, after the laboratory measurements were completed, cultured *D. labrax* juveniles were released into two simulated estuaries at densities that ensured vigorous intraspecific competition for food (60 fish per pond). Previous research had established that for fish and ponds of this size, density begins to limit growth at 30 fish

Table 1: Average conditions in the artificial estuaries during the months when fish were held there

Month	Average Daily Temperature (°C)	Average Minimum Temperature (°C)	Average Maximum Temperature (°C)	Average Daily Salinity (‰)	Average Minimum Salinity (‰)	Average Maximum Salinity (‰)
July	20.2	17.0	26.0	35.5	29.5	38.7
August	20.8	17.1	25.9	35.1	32.6	38.2
September	19.8	15.5	24.3	35.7	32.6	38
October	14.8	11.3	18.7	34.4	31.4	36.4
November	11.1	6.2	15.1	30.6	27.8	33

Note. Measurements were made by automated instrumentation. No attempts were made to systematically track oxygen levels, but sporadic measurements determined that the mesocosms were usually 100% saturated with oxygen and even on the most stagnant, warm days stayed above 50% saturation.

per pond (Cemagraf 1983). Avian predation was prevented in this experiment by covering the ponds with fine-mesh netting. The animals were in the estuaries from July 1, 2002, until December 4, 2002 (24 wk), and were removed to assess survivorship and growth on August 29, 2002, and October 17, 2002 (Table 1). The handling of fish at these intervals entailed anesthetizing each individual and measuring mass and standard length as described earlier. At the October 17, 2002, collection, mortality had approached 50%, and all surviving individuals had lost mass, so the decision was made to supplement the food in each pond with equal volumes of live, natural food seined from two adjacent artificial estuaries and to distribute it equally between the two experimental estuaries.

In the second 2004 experiment, juveniles were released into four simulated estuaries at much lower densities (20 fish per pond) but were exposed to avian predation. Forty wild fish and 40 cultured fish, randomly selected subsets of a larger sample, were stocked as two groups of 20 into four identical ponds. Fish were selected without any knowledge of performance but were then allocated to achieve equal biomass in each pond and held for 14 wk during the late summer and early autumn of 2004 (August 6–November 12, 2004). The ability to evade predators was tested by allowing local populations of *Ardea cinerea* (gray herons), *Egretta garzetta* (little egrets), and *Phalacrocorax*

carbo (great cormorants) unrestricted access to the simulated estuaries during this second experiment.

Data Analysis

Fish length, depth, and width were measured to the nearest millimeter (depth and width to correct for solid blocking; Claireaux et al. 2007) and mass to the nearest tenth of a gram. Statistical analyses were performed with Statgraphics 5 Plus (Manugistics) or Statistica 5.0 (Statsoft) except for logistic regression, which was performed with Stata 10 (StataCorp). Throughout the article, results are given as means \pm standard error. Where applicable, assumptions of normality and homogeneity of variance were assessed with the Kolmogorov-Smirnov and F_{\max} tests, respectively. The relationship between individual performances in swimming tests and ecological performance outcomes was tested with an ANCOVA model, after testing for adherence to ANCOVA assumptions, with fish size as a covariate and with logistic regression (Janzen and Stern 1998). Repeatability was tested nonparametrically with the Spearman rank order test between trials and a Kendall concordance coefficient (KCC) was calculated to assess repeatability across multiple trials. Differences in survival between mesocosms were evaluated by *t*-tests. In all cases, *P* values less

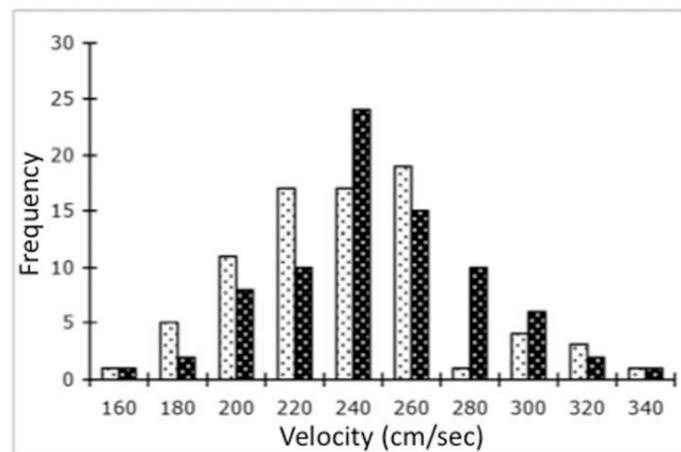


Figure 2. Histogram of variation in maximal sprint capacity among 158 juvenile *Dicentrarchus labrax* of both wild (dark bars; $n = 40$) and farm-reared (light bars; $n = 118$) origin. The percentage of the measured individuals within each group falling within a given interval is plotted.

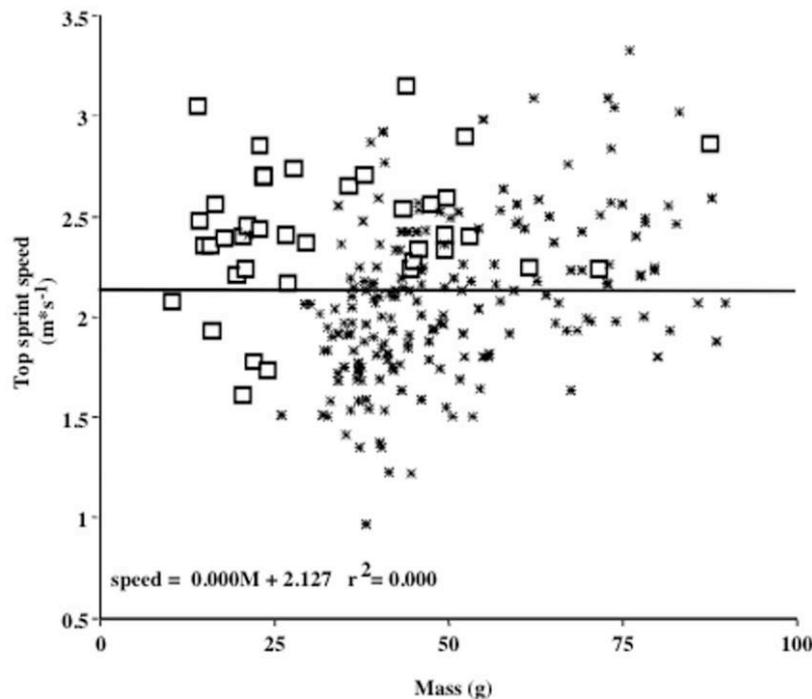


Figure 3. The top sprint performance of 228 juvenile sea bass as a function of body mass. Open squares represent animals captured in the wild ($n = 40$), and stars delineate animals reared in captivity. Size range was limited in cultured fish within a year, but no attempt was made to homogenize the sizes between 2002 and 2004 cultured fish producing the substantial size range; 2004 fish were selected to be of similar size to the anticipated catch of wild fish but were significantly larger. A least squares regression line, the equation thereof, and the r^2 value are presented.

than 0.05 indicated a statistically significant difference or correlation.

Results

Swimming Performance

Sprint Performance. As reported earlier for *Dicentrarchus labrax* (Nelson and Claireaux 2005; Claireaux et al. 2007), the sprint performance test was reproducible on a daily basis. Interindividual variation in performance far exceeded intraindividual variance in separate trials. The Spearman rank order coefficient was 0.83 for an animal's fastest trial versus that same animal's second-fastest trial ($P < 0.001$), 0.88 for the second-fastest versus third-fastest trials ($P < 0.001$), and the KCC was 0.992 across all three trials for the 120 cultured fish in 2002. The comparable numbers for the 2004 fish were as follows: first trial versus second trial, Spearman $r = 0.86$, $P < 0.001$; second trial versus third trial, Spearman $r = 0.91$, $P < 0.001$, and the KCC across all three trials was 0.947. The mean maximum sprint speed of the cultured fish in 2002 was 1.86 m s^{-1} and varied between 0.94 and 2.84 m s^{-1} (coefficient of variation [CV] of 17.5%). The comparable numbers for the subset of 40 cultured and 40 wild *D. labrax* released to the estuaries in 2004 were as follows: $\bar{X} = 2.35 \text{ m s}^{-1}$, with $CV = 14.9\%$, almost invariant from the complete group of animals sprinted in 2004; $n = 158$, $\bar{X} = 2.32 \text{ m s}^{-1}$, with $CV = 14.9\%$. Figure 2 presents the distribution

of sprint performances for all the fish sprinted in 2004 (2002 sprint distribution can be found in Claireaux et al. [2007]). Wild *D. labrax* exhibited a mean sprint capacity that was significantly higher than that of cultured fish, 15 cm s^{-1} faster on average for fish of identical size (ANCOVA, $F_{1,155} = 4.68$, $P = 0.032$), but because the wild fish were smaller, the absolute difference in mean sprint performance was not that great ($237 \pm 3.8 \text{ cm s}^{-1}$ wild vs. $228 \pm 3.9 \text{ cm s}^{-1}$ cultured). Both distributions were normally distributed (Kolmogorov-Smirnov test). Size was restricted as best as possible within a cohort, and there was no effect of size on sprint performance for either standard length or mass across the entire study (Fig. 3). Mass was considered the more accurate of the two metrics and is presented.

Endurance Performance. As reported in Claireaux et al. (2007), the U_{crit} protocol uncovered substantial interindividual variation in performance among cultured sea bass, and rank performances were significantly repeatable across the 24 wk of mesocosm occupancy. This test was mildly but significantly dependent on fish size: $U_{\text{crit}} (\text{m s}^{-1}) = 0.005 \text{ mass (g)} + 0.612$; $P < 0.01$. Whatever combination was considered (whole cohort, survivors, nonsurvivors, or before or after the stay in the estuaries), we found no significant relationship between U_{crit} and sprint speed (ANOVA: $P > 0.05$; Claireaux et al. 2007). Endur-

Table 2: Experiment 1: characteristics and performances of cultured sea bass survivors and nonsurvivors of various 8-wk intervals in two identical mesocosms, summer 2002, with initial high fish densities and no predation (means \pm SEM)

Measurement	First Estuary Interval (July 1–August 29, 2002)		Second Estuary Interval (August 29–October 17, 2002)		Third Estuary Interval (October 17–December 6, 2002)	
	Survivors	Fatalities	Survivors	Fatalities	Survivors	Fatalities
<i>n</i>	106	14	55	46	52	8
Mass _(init) (g)	49.6 \pm .57	43.0 \pm 1.13	50.9 \pm 1.08	48.5 \pm 1.32	55.8 \pm 1.53	52.5 \pm 3.24
Condition factor _(init)	1.03 \pm .01	.96 \pm .02 ^a	1.05 \pm .01	1.00 \pm .01 ^a	.93 \pm .01	.90 \pm .01
Sprint (m s ⁻¹)	1.86 \pm .03	1.85 \pm .09	1.91 \pm .04	1.84 \pm .04	1.89 \pm .05	1.94 \pm .10
Previous growth (g d ⁻¹)	.096	.053 ^b	.071	.009 ^b	-.27	-.35
<i>U</i> _{crit} (m s ⁻¹)	.81	.76	.82	.79	.82	.84

Note. Performance measurements were all made at the beginning of the experiment, and the remaining measurements are those recorded at the end of the previous interval (i.e., end of laboratory residence for the first interval). Because several fish remained undetected in the mud and “reappeared” after a subsequent interval, despite being recorded as dead, there is some imprecision in total fish number and recording the actual interval in which a fish expired. *U*_{crit} = critical swimming speed.

^a Condition factor at the start of a time interval in the estuaries was significantly different between eventual survivors and fatalities.

^b Growth rate in the period preceding a time interval in the estuaries was significantly different between eventual survivors and fatalities.

ance performance was not measured in the 2004 (second) experiment.

Ecological Performance

Artificial estuary number was always included as a covariate in an original analysis, and there were never any significant differences in length, mass, condition factor (CF), sprint, *U*_{crit}, or survival that could be attributed to which marsh a fish was in, so thereafter, the data for each marsh were analyzed together. Laboratory measurements of swimming performance were not predictive of survival for cultured fish in the mesocosms under the high-density conditions of 2002 (Table 2). The factors that best predicted survival of cultured fish were growth rate during the previous interval and condition factor of the fish at the onset of the interval (Table 2), although logistic regression did not support the predictive nature of CF (Table 3). During the interval of maximum mortality in the 2002 experiment (second estuarine interval), there was a slight tendency for survivors to be better swimmers than those fish that perished ($P \approx 0.15$ for both sprint performance and *U*_{crit}).

Food supplementation during the 2002 experiment (see above) allowed the remaining fish to achieve the highest growth rates of the experiment during the final 8 wk in the two estuaries. Interestingly, this enhanced growth rate was negatively correlated with the sprint performance of the 52 fish that survived the final marsh interval, measured after they were removed from the estuaries ($F_{1,50} = 14.3$; $P < 0.001$; Fig. 4). Growth rate was not significantly related to initial or final swim performance in any other estuarine interval. Overall, surviving individuals did not differ in condition factor, sprint performance, or *U*_{crit} from those that perished ($P > 0.05$; Tables 2, 4).

In the 2004 (second) experiment, no cultured fish survived 14 wk in the artificial estuaries exposed to avian predation, whereas 14 wild fish (35%; 8 in one estuary, 6 in the other) survived (Table 4). Since the wild fish differed significantly from the cultured fish in a number of the measured parameters (ontogenetic history, length, mass, sprint capacity, and body

shape; Table 4), it is difficult to ascribe the differential survival of wild fish to any one factor. The wild fish that survived 14 wk in the artificial estuaries ($n = 14$) did not exhibit significantly greater sprint capacity than those that perished ($n = 26$; $P = 0.135$). Close examination of the results suggests that it was important to be both small and fast to survive avian predation. The wild fish that survived 14 wk in the artificial estuaries actually had significantly greater sprint capacity when expressed in body lengths (BL) per second (17.2 BL s⁻¹ vs. 15.0 BL s⁻¹; $F_{1,38} = 4.43$, $P = 0.042$) were almost significantly smaller ($P = 0.09$) and had significantly lower condition factors ($P < 0.01$; Tables 3, 4).

Discussion

Swimming Performance

Several methods have been employed to look at sprint performance on the scale of seconds, but the SPC method described by Reidy et al. (2000) and Nelson et al. (2002) was employed because of the ease with which large numbers of fish could be repetitively measured and because this method has been shown to be significantly repeatable over time (Reidy et al. 2000; Martinez et al. 2002; Claireaux et al. 2007). We previously reported daily repeatability and substantial interindividual variability of maximal swimming speed in juvenile sea bass with this method (Claireaux et al. 2007); here, we confirm these results with the fish sprinted in 2004, showing significant daily repeatability and substantial variation in maximal sprinting speed (Fig. 2). This level of variation and repeatability was considered sufficient to test whether sprinting performance was subject to mortality selection in the simulated estuarine environment.

One interesting finding from these combined studies is the lack of scaling of maximal sprint speed as measured with a SPC. The prediction from the mutual dependency of both power output and the drag coefficient on the square of the linear dimension is the observed size independence of burst swimming speed (Vogel 2008). However, the increase in Reynolds number as fish size increases generally produces a scaling

Table 3: Logistic regression analysis of natural selection on European sea bass under simulated natural conditions with absolute fitness (survival) as the dependent variable

Variable	First Estuary Interval (July 1–August 29, 2002)				Second Estuary Interval (August 29–October 17, 2002)				2004 Experiment			
	α	SE	P	β_{avgrad}	α	SE	P	β_{avgrad}	α	SE	P	β_{avgrad}
Condition factor	4.366	2.350	.063	.2770	10.775	7.994	.178	.357	11.143	4.052	.006	−1.230
Sprint performance	.429	.660	.516	.0761	.128	1.166	.912	.023	1.479	.989	.135	.2850
U_{crit}	1.553	2.757	.547	.0777	−3.697	5.269	.483	−.185				

Note. For the 2002 competition experiment with no predation, the third estuary interval was not analyzed because of the small number of mortalities. α = logistic regression coefficient; β_{avgrad} = standardized regression coefficient as described by Janzen and Stern (1998); and U_{crit} = critical swimming speed.

coefficient for length of around +0.5 (Vogel 2008). Although it is common to observe no scaling of sprint swimming within the confines of a single study (Billerbeck et al. 2001; Langerhans et al. 2004; Nelson and Claireaux 2005), some authors report positive scaling of maximal sprint swimming speeds (Ojanguren and Brana 2003; Nelson et al. 2008), and other authors even report negative scaling (McGuigan et al. 2003). Thus, we conclude that, for intraspecific studies with narrow ranges of fish size, individual differences in physiology and morphology supersede the constraints of the physicochemical environment, minimizing scaling effects.

Our test of endurance performance, a modified U_{crit} procedure used only with the 2002 fish and reported on in Claireaux et al. (2007), also fulfilled the criteria of interindividual variability and intraindividual repeatability, even being repeatable across 6 mo of mesocosm residence (Claireaux et al. 2007). Farrell and colleagues (e.g., Farrell 2008) have evaluated similar modified U_{crit} procedures in salmonids and found that the numbers obtained are generally close to those obtained through traditional U_{crit} tests. Performance in this modified U_{crit} procedure was modestly size dependent, conforming to expectation (Beamish 1978). Thus, size-corrected values of this test were used for analysis.

Ecological Performance

Neither sprint nor endurance swimming performances of cultured fish, measured in the laboratory before the fish were released to the mesocosms, predicted ecological success (growth or survival) under high-density, predator-free conditions. Intraspecific competition for a limited forage base, environmental changes, and disease are the presumed challenges faced by juvenile sea bass under these conditions. During the first two intervals in the estuaries (July 1–October 17, 2002), when environmental temperature was high and the competition for resources was perceived to be the most intense, there were no significant relationships between swimming performance and any measure of ecological performance, although there was a slight tendency for survivors to be better swimmers during the interval of maximum mortality (second interval; Table 2; $P = 0.14$). These results suggest that modest levels of performance are sufficient for securing food in these mesocosm environments and that neither mode of swimming performance

is under directional selection at this age in the absence of predators (Irshick et al. 2008).

In contrast, exposure of juvenile European sea bass to avian predation in the simulated natural environments provided some indication that sprint swimming performance measured in the laboratory might contribute to success in the field. Fish captured from the wild were statistically better sprinters than cultured fish of the same size (Figs. 2, 3), and they survived 14 wk of avian predation in the artificial estuaries better than cultured fish (35% vs. 0%; Table 4). Obviously, there are many factors besides sprint performance that differed between wild and cultured sea bass (Malavasi et al. 2004), plus there were cultured fish that did not survive that swam as well as wild fish. However, considering that surviving wild fish tended to be faster than those that perished, we can posit an initial conclusion that sprint performance is important for mortality selection in juvenile sea bass inhabiting estuarine environments. Because wild fish were also significantly smaller than cultured fish and the surviving wild fish were significantly thinner and were also close to being significantly smaller than nonsurviving wild fish (Tables 3, 4), we can formulate an additional conjecture that, to avoid avian predation in these artificial estuaries, it is helpful to be neither noticed or preferred, but, if you are, it is advantageous then to be a good sprinter. How these results would change if piscine predation were included in the experimental design will have to await future studies.

Most other investigators have also found that wild fish outperform cultured conspecifics, primarily with U_{crit} or other endurance tests as the performance metric. For example, Vincent (1960) found that wild strains of brook trout (*Salvelinus fontinalis*) had better swimming performance than domestic conspecifics. Thomas and Donahoo (1977) found an inverse correlation between length of time under domestication and swimming endurance for three strains of hatchery rainbow trout (*Oncorhynchus mykiss*), and Basaran et al. (2007) found cultured sea bream (*Sparus aurata*) to have a lower U_{crit} than wild conspecifics. In contrast, Peake et al. (1997) report no difference between wild and hatchery-reared Atlantic salmon smolts. Data on the differences between wild and cultured fish on the timescale of predator-prey interactions are much harder to find but, generally, also favor wild-fish performance. For example, Gibson and Johnston (1995) show a reduced maximal velocity achieved from the escape response of farmed juvenile

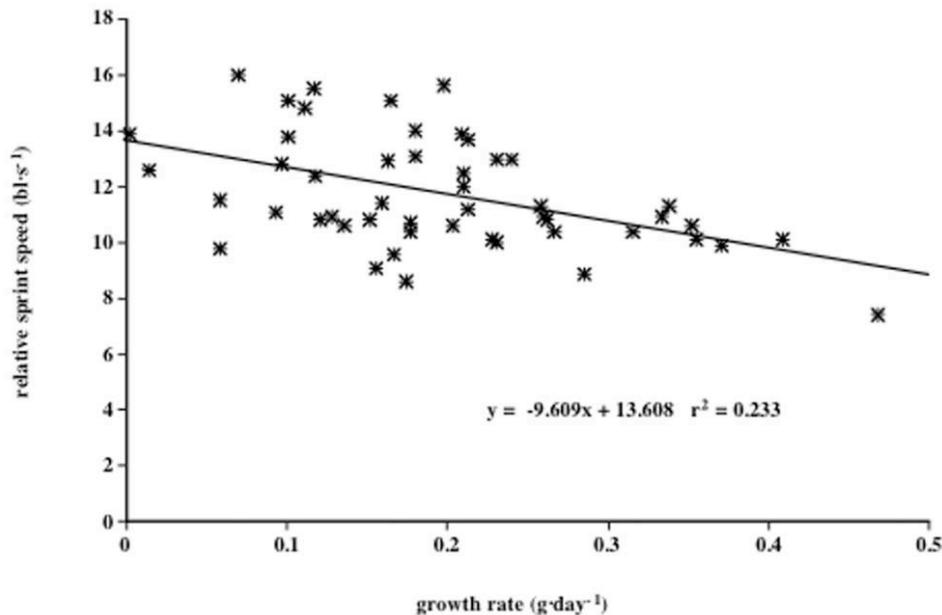


Figure 4. Relative sprint capacity of 52 cultured juvenile sea bass from the 2002 experiment, measured after they were removed from the estuaries, as a function of their growth rate during their last interval in the two experimental estuaries when forage was abundant and densities were low (third interval; November 17–December 6, 2002). A least squares regression line, the equation thereof, and the r^2 value are also presented.

turbot (*Scophthalmus maximus*) compared with wild juveniles, but only if the wild fish were freshly captured, which suggests a laboratory detraining effect (Nelson et al. 2008).

The complete lack of surviving cultured sea bass after 14 wk in the mesocosms subject to predation does not portend well for the survival prospects of released or escaped cultured fish of this species. Similar to locomotor performance, the general finding for release of cultured fish to the wild is that the cultured fish do not fair as well as comparison wild conspecifics (Carr et al. 2004; Fairchild and Howell 2004), although some studies report that cultured fish released to the wild actually do as well or even better than their wild counterparts (McGinnity et al. 2004; Paulsen and Støttrup 2004). Our results suggest that cultured sea bass belong to the former group. Their relatively poorer sprint performance and inability to survive 14 wk in

the mesocosms suggests that they would not fare well in natural environments.

Perhaps not surprisingly, the main predictors of survival under high densities without predation were the animal's condition and rate of growth at the beginning of a given time interval (Table 2). Significant growth and condition factor dependency of survival in the first intervals implies that animals that were more successful at getting food pellets in the laboratory tanks were also more successful at adapting to a natural diet in the mesocosms. One might suspect that this result implies that dominance hierarchies existed in our group tanks and that the most dominant individuals also did better in the mesocosm, but the constant reshuffling of animals between the three large holding tanks as they were swum should have minimized this effect. If more dominant individuals were over-

Table 4: Experiment 2: characteristics and performances of sea bass survivors and nonsurvivors of 14 wk in four identical mesocosms, summer 2004, with initial low fish densities and subject to avian predation

Measurement	Wild Fish 1		Wild Fish 2		Cultured Fish 1		Cultured Fish 2	
	Initial	Survivors	Initial	Survivors	Initial	Survivors	Initial	Survivors
n	20	8	20	6	20	0	20	0
Mass _(init) (g)	37.7 ± 4.24	75.2 ± 9.19	28.8 ± 4.24	36.2 ± 5.84	63.8 ± 1.91	NA	65.5 ± 3.80	NA
Condition factor _(init)	.74 ± .04	1.00 ± .02	.82 ± .01	1.02 ± .02	.94 ± .01	NA	1.00 ± .06	NA
Sprint (cm s ⁻¹)	2.35 ± .08	NA	2.41 ± .06	NA	2.38 ± .08	NA	2.26 ± .07	NA
Growth (g d ⁻¹)	NA	.48	NA	.17	NA	NA	NA	NA

Note. Each of the ponds was stocked with 20 cultured juveniles or 20 individuals captured from the wild. Sprint performance was measured at the beginning of the experiment, and the other measurements are reported for both entry and exit of the mesocosms. NA = not available.

represented among survivors, because there was no influence of sprinting performance on growth rate or survival, this would imply that dominant individuals were not necessarily better sprinters, as has been found in lizards (Garland et al. 2000; but see López and Martín 2002). The other interpretation of these results is that fish differed subtly in their health status or stress level before their release to the mesocosms. The continuation of significant differences between survivors and mortalities in the second mesocosm interval (Table 2) suggests the continuation of differential foraging ability or health in individuals across the first two measurement intervals.

Although initial swimming performance was not predictive of growth rates in the mesocosms, when food resources in the estuaries were ample and fish densities were reduced because of mortalities in the previous intervals (experiment 1: last interval October 18–December 6, 2002), a significant inverse relationship between growth rate in this last interval and sprint swimming performance measured after the fish were removed from the estuaries was observed (Fig. 4). This relationship derived from those nine animals with the highest growth rates having low sprint performances. This apparent trade-off between growth and swimming performance has been observed by a number of other investigators (Kolok and Oris 1995; Gregory and Wood 1998; Billerbeck et al. 2001; but see Royle et al. 2006 and Alvarez and Metcalfe 2007).

Limitations

Our mesocosms could not duplicate the field environment precisely. Temperature, salinity, depth, substrate, turbidity, dissolved oxygen, and the forage base were similar to what would be experienced by juvenile sea bass in the region, but the restricted dimensions and minimal currents were different. Whether the lack of deep-water refugia or substantial currents influenced the results reported here is unknown. Although there are some mild currents as the tide enters and leaves the artificial estuaries through piping, strong currents were never experienced during the experimental periods, a condition that may have masked the contribution of locomotor performance to survival and growth.

Another concern of this study is that laboratory measurements of sprint performance may not relate to locomotor performances used by juvenile sea bass in the wild. Some studies report that sprint capacity measurements made in laboratories are generally not maximal (Losos et al. 2002). Despite attempts to create optimal laboratory conditions for measuring performance (e.g., minimal human contact, realistic lighting conditions), there is no guarantee that maximum physiological performances were elicited. Similarly, there is the possibility that sea bass only use a small percentage of the measured sprint speeds in the mesocosms (Irschick 2003). Results from terrestrial studies suggest that, in some natural systems, maximal performance levels are rarely used (Irschick 2003; but see Husak 2006). Although in situ measurements of ecological performance in fishes are in their infancy (Hanson et al. 2008), it is unlikely that terrestrial results are applicable to the denser, more

viscous aquatic medium, where locomotor performances are subject to different constraints and may be under different selection intensities. We know of no in situ measurements of fast-start or burst performance of fishes during predator-prey encounters. However, Walker et al. (2005) measured improved survival chances for guppies (*Poecilia reticulata*) that performed better fast starts in staged laboratory predator-prey interactions, supporting our suspicions that maximal performance is routinely tested in a “fish eat fish” world.

In conclusion, we cautiously reject the null hypothesis that laboratory measurements of sprinting performance in European sea bass are unrelated to survival and growth in a simulated natural environment. Although the limitations of the artificial estuaries are acknowledged, this type of study is an important intermediate step for inferring the success of physiological phenotypes in nature until the technology exists for following the performance of large numbers of individuals of economically important species in the wild. We also reject the null hypothesis that our simulated estuarine environment is blind to where ontogeny occurred for these fish. Cultured fish, through either behavioral or physiological limitations, were unable to survive a 14-wk sojourn in the mesocosms that was survivable by 35% of the wild fish. One can only surmise that attempts at enhancement of wild European sea bass populations with the cultured stock we used would be a waste of resources.

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