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Quantitative genetic variation for post-stress cortisol and swimming performance in growth-selected and control populations of European sea bass (*Dicentrarchus labrax*)

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ABSTRACT

Sea bass is a major species in Mediterranean aquaculture, and is now being subject to selective breeding programmes for faster growth. In terrestrial species, it was demonstrated that fast growth may be linked to a correlated degradation of fitness traits. In this experiment, we evaluated 600 young sea bass from a factorial mating of 76 sires and 13 dams. The sires were from four genetic groups, wild (W), domesticated (D), and selected for growth (2 groups, M and P). The 600 offspring were submitted to two acute confinement stress challenges at 6 weeks intervals, and plasma cortisol at one hour post stress was measured. The same fish were also submitted to two swimming challenges at a 5 days interval, where the maximum sustained swimming speed (U_{max}) of each fish was evaluated. Parentage was assessed by genotyping of 12 microsatellites. 554 fish had both valid parentage and phenotypes. Cortisol had a low repeatability ($r = 0.30$ between the two successive measurements) while repeatability was moderate for U_{max} ($r = 0.62$). However, genetic correlations between successive measurements were very high (>0.96) for both traits, indicating that successive measurements were related to the same trait. Heritability was moderate for mean post-stress cortisol ($h^2 = 0.34 \pm 0.09$) and U_{max} ($h^2 = 0.48 \pm 0.08$). When U_{max} was expressed in $m.s^{-1}$, it was negatively correlated to cortisol ($r_A = -0.48 \pm 0.08$) and weakly correlated to body weight ($r_A = 0.12 \pm 0.16$), but figures changed when it was expressed in Body Lengths.s^{-1} ($h^2 = 0.55 \pm 0.08$, $r_A = -0.10 \pm 0.19$ with cortisol and $r_A = -0.64 \pm 0.07$ with body weight, respectively). Cortisol was moderately negatively correlated with body weight ($r_A = -0.36 \pm 0.18$). The four lines did not differ for cortisol or U_{max}, but when U_{max} was expressed in $BL.s^{-1}$ it tended to be lower in the two selected lines — which were also significantly larger. However, this is likely due to a phenotypic decrease of relative U_{max} with increasing body size. We conclude that selection for growth and/or domestication should not impact maximum sustained swimming speed in the European sea bass, but may tend to favour animals with low cortisol responsiveness. These traits could be used to orientate functional capabilities other than productivity in sea bass.

Statement of relevance: We estimate heritability of cortisol stress response and (for the first time) in European sea bass, as well as their correlations with growth. We show moderate correlations, and no correlated response to selection for growth. We also provide methods to evaluate these traits on large number of fishes. This can be useful to monitor and design breeding programmes.

1. Introduction

To sustain the fast growing demand for aquaculture products, selective breeding is increasingly employed particularly to improve productivity traits in farmed fish. As a result, important gains in growth rate in the range of 10–15% per generation have been achieved in several species (Gjedrem et al., 2012). In terrestrial animals where the history of selective breeding is much longer, very high cumulated gains in production traits have been achieved (e.g. broiler chicken, Havenstein et al., 2003 and turkey, Nestor et al., 1996), but sometimes at the expense of unfavourable correlated responses on traits such as reproductive traits, walking ability, susceptibility to heart failures, and resistance to diseases (Nestor et al., 1996; Rauw et al., 1998 for a review). In fish, cardiac failures have been recorded in salmonids (Mercier et al., 2000; Poppe et al., 2007) and raised

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attention to possible side effects of selection, although to date no link has been demonstrated between the use of selected strains and the occurrence of cardiac disorders. In rainbow trout *Oncorhynchus mykiss*, cardiac morphology and pumping ability were shown to be linked to swimming performance, which was suggested as a possible selection criterion to improve the livability of farmed trout (Claireaux et al., 2005). Accordingly, it was demonstrated in Atlantic salmon that individuals with inherent higher swimming capacity also displayed higher resistance to disease (Castro et al., 2013) and that aerobic training improved growth and disease resistance (Castro et al., 2011). However, apart from four studies, using sire half-sib families in brown trout (Blanc and Toulorge, 1981) or using few full-sib families in Atlantic salmon *Salmo salar* (Hurley and Schom, 1984), guppy *Poecilia reticulata* (Nicoletto, 1995) and threespine stickleback *Gasterosteus aculeatus* (Garenc et al., 1998), little is known on the genetic variation of swimming performance in fish and its correlation with production traits.

Another important trait when considering homeostasis and welfare of fish in aquaculture is the capacity to cope with acute stressful events inherent to farming. This is classically evaluated by post-stress plasma cortisol response (Wendelaar Bonga, 1997). Significant genetic variation in cortisol stress responsiveness has long been demonstrated in salmonids (Drew et al., 2007; Fevolden et al., 1993; Pottinger and Carrick, 1999; Quillet et al., 2014; Rexroad et al., 2012). Direct response to selection for high or low cortisol responsiveness has been demonstrated, together with correlated response on behavioural traits (Fevolden et al., 2002; Øverli et al., 2002).

The European sea bass is an important species for aquaculture in the Eastern Atlantic and in the Mediterranean area. Large genetic variation for growth exists in this species, and a considerable response of growth rate to selection (in the range of 20–40% per generation) has been demonstrated (Dupont-Nivet et al., 2008; Vandeputte et al., 2009). Few data exist showing limited genetic variation in cortisol stress response, with an heritability estimate of 0.08 ± 0.06 (Volckaert et al., 2012) and three suggestive QTLs (Massault et al., 2010). No heritability estimates exist for the swimming ability of this species.

In the present study, we aimed at estimating the genetic variation of cortisol stress response and swimming ability in the European sea bass, as well as their links with growth capacities. To this end, we used offspring from wild, domesticated and growth selected European sea bass, in a common garden experiment using a marker-based xpedigree. Fish were subjected to two successive acute crowding stress experiments where plasma cortisol response was evaluated, and two swimming challenges where maximum sustained swimming speed was assessed. The repeatability of the tests was evaluated, as well as the genetic variation of the traits and their correlations with growth.

2. Material and methods

2.1. Experimental animals

The sea bass used in this study was the offspring of four groups of sea bass sires:

- collected in the Atlantic Ocean on the coasts of Brittany: 20 W (wild) sires;
- domesticated for one generation (i.e. the offspring of the W fish, selected at random after one life cycle in the hatchery and recirculated on growing unit of Ifremer Palavas): 20 domesticated (D) sires;
- first generation mass-selected for growth (the top 5% in body length at 714 days of the offspring of W fish): 17 M (mass-selected) sires;
- first generation selected for growth in an industry breeding programme (Panittica Pugliese, Torre Canne di Fasano, Italy) using a Prosper-like individual selection scheme (Chevassus et al., 2004): 19 P (Prosper) sires, also originated from the same base population of W fish.

Sperm from all these 76 sires was individually cryopreserved (Fauvel et al., 1998) and they were mated in a full-factorial mating design with 13 wild West-Mediterranean sea bass dams. The eggs of the dams were mixed in equal volumes, and divided in 76 aliquots, each fertilized with the sperm of a single sire, thus producing a full factorial cross with an intended 988 full-sib families. After fertilization, the eggs were grouped by type of sire for incubation, and at 48 hour post-fertilization, equal volumes of (live) floating eggs were taken from each incubation tank, and dispatched in 12 larval tanks of 500 l each, i.e. 3 tanks per group (W, D, M, P), each seeded with approx. 27,000 eggs. The details of the selective breeding procedures and of the mating design have been described previously (Vandeputte et al., 2009).

Each of the four offspring groups (W, D, M, P) was reared separately in triplicates (12 tanks in total) until 268 days, where fish had a mean weight of 65 g. At that stage, 50 fish were sampled at random from each of the 12 tanks, and were individually weighed and PIT-tagged in the left dorsal muscle, while a fin clip was kept in ethanol for further genotyping. Three "mixed" tanks of 1.5 m^3 were stocked with 200 fish, coming from each of the four offspring groups (W, D, M, P, 50 fish per group).

2.2. Stress response experiment

Stress response experiments were performed twice at six weeks intervals (355–357 and 399–401 days). In each of the two experimental periods, each of the three mixed tanks was treated on a specific day, to avoid potential influence of the noise created by fishing and sampling in the other (nearby) tanks. In each tank, the water inlet was closed and the outlet was open wide in order to allow the water volume to quickly (within 10 mn) go down to 0.10 m^3, thus achieving a density of ca. 200 $kg.m^{-3}$, where the fish were kept for 1 h with pure oxygen supplementation. After 1 h, 10 ml 2-phenoxyethanol (0.1 $ml.l^{-1}$) was added to each tank to ease fish capture. Fish were then netted and anaesthetized in 0.3 $ml.l^{-1}$ 2-phenoxyethanol, identified (PIT-tag reading), and a blood sample withdrawn via the caudal vein (1 ml heparinized syringes). Individuals were then weighed before being returned to a 1.5 m^3 tank.

The duration of the phase between the end of the one hour confinement period and the collection of blood was measured for each fish and never exceeded 1 h.

Blood samples were centrifuged (1500 g, 10 min, 4 °C) and plasma was collected and kept at −20 °C pending cortisol dosage. Steroids were extracted from 50 μl plasma with 2 ml ethyl acetate/cyclohexane (1/1 *v*/*v*) and then suspended in 300 μl assay buffer (0.01 M NaH_2PO_4, 0.01 M Na_2HPO_4, 0.9% NaCl, and 0.1% gelatine, pH 7.25). Cortisol was assayed in duplicate according to the method described in Auperin et al. (1997). Plasma samples from each confinement stress were measured in four different assays. In order to avoid any possible bias related to sampling time that would be linked to different mean values between assays, samples from each stress experiment were split into two groups (odd and even sample order number) so that all sampling times were equally represented in each assay. Two references were added in each assay and allowed us to calculate inter-assay variability (respectively 7.63% for the reference 12.42 ng/tube and 9.80% for the reference 1.79 ng/tube) which fully validated our plasma cortisol measurements by these assays.

2.3. Swimming test

The swimming test was performed in a circular arena (Fig. 1) where water was progressively accelerated up to 1 $m.s^{-1}$ using two adjustable pumps. Fish were lightly anaesthetized in their rearing tank with 0.1 $ml.l^{-1}$ 2-phenoxyethanol during less than 5 min to facilitate fishing. All the fish from a given tank (max. 200 fish) were then transported to the swimming arena where they were left to habituate for 1 h, with oxygen supplied. In the last 15 min of the habituation period, the pumps

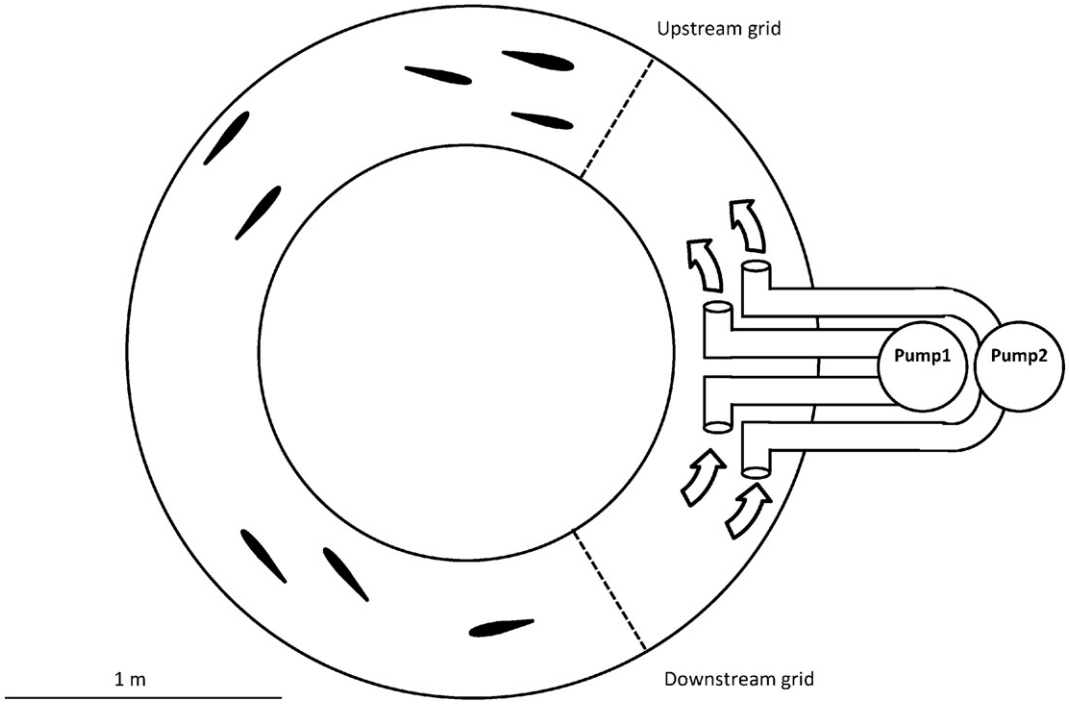

Fig. 1. The swimming trial arena. The external diameter was 2.50 m, the internal diameter 1.50 m, and the depth 40 cm, for a total volume of 1.26 m^3. The water current was progressively increased from 0.6 to 1.0 $m.s^{-1}$. Up to 200 fish of 180–200 mm average body length were tested in each individual swimming trial.

were started and the water current velocity increased to 0.25 $m.s^{-1}$. Water current velocity was measured using a flow meter (Hontzsch HFA, Germany). Oxygen was supplied to ensure a minimal oxygen content of the water of 5 $mg.l^{-1}$ (i.e., >70% air saturation), and water temperature was maintained between 20 and 23 °C during the trials. The increase in water velocity was made by steps to ensure a progressive fatigue of the fish and the increments were adapted to the swimming behaviour observed in order to avoid massive drops of exhausted fish. Trials lasted 85 to 173 min (115 on average), with 5 to 7 water velocity increments. Fish were considered exhausted when they were unable to remove themselves from the downstream grid of the swimming arena. At that time, they were netted and their PIT-tag the time were recorded. Water velocity at fatigue (or maximum sustained swimming speed U_{max}) was the water velocity during the last fully accomplished velocity level before fatigue, and was calculated in $m.s^{-1}$ (absolute U_{max}) or in Body Lengths.s^{-1} (relative U_{max}). For each tank, this test was repeated twice at 5 days interval, first at days 450–452 and then at days 455–457.

2.4. Genotyping and parentage assignment

Fish were genotyped for 11 microsatellite markers by LABOGENA (Jouy en Josas, France) and were assigned to their parents with the software VITASSIGN (Vandeputte et al., 2006), allowing for two allelic mismatches. Out of 599 fish with DNA available, 575 (96.0%) could be assigned to a single parental pair.

2.5. Statistical analyses

Post-stress cortisol in the two challenges performed on each tank at six weeks intervals was tested for potential sampling time effects by regressing cortisol on blood sampling time within each tank and for each experiment. In the first challenge, a significant correlation with sampling time was found only in tank 3 (Fig. 2c, $P < 0.001$). In the second challenge, there was a positive correlation of cortisol with sampling time in tank 1 (Fig. 2d, $P < 0.001$), and in tank 3 the first 98 samples had unusually low values for cortisol (Fig. 2f). Data from tank 3 in challenge 1 and tank 1 in challenge 2 were corrected to remove the correlations with time (corrected data = mean of the tank + residual of the regression), while the data from the first 98 samples in tank 3, challenge 2 were corrected by adding an uniform amount of 470 ng cortisol/ml, in order to bring their mean value (initially 444 ng/ml) to the mean of samples 99 to 173 (914 ng/ml). The resulting corrected value was not correlated with sampling time ($P > 0.40$).

To study the effects of genetic group, the mean values of the two challenge tests were used, both for post-stress cortisol and for U_{max}, while body length was only recorded at the first challenge for post-stress cortisol (356 days) and U_{max} (451 days).

The effect of the genetic groups (W, D, M, P) was assessed with the following model in SAS-Proc Mixed:

$$Y_{ijklm} = \mu + tank_i + group_j + sire_k\left(group_j\right) + dam_l + \varepsilon_{ijklm}$$

where Y_{ijklm} is the performance (body length, mean cortisol or mean U_{max}) of individual m, μ is the intercept, $tank_i$ is the fixed effect of tank i, $group_j$ is the fixed effect of genetic group j, $sire_k(group_j)$ is the random effect of sire k nested within group j, dam_l is the random effect of dam l and ε_{ijklm} is the random residual.

To estimate genetic parameters, the following model was used in VCE6.0 (Groeneveld et al., 2008):

$$Y_{ijkl} = \mu + tank_i + group_j + animal_k + \varepsilon_{ijkl}$$

with the same notations as above but with $animal_k$ the random additive genetic effect of animal k. Multi-trait animal models were used to estimate genetic and phenotypic correlations between traits.

3. Results

3.1. Phenotypic data base

A total of 554 fish had a proper parentage assignment and blood cortisol level determination for both stress challenges and were kept for analyses. Those fish represented offspring of 71 of the 76 sires used

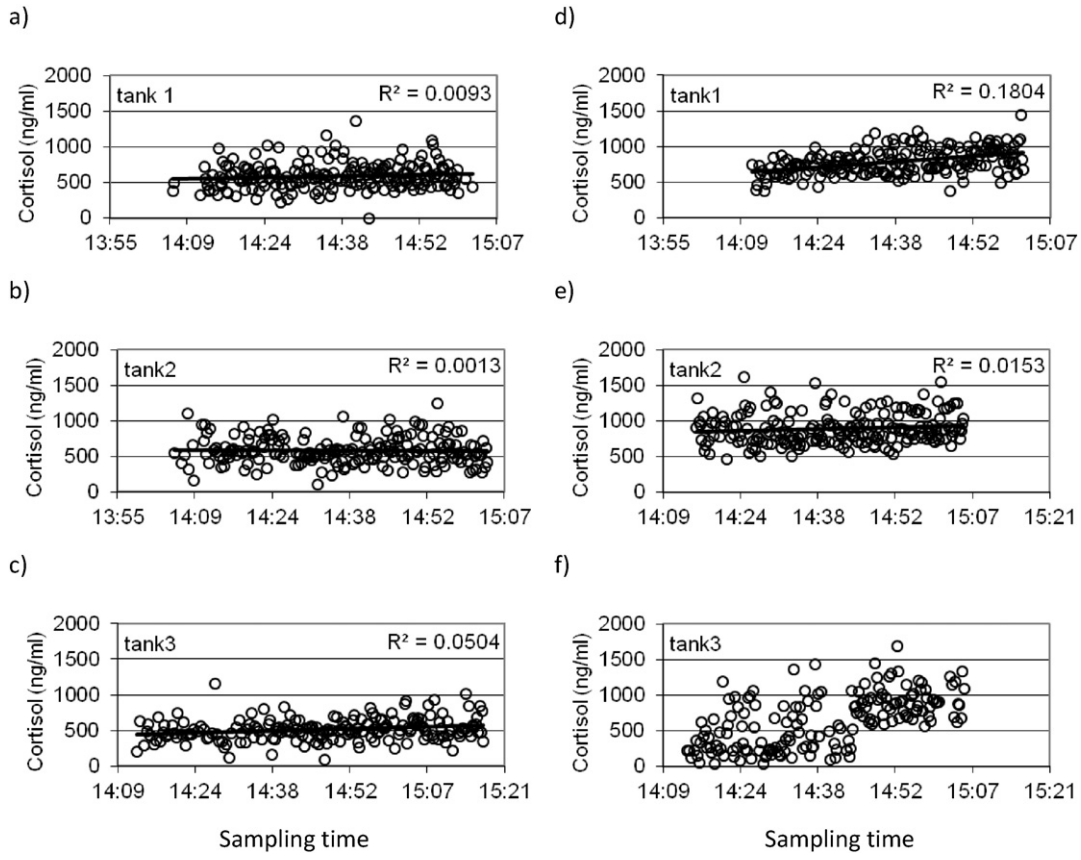

Fig. 2. Post-stress plasma cortisol concentration evolution over sampling time in three tanks with 200 sea bass each, for two samplings at 355–357 dpf (a, b, c) and 399–401 dpf (d, e, f).

(1–18 progeny per sire) and of 12 of the 13 dams used (18–73 progeny per dam), and a total of 366 full-sib families out of the 988 possible ones (1–7 progeny per full-sib family). The values of post-stress cortisol level were high, and were correlated with sampling time in tank 3 in challenge 1 ($P < 0.001$) and tank 1 in challenge 2 ($P < 0.001$), while there was a shift in the mean value in the first 98 samples of tank 3 in challenge2 (Fig. 2). Data were corrected to eliminate these links with sampling time, as explained before. The basic statistics for corrected cortisol are displayed in Table 1, and show that the average cortisol level in the second challenge was higher than in the first one. Swimming performances were available for 547 individuals in the first test and 510 individuals in the second test, and were rather similar in scale (Table 1).

3.2. Phenotypic and genetic correlations between two successive challenges

The phenotypic correlation (repeatability) between the two cortisol measurements was only 0.30 (Fig. 3a), while the genetic correlation was 0.99 ± 0.13. The phenotypic correlation observed for relative U_{max} (in BL/s) was higher (0.62 — Fig. 3b) and the genetic correlation was also very high (0.96 ± 0.05). Based on this, we decided to combine data from both challenges and use the mean cortisol level and the mean relative U_{max} as measurements of post-stress cortisol response and maximum sustained swimming speed respectively.

Table 1
Sample sizes and basic phenotypic parameters in the different tanks and different challenges for post-stress plasma cortisol (corrected for the effect of sampling time) and maximum sustained swimming speed in 554 sea bass.

Parameter	Age	N=	Mean	S.D.
Corrected cortisol (ng/ml)	356 dpf	554	560	170
	400 dpf	554	856	221
U_{max} (body lengths/s)	451 dpf	547	4.60	0.88
	456 dpf	510	4.92	0.84
Body weight (g)	356 dpf	554	109	42

3.3. Comparison of genetic groups

Genetic groups did not differ for their post-stress plasma cortisol level ($F_{3, 71.7} = 1.95$, $P = 0.13$ — Table 2), nor for their absolute maximum sustained swimming speed ($F_{3, 66.4} = 0.59$, $P = 0.62$). There was a tendency for relative U_{max} to differ between groups ($F_{3, 66.3} = 2.68$, $P = 0.054$), where the two growth selected groups (Massal, Prosper) tended to have a marginally lower relative U_{max} than the Wild and Domesticated controls (Table 2). This was paralleled by the fact that the growth-selected groups had a significantly higher body size than the two controls ($F_{3, 70.7} = 6.84$, $P = 0.0004$). When body length was introduced as a covariate in the model, the difference in relative U_{max} between lines vanished ($F_{3, 66.9} = 0.49$, $P = 0.69$).

3.4. Heritability and correlations among traits

Body weight and relative U_{max} had a high heritability (>0.50, see Table 3) while plasma cortisol had an intermediate heritability (0.33). The phenotypic correlations between body weight and the other two traits were negative, and this was even clearer with genetic correlations. There was no phenotypic correlation between cortisol and U_{max}, and the genetic correlation was not significantly different from zero. Heritabilities and correlations were also calculated with absolute U_{max} (data not shown in Table 3), and in this case the heritability was quite similar (0.48 ± 0.08), but the genetic correlation with body weight was slightly – but not significantly – positive (0.12 ± 0.16), and the genetic correlation with cortisol was clearly negative (−0.52 ± 0.16).

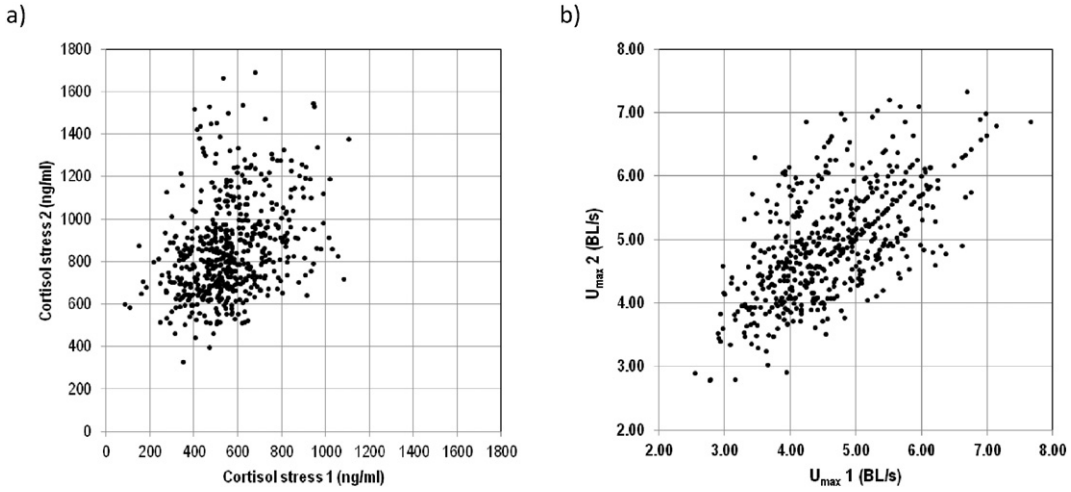

Fig. 3. Comparison of individual post-stress plasma cortisol (a, N = 554) and relative maximum sustained swimming speed (b, N = 510) in two successive challenges in European sea bass.

4. Discussion

In this paper, we provide estimates for narrow-sense heritability for swimming performance in fish, which appear to be rather high and clearly different from zero ($h^2 = 0.55 \pm 0.08$). It must be noted that due to the reaction time of the water mass to the increase of pumping intensity in the swimming arena, and to the irregular increase in water speed, we did not compute U_{crit} as defined by Brett (1964). Moreover, we did not attempt to correct for blocking effects as proposed by Keen and Farrell (1994). Therefore, our measurement of swimming performance may be seen as rather crude, but the high level of heritability (0.55), the limited standard error estimate (0.08), as well as the very high genetic correlation between the first and the second test (0.96) all show that this crude measurement corresponds to a stable genetic characteristic of the fish. Our narrow-sense heritability estimate was much higher than previously estimated for narrow-sense heritability of relative critical swimming speed in brown trout (0.34 ± 0.22, Blanc and Toulorge, 1981), broad-sense heritability of critical swimming speed in Atlantic salmon (0.24 ± 0.16 in Hurley and Schom, 1984) and guppy (0.24 ± 0.19 in Nicoletto, 1995) and more comparable to the broad-sense heritability estimates for burst-swimming speed in 2 months old threespine sticklebacks (0.37–0.41, Garenc et al., 1998) but not in the same fish at 3.6 months of age (0.00–0.02, same study).

The heritability of cortisol response to confinement stress was 0.33 ± 0.09, in the usual range (0.18–0.56) for the same trait in salmonids (Fevolden et al., 1999, 2002; Pottinger and Carrick, 1999; Weber et al., 2008), but well higher than the previous estimate available in sea bass (0.08 ± 0.06, Volckaert et al., 2012). It has to be noted that the estimate of Volckaert et al. (2012) was obtained from a limited number of families (mostly offspring of 10 sires and 2 dams), so our estimate is probably closer to reality. From a methodological point of view, we could see that in most cases there was no or very limited time trend in cortisol value during the one hour blood collection time following the one hour confinement stress. One exception was tank 3 in trial 2, where a change in mean value was seen around the middle of the sampling period, which may have been caused by sampling artefacts or some unidentified biological reason but not to the dosage, as dosages were split into different assays and the same trend was seen in all assays. The consequence on the results was very limited in any case as the genetic correlation between the two cortisol measurements was very high (0.96), and the heritability and genetic correlations with swimming performance and body weight estimated by 1) not taking into account the second cortisol measurement in tank 3 or 2) using uncorrected tank 3 data did not differ from those in Table 3 by more than ±0.03 for the estimates, and ±0.01 for their standard error, showing that the second cortisol measurement in tank 3 had limited impact on the results in any case. Generally speaking, the one hour confinement stress followed by one hour sampling time seems appropriate to evaluate many individuals for their cortisol response to confinement stress in sea bass. Here we could get individual performances for 200 fish in one 2 hour challenge (one hour stress + one hour blood sampling), quite comparable to a protocol successfully used in rainbow trout on groups of 100 fish tested at a time (Fevolden et al., 1993).

Our study provides genetic correlations between body weight, swimming ability and cortisol stress response in fish. Absolute U_{max} was weakly positively genetically correlated with body weight ($r_A = 0.12$) as seen in salmon ($r_G = 0.23$, Hurley and Schom, 1984), and relative U_{max} was strongly negatively genetically correlated with body weight ($r_A = -0.64 \pm 0.08$). The phenotypic ($r_P = -0.56$) and environmental ($r_E = -0.45 \pm 0.07$) correlations between relative U_{max} and body weight were of similar magnitude. This suggests that there is a phenotypic decrease in relative U_{max} with increasing body size, and that the genetic correlation observed is a consequence of this rather than of a negative pleiotropic effect of growth-favouring genes on swimming ability. This was confirmed by the total absence of difference between control and selected strains when body length was added as a covariate in the ANOVA model. This negative relationship of relative swimming speed and body size is well known and established in the literature (Bainbridge, 1958; Bellwood and Fisher, 2001). It is classically observed that length-specific (relative) maximal swimming speed

Table 2
Least square means (± standard error) of differences between genetic groups for mean cortisol stress response and mean relative U_{max}. Different superscripts within the same row indicate significant differences ($P < 0.05$).

Parameter	Wild	Dom	Massal	Prosper
Mean corrected cortisol (ng/ml)	732 ± 19^a	706 ± 19^a	673 ± 20^a	711 ± 20^a
Absolute mean U_{max} (m/s)	0.819 ± 0.013^a	0.799 ± 0.013^a	0.803 ± 0.014^a	0.816 ± 0.013^a
Relative mean U_{max} (BL/s)	4.42 ± 0.10^a	4.41 ± 0.10^a	4.19 ± 0.11^a	4.15 ± 0.10^a
Body length at 451 dpf (mm)	187.1 ± 3.4^a	183.0 ± 3.4^a	193.2 ± 3.6^b	198.1 ± 3.5^b

Table 3
Heritability (diagonal), genetic correlations (upper triangle) and phenotypic correlations (lower triangle of body weight at 356 dpf, mean post-stress plasma cortisol and mean relative maximum sustained swimming speed.

	Body weight	Mean cortisol	Mean relative U_{max}
Body weight	**0.62 ± 0.07**	−0.36 ± 0.16	−0.64 ± 0.07
Mean cortisol	−0.13	**0.33 ± 0.09**	−0.10 ± 0.19
Mean relative U_{max}	−0.56	0.01	**0.55 ± 0.08**

decreases with body size. One major reason for that observation is that the speed of fish myotomal muscle contraction decreases with increasing body mass (Altringham and Johnston, 1990). Therefore, larger fish attain lower tail beat frequencies, and assuming that relative stride length, the proportion of body length moved per tail beat, remains constant, then length-specific speed must necessarily decrease with size.

Cortisol stress response was moderately negatively genetically correlated with body weight ($r_A = -0.36 \pm 0.16$), confirming previous results in the same species, where r_A was estimated at -0.60 ± 0.44 (Volckaert et al., 2012), while results in rainbow trout show no or slightly negative effects of cortisol responsiveness on growth (Drew et al., 2007; Fevolden et al., 2002; Quillet et al., 2014). However, there was no effect of selection for growth on the average post-stress cortisol level of the lines tested (Table 2), so the modification of cortisol responsiveness by selection for growth is not expected to happen very quickly. Nevertheless, the sign of this correlation tends to show that selection for growth will tend to co-select fish with low cortisol responsiveness, which is expected by the Pace of Life Syndrome theory (Réale et al., 2010). However, it is not clear whether the favoured phenotype would be low-responsive fish, which are expected to have a high metabolism but also a high aggressiveness and a low immune response – potentially highly productive in a protected farming environment – or high responsive fish which would be less aggressive and more robust.

This study also provides the first estimates of genetic correlations between cortisol responsiveness and swimming ability. Theoretical expectations are that high growth rate should correlate with low cortisol responsiveness and high exploratory ability and metabolic rate (Réale et al., 2010). Here, we show that relative U_{max} is strongly negatively correlated with body weight and not significantly correlated with cortisol responsiveness ($r_A = -0.10 \pm 0.19$, $r_P = 0.01$), which seems to contradict theory. However, we saw that this negative correlation with growth was mostly linked to a phenotypic effect of size whereby large fish have a lower relative U_{max}. When relative U_{max} was corrected for this effect of size, no difference between selected lines was apparent. Moreover, U_{max} may not be a good indicator of metabolic rate and metabolic scope in sea bass, as previous results show that animals with a high routine metabolic rate and aerobic scope are not the ones able to reach the highest swimming speed (Marras et al., 2010). Indeed, U_{max} also includes part of anaerobic performance, especially at higher swimming speeds. Finally, it may also be possible that our crude measurement of U_{max} be biased by other factors, still its high heritability indicates that it really represents a characteristic of the fish which has a strong genetic basis. As this trait has been demonstrated to be positively correlated with cardiac capacities in rainbow trout (Claireaux et al., 2005), it could then be used to counteract potential detrimental effects of fast growth on the cardiac system, like those that were earlier suspected in brown trout *Salmo trutta* and Atlantic salmon (Mercier et al., 2000; Poppe et al., 2007).

5. Conclusion

This study showed that significant genetic variability for swimming ability and cortisol stress response exist in the European sea bass. These traits were negatively genetically correlated with growth, but in the case of swimming ability this seemed to be essentially a phenotypic effect of larger size. The correlated responses on those traits were not large enough to be evidenced in one generation of selection. Recording and selecting those traits potentially provide new opportunities to orientate domestication and selection of fish, and counteract potential negative effects of selection for improved productivity by selecting faster swimmers. For cortisol response, it is not clear whether high or low responsive fish would be the preferred phenotype, depending on the level of control of the rearing environment.

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